

THE EFFECTS OF SOCIAL CONTEXT & CACHE SURVIVAL ON PINYON JAY
CACHING BEHAVIOR

by

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I examined how pinyon jays (*Gymnorhinus cyanocephalus*) assess and determine the risk of pilferage to their caches. Jays were allowed to cache in an open room while alone or while being observed by a conspecific. In a counterbalanced design, jays cached in the opposite treatment once they had finished recovering their caches. I compared birds' behaviors between treatments in order to determine whether jays consider the presence of an observer in measuring the local competitive environment. Once all jays had completed alone- and observed- treatments, I ran the experiment once more to determine if individuals were consistent in their cache protection strategies. Results from this experiment reveal that pinyon jays did not respond to audience effects. Birds showed distinct patterns of behavior, but individuals were consistent in their behavior across treatments and replications. Jays serving as observers were tested for their ability to recover caches they had watched being made. These birds were able to accurately recover observed caches, though not as reliably as cachers.

I then used base levels of cache protection activity as assessed from the first experiment to divide birds into two groups so each had similar mean levels of cache protection behaviors. To evaluate whether pinyon jays directly assess pilferage through cache-loss, I removed 50% of the seeds cached for birds receiving the cache-removal treatment, while birds receiving the non-removal treatment were allowed to recover all the seeds they cached. Birds that participated in the non-removal treatment later participated in a cache-removal treatment so I could compare the responses to cache-removal between the two groups. To assess whether experience pilfering might influence caching decisions, I compared responses between previous observers and previous cachers. Jays that had their caches removed ate fewer seeds and cached fewer seeds when compared to the non-

removal group. Of the seeds they cached, more of those seeds were cached behind shielding landmarks. These behavioral patterns were not evident in the group that participated in both treatments. Birds with experience as pilferers were more exploratory, ate more food, and expressed higher levels of cache protection behaviors during the removal treatment.

“It is the supreme art of the teacher to awaken joy in creative expression and knowledge.”

--Albert Einstein

It is with deepest gratitude and respect that
I dedicate this thesis to the many teachers in my life.

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TABLE OF CONTENTS

Abstract	i
Acknowledgements.....	iv
Grant Information	v
Chapter 1: Introduction	2
References.....	6
Chapter 2: The effects of social context on caching behaviors	10
Methods	12
Results: Cachers	17
Results: Observers	19
Discussion: Caching	21
Discussion: Pilfering	23
Conclusions	27
References	29
Chapter 3: The effects of cache survival on caching behaviors	34
Methods	35
Results: Habituation	41
Results: Comparing Previous History	44
Results: Comparing Treatments	48
Discussion: General Behavior	52
Discussion: Previous History	56
Discussion: Comparing Treatments	58
Conclusions	65
References	67
Chapter 4: Conclusions	70
Cachers.....	70
Pilferers.....	72
References	74
Appendix	76

LIST OF FIGURES

Figure 2.1	19
Figure 2.2	20
Figure 3.1	38
Figure 3.2	42
Figure 3.3	43
Figure 3.4, a, b & c	45
Figure 3.5	46
Figure 3.6	47
Figure 3.7	48
Figure 3.8, a & b	49
Figure 3.9	50
Figure 3.10	51
Figure 3.11	51

CHAPTER 1: INTRODUCTION

Many animals that depend on seasonally variable food supplies store food when it is abundant, then retrieve it for consumption when food is otherwise unavailable. Food caching provides potential benefits, particularly by allowing more predictable access to food over space and time (see Vander Wall 1990 and references therein). But caching also poses risks, including loss of the stored food through pilferage by other animals. This risk is particularly great for animals that live in large groups—highly social animals must balance the many benefits of group living with increased intraspecific competition (Andersson & Krebs 1978, Vander Wall 1990). In species that scatter-hoard, or create many small food stores over a large area, there are many opportunities for cache pilferage. Despite the fact that each scatter hoarder faces hundreds to thousands of cache decisions per caching season, little is known regarding how food-storing animals assess and determine the risk of pilferage.

Studies performed with scatter hoarders indicate that some species may indirectly assess caching environment by measuring the social environment. When conspecifics are present, ravens, scrub jays, and chickadees preferentially cache behind shielding landmarks (Bugnyar & Kortschal 2002, Dally et al. 2005, Pravosudov 2008, Pravosudov et al. 2010), and crows and ravens “false-cache,” or probe into the substrate without depositing any food (James & Verbeek 1983, Heinrich 1999). A plethora of scatter-hoarding species return to their caches after conspecifics have departed and “re-cache” their food, moving it to a new location (e.g. Goodwin 1956, MacDonald 1976, DeGange et al. 1989, Bardin & Markovets 1991, Jenkins & Peters 1992, Jenkins et al. 1995,

Heinrich 1999, Emery & Clayton 2001, Bugnyar & Kortschal 2002). Other species respond to conspecific presence by reducing the amount they cache (Stone & Baker 1989, Brontons 2000, Pravusodov & Lucas 2000), while other species delay caching or stop caching all together (James & Verbeek 1983, Burnell & Tomback 1985, Kallandar 1978).

Not all scatter hoarding species respond solely to the presence of an observer. Instead, it appears that some cachers assess pilferage threat directly by measuring cache survival then adjusting their caching behaviors later. Marsh tits (Stevens 1984), mountain chickadees (Pravusodov 2001), black-capped chickadees (Hampton & Sherry 1994) and kangaroo rats (Preston & Jacobs 2001, 2005) failed to modified their caching behaviors in the presence of conspecifics. In each of these cases, experimenters demonstrated that cachers were indeed capable of adjusting their caching behaviors but additional stimulus was required to elicit such a response. Whether in the field (Stevens 1984, Pravusodov 2001) or in lab-based settings (Hampton & Sherry 1994, Preston & Jacobs 2001, 2005), cachers required cache-removal with the presence of an observer to begin to engage in caching behaviors.

Cachers should assess the caching environment relative to how sensitive they are to audience affects, so we expect the variation seen in the above examples. Evolutionary theory predicts that factors such as memory and motivation should vary across species according to how dependent each species are upon cached food for survival. It could be particularly revealing to study a system that relied heavily, if not exclusively, on cached food for a portion of its life- or yearly- cycle. In such a case, cache-survival could be a reliable proxy for fitness. In such a system, we should be more likely to detect changes in

caching behaviors if the cacher assessed a threat of pilferage since higher costs would be associated with cache loss.

Pinyon jays (*Gymnorhynchus cyanocephalus*) provide such a system. Food caching is exceptionally important for pinyon jay survival and fitness since cached pinyon pine (*Pinus edulis*) seeds comprise up to 95% of the diet in the winter months (Ligon 1978). Jays are also highly dependent on food caches during the mating and breeding seasons when other resources are sparse; recovered pine seed caches comprise up to 33% of their young's diet. I therefore expect jays to make caching decisions with care, given the steep costs of cache-loss.

As expected from their ecology, pinyon jays have excellent spatial memory (Olson et al. 1995, Bednekoff et al. 1997). Caches are located entirely by means of spatial memory, using landmarks to locate caches even when the ground is covered in snow (Balda & Kamil 1989). Pinyon jays use spatial cues to locate previous caches even when additional odor cues are present (Vander Wall 1982; Balda & Kamil 1989). Pinyon jays are not limited to recovering their own food. Jays can recover caches using observational memory—in some cases this enhances fitness, since mated pairs are known to retrieve one another's caches via observational memory (Dunlap et al. 2006). This means that pilferage by conspecific competitors is also a constant risk. Field observations have reported that jays pilfer from each other (Stotz & Balda 1995), and daily pilferage rates in the field can range up to 30% (Vander Wall 1990). Therefore cognitive abilities involved in pilferage prevention may have been subject to strong natural selection (Vander Wall & Smith 1987). Indeed pinyon jays commonly show various cache protection strategies in both field and lab settings (e.g. Balda & Bateman 1971, Bednekoff et al. 1997).

Any member of social group may act as cacher or pilferer, perhaps performing both roles. These roles may require different cognitive abilities. While caching demands abilities that enable one to better avoid cache pilferage, pilfering strategies may require better observational recovery, or aggressive tactics which allow pilferers to more effectively recover caches which are not their own.

Questions Addressed in This Dissertation

To determine factors that influence pinyon jay caching decisions, I focused on three main variables. First I manipulated social context during caching, examining whether the social environment was used as an indirect measure of current competitive environment, and also a measure of pilferage threat. In the second study, I manipulated cache-survival to examine whether pinyon jays used a more direct sampling method to quantify the threat to their caches. Finally, I examined the effects of experimental history to determine whether past experience as a pilferer affects subsequent caching behaviors.

To gain a more complete picture of which cognitive abilities pinyon jays use for food management, pilferers were tested for recovery accuracy. Previous lab-based studies with pinyon jays have determined that mated males can recover their mates' caches, but results from this same study indicate that females (mated or single) and unmated males did not exhibit the same proficiency for cache pilferage (Dunlap et al. 2006). Field studies also indicate that pinyon jays are capable of pilferage via observational spatial memory (Stotz & Balda 1995), but these studies did not track the fate of individual caches.

To more fully grasp the challenges faced by cachers, I sought to understand some of the cognitive processes used by pilferers to recover other jays' caches. First, I tested whether socially unrelated (non-mated) jays could recover observed caches at levels significantly above chance. I also determined if so-called "cache-protection behaviors" decreased pilferer recovery accuracy. Behaviors such as re-caching and false caching have been assumed to be functionally deceptive, but there are no studies linking the action of the cacher with a decrease in pilferer recovery. Finally (as stated above) pilferers' progress through the second experiment were tracked as they became the cachers. Their behaviors were compared to birds that lacked such history (i.e. birds that were cachers in the first experiment). Since pilferers were selected at random from a larger/general pool of birds, I expect that if results show consistent effect of history across a set of birds selected to have that history, then behavioral phenotypes may be discounted.

REFERENCES

- Andersson, M. & Krebs, J. R.** 1978. On the evolution of hoarding behaviour. *Animal Behaviour*, 26, 707-711.
- Balda, R. P. & Bateman, G. C.** 1971. Flocking and annual cycle of the pinon jay, *Gymnorhinus cyanocephalus*. *The Condor*, 73, 287-302.
- Balda, R. P. & Kamil, A. C.** 1989. A comparative study of cache recovery by three corvid species. *Animal Behavior*, 38, 486-495.
- Bardin, A. V. & Markovets, M. Y.** 1991. Rate of plundering of reserves stored by tits: experimental investigation. *Soviet Journal of Ecology*, 21, 332-336.
- Bednekoff, P. A., Balda, R. P., Kamil, A. C. & Hile, A. G.** 1997. Long-term spatial memory in four seed-caching corvid species. *Animal Behaviour*, 53, 335-341.
- Brotons, L.** 2000. Individual food-hoarding decisions in a nonterritorial coal tit population: the role of social context. *Animal Behaviour*, 60, 395-402.
- Brunell, K. L. & Tomback, D. F.** 1985. Steller's jays steal gray jay caches: field and laboratory observations. *Auk*, 102, 417-419.
- Bugnyar, T. & Kotrschal, K.** 2002. Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? *Animal Behaviour*, 64, 185-195.
- Dunlap, A. S., Chen, B. B., Bednekoff, P. A., Greene, T. M. & Balda, R. P.** 2006. A state-dependent sex difference in spatial memory in pinyon jays, *Gymnorhinus cyanocephalus*: mated females forget as predicted by natural history. *Animal Behaviour*, 72, 401-411.
- Dally, J. M., Emery, N. J. & Clayton, N. S.** 2005. Cache protection strategies by western scrub-jays, *Aphelocoma californica*: implications for social cognition. *Animal Behaviour*, 70, 1251-1263.
- DeGange, A. R., Fitzpatrick, J. W., Layne, J. N. & Woolfenden, G. E.** 1989. Acorn harvesting by Florida scrub jays. *Ecology*, 70, 348-356.
- Emery, N. J. & Clayton, N. S.** 2001. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, 414, 443-446.
- Goodwin, D.** 1956. Further Observations on the Behaviour of the Jay *Garrulus glandarius*. *Ibis*, 98, 186-219.

- Hampton, R. R. & Sherry, D. F.** 1994. The effects of cache loss on choice of cache sites in black-capped chickadees. *Behavioral Ecology*, 5, 44-50.
- Heinrich, B.** 1999. *Mind of the Raven*. New York: Harper.
- James, P. C. & Verbeek, N. A. M.** 1983. Food storage behavior of northwestern crow. *Behaviour*, 85, 276-290.
- Jenkins, S. H. & Peters, R. A.** 1992. Spatial patterns of food storage by Merriam's kangaroo rats. *Behavioral Ecology*, 3, 60-65.
- Jenkins, S. H., Rothstein, A. & Green, W. C. H.** 1995. Food Hoarding by Merriam's Kangaroo Rats: A Test of Alternative Hypotheses. *Ecology*, 76, 2470-2481.
- Ligon, J. D.** 1978. Reproductive interdependence of piñon jays and piñon pines. *Ecological Monographs*, 48, 111-126.
- MacDonald, D. W.** 1976. Food caching by red foxes and some other carnivores. *Z. Tierpsychol.*, 42, 170-185.
- Olson, D. J., Kamil, A. C., Balda, R. P. & Nims, P. J.** 1995. Performance of 4 Seed-Caching Corvid Species in Operant Tests of Nonspatial and Spatial Memory. *Journal of Comparative Psychology*, 109, 173-181.
- Pravusodov, V. V.** 2008. Mountain chickadees discriminate between potential cache pilferers and non-pilferers. *Proceedings of the Royal Society B-Biological Sciences*, 275, 55-61.
- Pravusodov, V. V. & Clayton, N. S.** 2001. Effects of demanding foraging conditions on cache retrieval accuracy in food-caching mountain chickadees (*Poecile gambeli*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268, 363-368.
- Pravusodov, V. V. & Lucas, J. R.** 2000. The effect of social dominance on fattening and food-caching behaviour in Carolina chickadees, *Poecile carolinensis*. *Animal Behaviour*, 60, 483-493.
- Pravusodov, V. V., Roth, T. C. & LaDage, L. D.** 2010. Chickadees are selfish group members when it comes to food caching. *Animal Behavior*, 80, 175-180.
- Preston, S. D. & Jacobs, L. F.** 2005. Cache decision making: the effects of competition on cache decisions in merriam's kangaroo rat (*dipodomys merriami*). *Journal of Comparative Psychology*, 119, 187-196.
- Preseton, S. D. & Jacobs, L. F.** 2001. Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy. *Behavioral Ecology*, 12, 517-523.

- Stevens, T. A.** 1984. Food storing by marsh tits and shrikes, Oxford University.
- Stone, E. R. & Baker, M. C.** 1989. The Effects of Conspecifics on Food Caching by Black-Capped Chickadees. *Condor*, 91, 886-890.
- Vander Wall, S. B.** 1990. *Food Hoarding in Animals*. Chicago: University of Chicago Press.
- Vander Wall, S. B.** 1982. An experimental analysis of cache recover in Clark's Nutcracker. *Animal Behavior*, 30, 84-94.
- Stotz, N. & Balda, J.** 1995. Cache and recovery behavior of wild pinyon jays in Northern Arizona. *The Southwestern Naturalist*, 40, 180-184.

CHAPTER 2: THE EFFECTS OF SOCIAL CONTEXT ON CACHING BEHAVIORS

Any behavioral or cognitive strategy that increases cache recovery, whether through enhanced memory or decreased pilferage will be strongly selected for since they are important components of the adaptive strategies in many animals. Here I experimentally examine individuals playing the roles of cacher or pilferer, though in nature individuals play both these roles within the same season or caching bout. First I examine how the presence of an observer affects caching behavior, then I investigate the effectiveness of cache protection behaviors on pilferage attempts by the observer.

A number of studies have reported changes in caching behavior due to audience effects, changes that may interfere with an observer's ability to locate cached food (e.g. northwestern crows, James & Verbeek 1983; voles, Geyer 1984; black-capped chickadees, Hitchcock & Sherry 1990; yellow pine chipmunks, Vander Wall 1995; scrub jays, Emery & Clayton 2001; red squirrels, Gerhardt 2005; grey squirrels, Leaver et al. 2007). Such effects have not been studied extensively in highly social species. Because intraspecific competition is greater in social species, caching defense might be expected to be more conspicuous.

One such social species, the pinyon jay, opens pinecones, harvests, transports, and caches the seeds surrounded by flocks of 50-500 conspecifics (Balda & Balda 1978; Balda 2002). These flocks consist of extended family and non-related individuals, which are formed into a well-developed social hierarchy (Marzluff & Balda 1992). These jays are particularly well suited for laboratory experiments on caching since this important, ecologically relevant behavior is commonly displayed in captivity (e. g., Balda & Kamil

1989; Bednekoff & Balda 1996a; Balda & Kamil 2006). This system provides an exceptional opportunity to examine social context in food hoarding behavior.

I carried out experiments to determine if social context influenced cache management behaviors in the pinyon jay by testing whether the presence of a conspecific observer would cause a change in caching. Since many other social parids and corvids demonstrate audience effects (see Chapter 1), one might predict that pinyon jays will adjust caching behavior in the presence of an observer. By contrast, one might predict that pinyon jays would not demonstrate audience effects since they are never truly alone during caching.

In order to test if observers can recover seeds they have seen being cached, I compared the ability of cachers and their observers to find stored seeds. Previous studies have assumed that observers that have seen another bird cache seeds can later locate the caches, though there is little direct evidence for this assumption. In an aviary study, ravens only recovered caches they had observed being made, leaving planted (unobserved) caches unexplored (Bugnyar & Kotrschal 2002). A comparative lab-based study of Clark's nutcrackers and Mexican jays revealed that both species were able to recover observed caches (Bednekoff & Balda 1996b). Additionally, a similar lab-based study demonstrated that mated pinyon jays cached near each other, and could also later recover each other's caches (Bednekoff & Balda 1996a). There has not been any further research conducted with pinyon jays to determine whether unrelated jays could recover one another's caches.

METHODS

Subjects: For this study, 13 jays were taken from the wild as adults from field populations around Flagstaff, Arizona in 1996 – 2007. At the time of this study, the ages of the experimental birds ranged from at least 2 - 10 years (A. Kamil, unpublished data). Four birds had served in a previous social inference experiment (Paz-y-Miño et al. 2004), the other nine were experimentally naïve. Birds were housed in individual 42 cm x 42 cm x 67 cm cages and maintained at 90% of ad libitum weight on a combination of medicated poultry feed (HomeFresh™, Londonderry, NH, U.S.A.), parrot feed (Lafeber's® Omega 3 + 6 Balanced Premium Daily Diet, Cornell, IL, U.S.A.), sunflower seeds (Cardinal Brand™ Striped Sunflower Seed, Oakes, ND, U.S.A.), pinyon pine seeds, mealworms, and a vitamin supplement (Lafeber's® Avi-era™ Bird Vitamin, Cornell, IL, U.S.A.). Water and grit were available at all times. The light cycle in the rooms was 14L:10D with natural spectrum lighting.

Experimental Room: Habituation, caching, and recovery sessions were conducted in a 2.7 m x 4.8 m room built for behavioral testing. The floor of the experimental room held 117 holes (5.5 cm diameter), spaced at 20 cm intervals and arranged in a grid of 9 rows by 13 columns. Each hole contained either a sand-filled cup ($N = 51$) or a plaster-filled cup ($N = 62$) painted to match the floor. To determine which holes would remain filled and which would serve as potential cache sites, I used a noise-based random number generator (RANDOM.ORG). Painted plastic and wooden objects were scattered around the room, and posters were hung on the walls to serve as landmarks. A cage for an observer bird was placed against the south wall of the room, two perches were placed on the ground near the potential cache sites, and a pole that crossed the length of the room perpendicular

to the observer's cage served as a perch and feeding site. Test birds entered and exited the experimental room through a porthole.

Birds' behavior was recorded manually through a smoked glass window near the entrance of the experimental room. I also recorded all sessions to digital videodisks with a surveillance video camera mounted in the ceiling.

Habituation: Prior to beginning the experiment, I habituated the birds to the experimental room by introducing them to the room in pairs and providing them with 85 ml of pinyon pine seeds (~ 130 seeds) in a central feeding dish attached to a perch. If a bird was initially slow to venture onto the floor or probe into holes, I also placed food in a Petri dish on the floor. Additionally, test birds were trained to fly towards light. I accomplished this by turning lights off in the section birds were meant to leave, and turning lights on in the area birds were meant to fly to. Habituation was complete when a bird had eaten about 10 seeds off the floor and probed in ten or more holes around the room within one visit to the room.

General Overview: To evaluate the effect of an observer on caching behaviors, I observed jays caching both alone and in the presence of another pinyon jay. I also ran recovery tests for both cachers and observers to compare accuracy for self-made caches and observed caches. Thus the study included caching sessions with and without observing jays, and recovery sessions of both observer and cachers. All experiments were conducted between 0700 and 1200 hours, since pinyon jays typically forage during the morning. To decrease variability between cachers, I selected individuals of all one sex. I

used all male pinyon jays as cachers, and two male and two female jays as observers. Previous studies have demonstrated that males reliably recover more of their caches at certain times of the year when compared to mated females (Dunlap et al. 2006). Observers' sexes were unknown at the beginning of the study, but the male-female split allowed us to study observational recovery ability for both sexes.

Procedure: During caching trials, I released the caching bird into the room and allowed it to eat, leave, or cache seeds that were either already sitting in the central feeder (in the alone condition), or added after a 15 m socialization period, during which the test bird was allowed to interact with the observer bird. Since these very social birds were housed in individual cages when not participating in the experiment, this meant that they were only allowed to closely interact during the observed treatment. In an attempt to prevent the presence of an observer (i.e. direct social interaction) from having any confounding effects on our measurements of caching behavior, such as latency to first cache, etc., we allowed the birds time to interact before seeds were added to the room. During the caching trials without the presence of an observer, a caged, non-experimental companion bird was in vocal, but not visual contact with the caching bird. A companion bird was provided because previous studies have shown that pinyon jays will not habituate to a room without a conspecific present (i.e. Balda & Kamil 1989).

To measure caching behavior, each caching trial continued until a bird had cached at least 15 seeds, or until a bird had perched for 20 min. During each trial, I recorded the number and location of holes probed, as well as the number and location of the caches made. After each trial, I verified cache location and number of seeds per site by sifting

the sand and recording the seeds present in each of the sand-filled cups visited by the caching bird. False-caches were determined after the fact, when I reconciled scoring marks with sifted cups; if a cup had been marked as having a cache, yet no seed was present, I marked a false-cache.

To evaluate the cacher's recovery ability, I waited until the cacher bird had returned to 90% ad libitum weight (2 – 7 d), then released it into the same experimental room and set-up in which we had re-established its caches, using the seeds it had cached. I controlled percentage body weight to keep birds' motivational states equivalent. Other studies of similar design have kept retention intervals constant, but pinyon jays have outstanding spatial memory, which lasts on the order of months (Bednekoff et al.1997), so I was not concerned that some bird retrieved within two days, while others retrieved up to five days later.

During recovery sessions, the bird recovered, left, or re-cached previously made caches. This second trial lasted until the bird re-cached a seed in the same cup twice in a row, recovered all of its caches, or began a sequential search pattern (visiting the nearest neighboring cache site six times in a row), indicating the bird had ceased using spatial memory to recover its own caches. If any seeds remained after this initial recovery session, the bird was re-released into the room for a second recovery session once it had reached 90% ad libitum weight. Again, in this last recovery session, the jay was allowed to recover any remaining seeds.

Half of the birds were randomly assigned to start in the observed caching treatment, while the other half initially cached without an observer. When recovery was complete, each test bird was allowed to cache in the alternate caching condition. I

conducted two replicates of each cache-recovery cycle with each treatment for each cacher bird, once in winter 2007, and once in summer 2008. Each cacher bird therefore cached on a total of four occasions, twice in the presence of another jay, and twice with only a companion jay outside the room. Each replicate of the observed state was conducted with a different observer bird in order to control for any effects of an individual observer.

To evaluate an observer's recovery ability, I removed both the cacher bird and its observer bird from the room after a caching bout. After sifting cups to verify the cache locations and sizes, I re-set the caches using new seeds. I placed seeds in the same pattern as the cacher bird had previously established them, but saved the original seeds for the cacher's recovery trial (see above). No extra seeds were available during the observer recovery trial. I did not allow observers (=pilferers) to recover the original seeds cached since birds preferentially cached the heavier seeds from among those provided in the feeder (see results). Caching birds occasionally put more than one pine nut in a site. When they did, we replaced the multiple seeds with a single seed to prevent pilferers from becoming sated at a single recovery site. I removed all traces of the previous cache session, and released the observer bird into the room through the porthole to allow him or her an opportunity to pilfer the original cacher bird's caches. The pilferer could then recover, eat, re-cache, or leave seeds as placed by the cacher. This trial lasted until the pilferer bird recovered all of the test bird caches, began a systematic search pattern, re-cached a seed in the same location twice in a row, or perched without moving for 20 m. I recorded the order of holes probed during recovery and re-caching, as well as the number and location of any re-caches made.

Statistical Analyses: To determine if birds recovered caches more frequently than expected by chance, I used the hypergeometric probability distribution (as in Balda et al. 1986; Sokal & Rohlf 1995). I did not include revisits to holes within a trial, so recovery patterns resembled sampling without replacement. I calculated the number of cache recoveries expected by chance given the number of correct and incorrect sites available and the number of recoveries that were attempted using Number Cruncher Statistical Systems™ 3.1 statistical and data analysis system (© J. Hintze, Kaysville, UT, www.ncss.com). To determine if pilferer birds visited correct and incorrect holes with differing frequencies, I compared the probability of a visit to a given hole-type (cache site, false cache site, or non-cache site) using the Friedman and post-hoc Wilcoxon signed-rank tests. To compare cache protection behaviors between treatments, I used Wilcoxon rank-sum tests. I compared these differences across replications of the experiment using a Spearman's rank correlation. For these latter tests we used STATISTICA (StatSoft, Inc. 2004, version 7).

RESULTS

Cacher Birds: During caching sessions, pinyon jays cached quite readily whether or not an observer was present. Latency to first cache by the cacher bird did not differ between social conditions. When observers were present, jays cached their first pine nut within 18.0 ± 3.19 m ($N = 18$, $\bar{x} \pm SE$); when no observer was present, jays made their first cache within 14.7 m ± 1.53 ($N = 18$) (Wilcoxon rank-sum: $T = 257$, $N = 9$, $P = 0.51$). When observers were present, the jays required a mean of 34.2 ± 4.63 m ($N = 18$) to

complete their 15 caches. When no observer was present, 35.5 ± 3.03 m ($N = 18$) were required (Wilcoxon rank-sum: $T = 263$, $N = 9$, $P = 0.20$). Caching birds did not delay caching or change their overall rate of caching in the presence of an observer bird.

Caching jays also did not adjust their frequency of functionally deceptive behaviors between treatments. In the presence of an observer bird, cachers false-cached 2.08 ± 0.08 times ($N = 18$). When caching alone, cacher birds false-cached 1.39 ± 0.03 times ($N = 18$) (Wilcoxon rank-sum: $T = 230$, $N = 9$, $P = 0.15$). When an observer was present during caching, cacher birds re-cached 4.67 ± 0.66 times, when alone during caching, cacher birds re-cached 3.77 ± 0.30 times (Wilcoxon rank-sum: $T = 208$, $N = 9$, $P = 0.43$).

Individual jays false-cached at consistent rates during both caching and recovery trials within a single cache-recovery cycle. Birds that false-cached often during the caching session also false-cached frequently during the recovery trial, though no other pinyon jay was present. Likewise, birds that did not exhibit false-caching behavior during the caching session (or only did so at low levels) did not do so during the recovery session either (Spearman's Rank correlation: replication one, $r_s = 0.75$, $N = 9$, $P < 0.05$; replication two, $r_s = 0.95$, $N = 9$, $P < 0.05$). Thus, I found no change in the rate of false-caching or re-caching in the presence of an observer, and individual birds were consistent in their behavior within a cache-recovery cycle.

There was a trend for individuals that exhibited high rates of false-caching to also re-cache seeds more frequently. I tested for consistency of both behavioral traits by calculating the correlation between the cache and recovery trials within a cache-recovery cycle (Spearman's Rank correlation: replication one, $r_s = 0.57$, $N = 9$, $P > 0.05$;

replication two, $r_s = 0.60$, $N = 9$, $P > 0.05$). Correspondingly, birds that did not false-cache often tended not to re-cache frequently either. However, re-caching frequency was so low for both treatments that the correlations were not significant.

These results demonstrate that the presence of an observer did not affect cache-management decisions by pinyon jays in this study. Individuals tended to be consistent in their caching behaviors both across time (within caching and recovery trials within a single cache-recovery cycle, as well as between the first and second replications of the experiment), and between social contexts (alone or observed during caching).

Observer Birds: Observers were able to discover and remove some of the caches they observed being made (Fig. 2.1), and pilferer birds did recover caches as accurately as

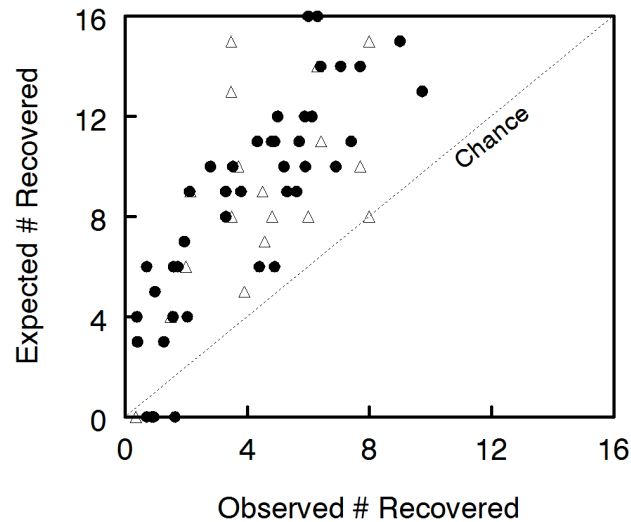


Figure 2.1. Jays generally recovered cached seeds at levels significantly above chance. Jays recovering their own caches are represented by ●, and birds recovering observed caches are represented by △. We calculated recovery accuracy via hypergeometric analyses using the number of caches recovered (X), and holes probed (R) out of 51 open holes (N) by each bird in each trial.

cachers recovered their own caches (Fig. 2.1). Unexpectedly, pilferer cache recovery did not decrease significantly in trials where cacher birds engaged in cache protection behaviors (Wilcoxon rank-sum: $T = 18$, $N = 9$, $P = 0.22$).

Pilferers were more likely to visit actual cache sites than false-cache sites (Wilcoxon rank-sum: $T = 17$, $N = 16$, $P = 0.014$, Fig. 2.2). However, pilferers also demonstrated a significant preference for visiting false-cache sites before visiting non-cache sites (Wilcoxon rank-sum: $T = 5$, $N = 16$, $P = 0.001$, Fig. 2.2). Certain pilferers visited false-cache sites more often than other sites. Due to our small sample size ($N = 4$), we were not able to statistically evaluate these results.

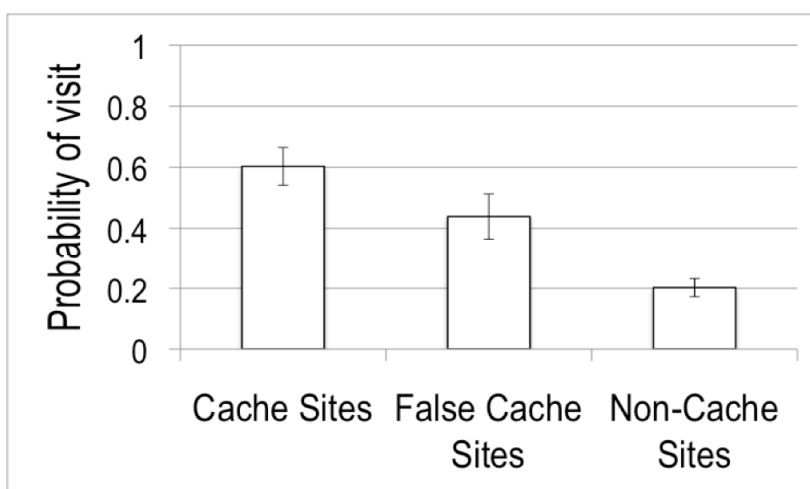


Figure 2.2. Probability of pilferer birds visiting an observed cache site, an observed false cache site, and a non-cache site. Friedman's rank ANOVA revealed overall significance between groups ($X^{2,16} = 20.67$, $P < 0.001$). Pilferers were more likely to visit sites that cachers had probed in (cache- and false-cache sites) than sites that cacher birds had not probed (non-cache sites). They were also more likely to visit cache sites than false cache sites.

DISCUSSION

Caching Behavior

Pinyon jays did not alter their caching behaviors in the presence of an observer. Caching birds did not begin to cache items more quickly when a conspecific observer was present, nor did they noticeably delay caching. Cacher birds did not alter their patterns of caching either; overall caching rates were similar between treatments, as were levels of false caching and re-caching. These findings contradict previous results for corvids, such as scrub jays (Dally et al. 2005), gray jays (Waite 1992) and ravens (Heinrich & Pepper 1998; Bugnyar & Kortschal 2004; Bugnyar & Heinrich 2005), as well as for other animals that cache, such as grey squirrels (Leaver et al. 2007) and mountain chickadees (Pravosudov 2008).

The lack of response to the presence of an observer could be explained by several alternative explanations. Maintenance conditions could have influenced behavior during the study. When not participating in experiments, all birds were maintained on ad libitum diets. Although the test birds were housed in individual home cages, and ideally should not have been able to interact outside of the experimental interactions, they have been known to feed each other through the cage screens when on a restricted diet if cages were placed closely together (C. Keefe, personal observation). Therefore, for the majority of the time (under non-test conditions), food was plentiful, and when food was scarce, other birds were able to provide food but not pilfer it. The next study will explore whether pinyon jays ever alter their cache protection behaviors when given a chance to associate the presence of an observer with cache pilferage.

Another possibility is that both the presence of an observer and the direct experience of pilferage are necessary precursors to eliciting cache protection strategies. Birds may have created an association between the presence of an observer and cache-survival, since I re-set all caches prior to the re-test of a caching bird. Such an association is unlikely to have been previously reinforced in the field since pilferage by both conspecifics and heterospecifics has been reported to be relatively high (30% or more) (Vander Wall 1990; Marzluff & Balda 1992; Stotz & Balda 1995). Pinyon jays should pay attention to cache survival, as cache management is tightly linked to mate and offspring survival (Balda & Bateman 1971; Bateman & Balda 1973; Ligon 1978). My next study directly evaluates the alternative hypothesis that pinyon jays can associate an observer with pilferage over a period of consistent reinforcement.

One explanation is that pinyon jays in this experiment did not associate the presence of an observer bird with cache pilferage. Pinyon jays may not have responded to audience effects due to their highly social nature. Since they harvest and cache in flocks, perhaps they require the additional stimulus of witnessing pilferage to alter their behaviors—after all, cache protection strategies in the presence of conspecifics are observed in the field (Marzluff & Balda 1992, Stotz & Balda 1995).

One could argue that pinyon jays tolerate cache theft, but cache pilferage has potentially high costs on survivorship and reproductive success within this system. Breeding and fledging of young occur during months of scarcity, so adult and hatchling diets are comprised of up to 95% cached pine nuts (Ligon 1978). Given the value of cached food, it does not seem likely to us that pinyon jays would be insensitive to an association as salient and as consequential to fitness as cache pilferage. Caching birds

tested have not experienced the cost of pilferage within the context of any studies being conducted in our laboratory, and some individuals have not experienced cache pilferage in up to 12 caching seasons (years). However, given their long evolutionary history (and coevolution) with pinyon pine (Ligon 1974, 1978), we doubt jays would develop an insensitivity to cache threats.

It does appear that pinyon jays may exhibit behavioral types; there were consistent individual differences across contexts (Hessing et al. 1993, van der Kooij et al. 2002, Sih et al. 2004). Birds were consistent within their re-caching and false caching behavior during repeat runs of the experiment. These behaviors were consistent in different seasons and in different caching conditions. Consistent behaviors might be favored within the stable dominance hierarchy of a pinyon jay flock. That is, social roles could vary as a function of behavioral types (Sih & Watters 2005). We already know that pinyon jays flocks are arranged with dominance hierarchies; to navigate the social landscape jays exhibit individual recognition (Bond et al. 2003), and track dominance relationships within the flock via transitive inference (Paz-y-Miño et al. 2004). There may be a relationship between dominance rank, behavioral type, and cache management strategy. Field studies of pinyon jays have found that dominant birds tended to pilfer from subordinates (Marzluff & Balda 1992) as is also the case in scrub jays (Dally et al. 2006). It would not be surprising if subordinate individuals invested more in pilferage-avoidance strategies than dominant birds as has been found in scrub jays (Dally et al. 2005), black-capped chickadees, and willow tits (Lahti 1998). Individuals higher up in the hierarchy could opt for active cache-defense, while birds lower on the social scale might choose preventative cache-protection strategies in order to avoid direct conflict

with conspecifics. Future studies should therefore investigate the relation of cache management strategies to dominance rank.

This study demonstrated that pinyon jays behave consistently across different “situations,” as defined by Sih and colleagues (Sih et al. 2004). Additional data on pinyon jay behavior in different “contexts,” such as correlations between general levels of aggressiveness during handling, with activity in home cages or rates of acquisition (learning), could provide us with an axis describing a behavioral syndrome; a suite of correlated behaviors that are consistent across situations and contexts (Sih & Bell 2008). A bird’s location on this axis would describe its behavioral type with respect to that syndrome, and would provide an independent test of the behavioral syndrome hypothesis.

In conclusion, the caching test showed that the presence of an observer had no effect on pinyon jays’ caching behavior. In a species where individuals are never truly alone during caching, perhaps jays use other information to make caching decisions. Our test revealed baseline differences between individuals in re-caching and false caching levels. These individual differences remained both between replications of the test and between social conditions during caching. Even if constancy in behavior between social conditions can be ascribed to our experimental design, our results still demonstrate interesting, unexpected differences between pinyon jays and other caching corvids, which could reflect differences in their degree of sociality.

Pilferage Behavior

As mentioned above, pinyon jays cache as a flock (Marzluff & Balda 1988). The pine nuts are therefore subject to producer-scrounger dynamics between cacher and pilferer.

Though the behaviors of caching and pilfering may seem disparate, they can occur in the same organism within the same food-recovery bout (Vander Wall 2003; Van Horick & Burns 2007) so it is important to note that producer/scrounger dynamics could play out on the level of the individual rather than the population. Although many studies have looked at the effects of an observer on caching behavior, most of these have assumed that the observer could recover at least some of the caches it had observed being created (which we will call “observed caches”). In systems where olfactory cues are not available, and spatial memory is the primary mechanism of cache retrieval (rather than home-range searching) this becomes a rather large assumption since cachers and observers probably do not encode the same spatial information because of the difference in perspective (Kamil & Cheng 2001).

Pilferers were able to recover observed caches better than expected by chance (Figure 2.2). This represents an impressive spatio-cognitive feat. For the pilferer to accurately recover observed caches, they must somehow transform their spatial information in addition to retaining the information over time. Behaviors during cache-retrieval indicate that pilferers did not travel fixed paths when recovering observed caches. Instead birds recovered caches immediately upon entering the room, from whichever angle yielded the fastest approach from the porthole. Pilferers did not recreate a “snapshot” of the caches as they had observed them being made from the cage inside the room. Rather than fly from the porthole to the cage then to the cache locations, pilferers began recovering caches immediately upon being released into the room. These observations indicate that pilfering pinyon jays use multiple landmarks (as caching pinyon jays do) to encode the location of observed caches.

Pilferers did not recover observed caches as accurately as cachers recovered their own caches (Figure 2.2). These findings are consistent with those of previous studies of wild-caught pinyon jays (Bednekoff & Balda 1996a), and make sense when considering the extra spatio-cognitive processing that may be required when tracking a competitor's food stores from a distant location.

One key result was that pilferers responded to false caching behavior by preferentially probing in false cache locations over non-cache locations (Fig. 2.1). False caching has been reported in field and lab numerous times for many scatter hoarding species (Stotz & Balda 1995, Heinrich 1999, Steele et al. 2006, etc.). Although “false caching” behavior has been assumed to be a functionally deceptive behavior, these are the first data for any species demonstrating the link between the apparent cache protection behavior and a responsive pilferer.

Pilferers visited false-cache sites less frequently than cache sites but more frequently than non-cache sites (Figure 2.1). This provides direct evidence that false-caching increases the cost of pilfering observed caches. It also demonstrates that pinyon jays can sometimes distinguish false- from true cache sites. Pilferers may reduce some of the costs of incurred by playing the scrounger role by prioritizing their search; probing cache sites more often than false-cache sites, then by checking false-cache sites secondarily; or by simply checking all holes that the cacher bird has probed.

Overall, pilferers were able to recover observed caches, and they differentiated between false-, non-, and true cache sites. Even at short retention intervals (20m – 1h), pilfering birds did not recover observed caches as accurately as cachers, who recovered their caches 2 – 5 d later. These patterns are similar to those found in Clark's

Nutcrackers and Mexican Jays (Bednekoff & Balda 1996b). Individuals using observational memory did not perform as well as those recovering caches made first-hand. Pilferers recovered caches in a pattern that indicated they used multiple spatial landmarks to encode cache locations, rather than using path integration, recreating a mental snapshot of the caches, or retracing the cacher's path.

Conclusions

The primary goals of my first experiment were to determine if pinyon jays alter their caching behaviors in the presence of a conspecific observer, and to examine cache recovery by observer birds. Pinyon jays engaged in a variety of cache protection behaviors, including false caching and re-caching pinyon pine seeds. Levels of cache-protection behaviors varied greatly between individuals. However, individual jays did not alter their basic behavior patterns between replications of the experiment over time, nor did they alter their behavior patterns when caching in the presence of an observer. Contrary to the majority of results from other caching species, these findings suggest that cache protection behavior in the highly social pinyon jay may be controlled by individually stable responses rather than social experience.

The success of observer birds in recovering test birds' caches exceeded that expected by chance, indicating that they represent competition to caching birds. Finally, an unexpected discovery from the control pilferage test was that false caching behaviors by test birds served to functionally deceive the observer (pilferer) birds. Observers visited false-cache sites before non-cache sites. Together these findings strongly suggest that the

social interplay between cacher and pilferer, or producer and scrounger, may be more complex than previously assumed.

REFERENCES

- Andersson, M. & Krebs, J.R.** 1978. On the evolution of hoarding behavior. *Animal Behaviour*, 26, 707-711.
- Balda, R.P.** 2002. Pinyon Jay (*Gymnorhinus cyanocephalus*). In: *Birds of North America* (Ed. By Poole A. and Gill, F.) Philadelphia.
- Balda, R.P., & Balda, J.** 1978. The care of young pinyon jays and their integration into the flock. *Journal of Ornithology*, 119, 146-171.
- Balda, R.P. & Bateman, G.C.** 1971. Flocking and annual cycle of the pinyon jay, *Gymnorhinus cyanocephalus*. *The Condor*, 73, 287-302.
- Balda, R. P., Kamil, A.C., & Grim, K.** 1986. Revisits to emptied cache sites by Clark's nutcrackers (*Nucifraga Columbiana*). *Animal Behavior*, 34, 1289-1298.
- Balda, R. P. & Kamil, A.C.** 1989. A comparative study of cache recovery by three corvid species. *Animal Behavior*, 38, 486-495.
- Balda, R.P. & Kamil, A.C.** 1992. Spatial memory in Clark's Nutcracker, *Nucifraga-columbiana*. *Animal Behaviour*, 44, 761-769.
- Balda, R.P. & Kamil, A.C.** 2006. The ecology and life history of seed caching corvids. <http://www.pigeon.psy.tufts.edu/asc/Balda/Default.htm> Accessed 3 November 2007.
- Bateman, G. C. & Balda, R. P.** 1973. Growth, development, and food habits of young pinoñ jays. *Auk* 90: 39-61.
- Bednekoff, P.A., & Balda, R.P.** 1996a. Social caching and observational spatial memory in pinyon jays. *Behavior*, 133, 807-826.
- Bednekoff, P. A. & Balda, R. P.** 1996b. Observational spatial memory in Clark's nutcrackers and Mexican jays. *Animal Behaviour*, 52, 833-839.
- Berger, L.R. & Ligon, J.D.** 1977. Vocal communication and individual recognition in the pinyon jay. *Animal Behavior*, 25, 567-584.
- Bond, A.B., Kamil, A.C., & Balda, R.P.** 2003. Social complexity and transitive inference in corvids. *Animal Behavior*, 65, 479-487.
- Brunell, R.K. & Tomback, D.F.** 1985. Steller's jays steal gray jay caches: field and laboratory observations. *Auk*, 102, 417-419.
- Bugnyar, T. & Heinrich, B.** 2005. Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proceedings of the Royal Society B-Biological Sciences*, 272, 1641-1646.

- Bugnyar, T. & Kotrschal, K.** 2004. Leading a conspecific away from food in ravens (*Corvus corax*)? *Animal Cognition*, 7, 69-76.
- Bugnyar, T. & Kotrschal, K.** 2002. Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? *Animal Behaviour*, 64, 185-195.
- Clayton, N.S., Dally, J.M. & Emery, N.J.** 2007. Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362, 507-522.
- Coolen, I.** 2002. Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (*Lonchura punctulata*). *Behavioral Ecology and Sociobiology*, 52, 232-238.
- Coolen, I., Giraldeau, L. A. & Lavoie, M.** 2001. Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. *Animal Behaviour*, 61, 895-903.
- Dally, J.M., Clayton, N.S. & Emery, N.J.** 2006. The behaviour and evolution of cache protection and pilferage. *Animal Behaviour*, 72, 13-23.
- Dally, J.M. & Emery, N. J. & Clayton, N. S.** 2004. Cache protection strategies by western scrub-jays (*Aphelocoma californica*): hiding food in the shade. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271, S387-S390.
- Dally, J.M., Emery, N.J. & Clayton, N.S.** 2005. The social suppression of caching in western scrub-jays (*Aphelocoma californica*). *Behaviour*, 142, 961-977.
- Darwin, C.** 1872. *The expression of the emotions in man and animals*. London: Murray.
- Dukas, R.** 2004. Evolutionary biology of animal cognition. *Annual Review of Ecology Evolution and Systematics*, 35, 347-374.
- Dunbar, R. I. M.** 1998. The social brain hypothesis. *Evolutionary Anthropology*, 6, 178-190.
- Dunbar, R. I. M.** 1986. The social ecology of gelada baboons. In: Rubenstein DI, Wrangham RW, editors. *Ecological aspects of social evolution: birds and mammals*. Princeton: Princeton University Press.
- Dunlap, A.S., Chen, B.B., Bednekoff, P.A., Greene, T.M. & Balda, R.P.** 2006. A state-dependant sex-difference in spatial memory in pinyon jays, *Gymnorhinus cyanocephalus*: mated females forget as predicted by natural history. *Animal Behavior*, 72, 401-411.

- Emery, N.J.** 2006. Cognitive ornithology: the evolution of avian intelligence. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 361, 23-43.
- Emery, N.J. & Clayton, N.S.** 2001. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, 414, 443-446.
- Gerhardt, F.** 2005. Food pilfering in larder-hoarding red squirrels (*Tamiasciurus hudsonicus*). *Journal of Mammalogy*, 86, 108-144.
- Geyer, L.A.** 1984. Factors affecting caching in the pine vole, *Microtus pinetroum*. *Mammalia*, 48, 165-172.
- Heinrich, B. & Pepper, J.W.** 1998. Influence of competitors on caching behaviour in the common raven, *Corvus corax*. *Animal Behaviour*, 56, 1083-1090.
- Heinrich, B.** 1999. *Mind of the raven*. Harper, New York.
- Hessing, M. J. C., Hagelso, A. M., Vanbeek, J. A. M., Wiepkema, P. R., Schouten, W. G. P. & Krukow, R.** 1993. Individual Behavioral-Characteristics in Pigs. *Applied Animal Behaviour Science*, 37, 285-295.
- Hitchcock, C.L. & Sherry, D. F.** 1990. Long-term-memory for cache sites in the black-capped chickadee. *Animal Behaviour*, 40, 701-712.
- Humphrey, N. K.** 1976. The Social Function of Intellect. In: *Growing Points in Ethology* (Ed. By Bateson, P.P.G. & Hinde, R. A.), pp. 303-317: Cambridge University Press.
- James, P.C. & Verbeek, N.A.M.** 1983. Food storage behavior of northwestern crow. *Behavior*, 85, 276-290.
- Kamil, A. C.** 1983. Optimal foraging theory and the psychology of learning. *American Zoologist*, 23, 291-302.
- Kamil A. C. & Cheng, K.** 2001. Way-finding and landmarks: The multiple-bearings hypothesis. *Journal of Experimental Biology*, 204:103–113.
- Kilham, L.** 1958. Sealed-in winter stores of red-headed woodpeckers. *Wilson Bulletin*, 70, 107-113.
- King, A. J., Isaac, N. J. B. & Cowlshaw, G.** 2009. Ecological, social, and reproductive factors shape producer-scrounger dynamics in baboons. *Behavioral Ecology*, 20, 1039-1049.
- Lahti, K., Koivula, K., Rytönen, S., Mustonen, T., Welling, P., Pravosudov, V. V. &**

- Orell, M.** 1998. Social influences on food caching in willow tits: A field experiment. *Behavioral Ecology*, 9, 122-129.
- Leaver, L.A., Hopewell, L., Caldwell, C. & Mallarky, L.** 2007. Audience effects on food caching in grey squirrels (*Sciurus carolinensis*): evidence for pilferage avoidance strategies. *Animal Cognition*, 10, 23-27.
- Ligon, J.D.** 1978. Reproductive interdependence of pinyon jays and pinyon pines. *Ecological Monographs*, 48, 111-126.
- Marzluff, J.M. & Balda, R. P.** 1992. *The pinyon jay: Behavioral ecology of a colonial and cooperative corvid*. London: T. & A.D. Poyser.
- Mitchell, R.W.** 1986. A framework for discussing deception. In: *Deception: Perspectives in Human and Non Human Deceit*. (Ed. By Mitchell, R. W. a N.S.) p. 388. Albany: SUNY Press.
- Morand-Ferron, J., Sol, D. & Lefebvre, L.** 2007. Food stealing in birds: brain or brawn? *Animal Behaviour*, 74, 1725-1734.
- Paz-y-Mino, G., Bond, A.B., Kamil, A.C. & Balda, R.P.** 2004. Pinyon jays use transitive inference to predict social dominance. *Nature*, 430, 778-781.
- Pravosudov, V.V.** 2008. Mountain chickadees discriminate between potential cache pilferers and non-pilferers. *Proceedings of the Royal Society B-Biological Sciences*, 275, 55-61.
- Romane, G.** 1882. *Animal Intelligence*. London: Kegan, Paul.
- Sih, A. & Bell, A.M.** 2008. Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior*, Vol. 38, 38, 227-281.
- Sih, A., Bell, A., & Johnson, J.C.** 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19, 372-378.
- Sih, A., & Watters, J.V.** 2005. The mix matters: behavioural types and group dynamics in water striders. *Behaviour*, 142, 1417-1431.
- Sokal, R. R., & Rohlf, F. J.** 1995. *Biometry*, 3rd edn. New York: W. H. Freedman & Co.
- Stephens, D.W. & Krebs, J. R.** 1986. *Foraging theory*. Princeton, New Jersey: Princeton University Press.
- Stotz, N. & Balda, J.** 1995. Cache and recovery behavior of wild pinyon jays in Northern Arizona. *The Southwestern Naturalist*.

- Toomey, M.B., Bowman, R. & Woolfenden, G.E.** 2007. The effects of social context on the food-caching behavior of florida scrub-jays (*Aphelocoma coerulescens*). *Ethology*, 113, 521-527.
- Vander Wall, S.B.** 1995. The effects of seed value on the caching behavior of yellow pine chipmunks. *Oikos*, 74, 533-537.
- Vander Wall, S. B.** 1990. *Food Hoarding in Animals*. Chicago: University of Chicago Press.
- Vander Wall, S.B.** 1982. An experimental analysis of cache recovery in Clark's Nutcracker. *Animal Behaviour*, 30, 84-94.
- Vander Wall, S. B. & Jenkins, S. H.** 2003. Reciprocal pilferage and the evolution of food hoarding behavior. *Behavioral Ecology*, 14, 656-667.
- Vander Wall, S. B. & Smith, K.G.** 1987. Cache protecting behavior of food-hoarding animals. In: *Foraging behavior*, ed. A. C. Kamil, J. R. Krebs, and R. H. Pulliam, pp. 611-644. New York: Plenum Press.
- Van der Kooij, E. V., Kuijpers, A. H., Schrama, J. W., van Eerdenburg, F. J. C. M., Schouten, W. G. P. & Tielen, M. J. M.** 2002. Can we predict behaviour in pigs? Searching for consistency in behaviour over time and across situations. *Applied Animal Behaviour Science*, 75, 293-305.
- Waite, T.A.** 1992. Social hoarding and a load-size-distance in gray jays. *The Condor*, 94, 995-999.

CHAPTER 3: THE EFFECTS OF CACHE SURVIVAL ON CACHING BEHAVIOR

If pinyon jays do not respond to the cache threat posed by the presence of a conspecific (see Chapter 2), perhaps they monitor cache threat directly by tracking the survival of their caches. Verifying the percentage of caches remaining would give jays a direct measure of the threat posed to their caches. Some species of scatter-hoarders assess pilferage threat through a combination of direct and indirect means. Some of these species include marsh tits (Stevens 1984), black-capped and mountain chickadees (Hampton & Sherry 1994, Pravusodov 2001), and kangaroo rats (Preston 2001, Preston & Jacobs 2005). These species received exposure to an observer, but did not respond until after they had experienced pilferage paired with the presence of an observer. Pinyon jays may respond in a similar fashion since they harvest, transport and cache food in a highly social environment (Balda & Bednekoff 1971). Since jays are virtually always in contact with other members of their flock, the presence of conspecifics may not be meaningfully related to pilferage. This may force the jays to gather more information about the competitive environment by monitoring their caches over time, and responding to cache survival. To determine if pinyon jays use information on cache-survival to make decisions about which caching strategies to use, I subjected birds to heavy cache loss, then quantified any changes in their caching behaviors.

Collecting information about cache-survival can inform cache-management decisions with real-time data. However, if pinyon jays could learn from previous experience with pilferage, they may reduce pilferage risk by employing pilferage avoidance strategies. Experiments with scrub jays (Emery & Clayton 2001) indicate that

individuals with experience pilfering react more strongly to the social environment during caching when compared to birds who have never recovered another birds' caches (in an experimental context). In their studies, Emery and Clayton's team allowed scrub jays to cache food in observed and unobserved conditions (a design conceptually similar to that found in Chapter 2). Although all birds re-cached food more in the observed condition compared to the unobserved caching condition, jays that had been allowed to recover other jays' caches re-cached their food at even higher rates when compared to birds lacking such experience. To determine if pinyon jays with experience as pilferers transfer that information to avoid cache pilferage when behaving as cachers, the pilferers from the first experiment (Chapter 2) participated in this cache-removal experiment. I then compared their behaviors to the behaviors of birds that had acted as cachers in the prior experiment to determine whether there were behavioral differences between the two groups.

METHODS

Ten jays were used from our first experiment (see Chapter 2). I conducted all experiments between 0800 and 1200 since pinyon jays typically forage, cache, and pilfer during these times. Jays were fed the same maintenance diet as outlined in chapter two, and cached in the same experimental room. However, different landmarks were placed in new locations on the floor and walls in order to prevent spatial memory interference (Lewis 2005).

Habituation & Training: Jays had not been in the experimental room for 6-8 months when this second experiment began. The jays therefore needed to be re-acclimated to the room. First, individual jays were put in the room for an hour with a water dish in the center of the room. I recorded whether the bird explored and drank from the water dish (a novel object in this context), how often they visited the dish in a given session, and how they interacted with the dish (e.g. pecking at it, moving it, drinking water from it, etc.). Additionally, I recorded the type and frequency of vocalizations jays used while exploring the room (see Marzluff & Balda 1992 for a detailed description of pinyon jay calls). I recorded jays approach to seed selection, including whether or not they tested seed quality (“bill-weighing” and “bill clicking” as described in Lignon & Martin 1974), and how many seeds they discarded to the floor while selecting food to eat and cache. Finally, I recorded each individual’s approach to seed caching (e.g. re-caching, frequency of false-caching, etc.). Birds remained in the experimental room until they had explored and walked on the floor, probing at least 10 holes during the visit. If birds did not habituate during the first visit to the room, they repeated habituation sessions until they met criteria.

Once birds readily explored the room, they entered the second stage of training. I placed 100 pinyon pine seeds in a food dish attached to a perch. Jays were allowed to explore the room, eat, cache, and re-cache seeds until they had stopped and perched for 10 consecutive minutes. If a bird cached any seeds, I allowed them to recover these seeds once they had returned to 90% weight (1 – 2 d), then began another cache-training cycle with 100 seeds once the bird had returned to 90% weight. A was considered fully trained once they cached 16 seeds within 1h.

General Overview: Using base levels of cache protection activity (including false-caching and re-caching levels) as assessed in our first experiment (see Chapter 2), I divided the birds into two groups so that each had similar mean levels of cache protection behaviors. My goal was to evaluate the effects of heavy cache removal on caching and retrieval behaviors. To this end, I removed 50% of the seeds cached by birds receiving the cache-removal treatment, while birds receiving the control treatment were allowed to recover all of the seeds they cached. Unlike the first experiment, all caches were made in the presence of an observer.

Birds received a series of five cache-recovery cycles. During the fifth cache-recovery cycle of the cache-removal treatment birds received a probe trial. To determine whether recovery behaviors were a function of cache removal, or merely a side-effect of environmental conditions, we did not remove any seeds, nor did we allow the observer bird into the room to pilfer any seeds. Therefore the fifth cache-recovery cycle in the cache-removal treatment was procedurally identical to one in the control, non-removal treatment.

Once the control group of birds had completed their cache-recovery blocks, they then received a series of 5 cache-recovery cycles with the cache-removal treatment as described above. All the data from birds that had first received the control treatment, then the cache-removal treatment were analyzed separately from birds that only received the cache-removal treatment in anticipation of order effects. Birds that received the cache-removal treatment second may exhibit behavioral patterns distinctive from those that received the treatment first due to the effects of time and increasing age.

I then compared a suite of behaviors between the two groups to determine whether pinyon jays adjusted their behaviors in the face of heavy cache predation. These metrics of behavior included: latency to first cache, number of seeds cached and consumed, number of cache sites used, number of caches made behind shielding landmarks, frequency of re-caching and false-caching, and total session time.

Birds who had recent experience pilfering in our first experiment also participated in the second experiment. Each of these birds received both control and cache-removal treatments. To control for order effects, the order of treatment was reversed for 2 of 4 birds. Unfortunately, one of the birds did not complete the trials and had to be dropped from the study. Time and monetary constraints prevented a design in which we trained and used additional pilferers. A schematic of birds' experience may be seen below in

Figure 3.1:

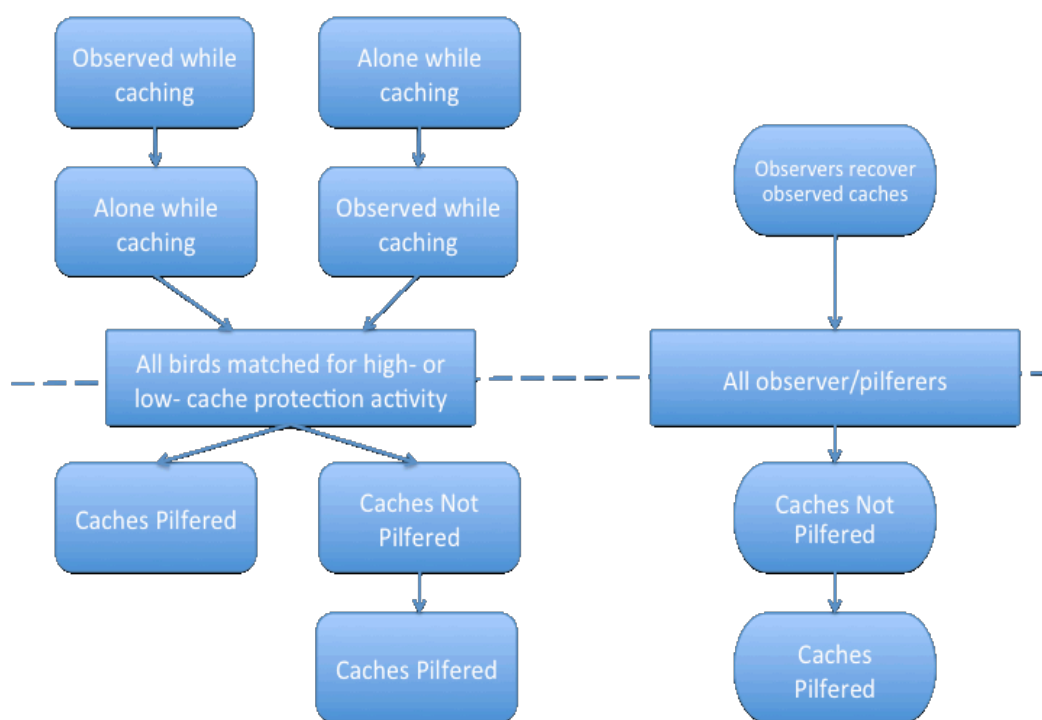


Figure 3.1. Sequence of treatments through experiment one (above the dotted line) and experiment two (below the dotted line). Observer jays (on the right) that acted as pilferers had observed cachers (on the left) as they made their caches. In the second experiment, all test birds acted as cachers, and all birds cached in the presence of an observer.

Control Treatment: During all caching trials a caged observer, Mote, was present. We chose to use a single observer despite the design drawbacks of pseudoreplication since we wished to control variance in the behavior of the pilferer. I released the caching bird into the room and allowed it to eat, cache, or leave 100 seeds provided in the central feeder on the perch. Each caching trial continued until a bird had perched for 10 consecutive minutes. After each trial, I verified cache location and number of seeds per site by sifting and recording the seeds present in each of the sand-filled cups visited by the caching bird.

To evaluate the cacher's recovery ability, I waited until the cacher bird had returned to 90% ad libitum weight (2 – 4 d), then released it into the same experimental room and set-up in which we had re-established its caches, using the seeds it had cached. The bird then recovered, re-cached, or left its previously made caches. This second trial lasted until the bird recovered all of its caches, re-cached a seed in the same cup twice in a row (leaving the hole in between caching visits), or began a sequential search pattern (visiting the nearest neighboring cache site six times in a row). These criteria were chosen because re-caching a seed twice in a row in the same location indicated that the bird was no longer sufficiently motivated to recover its caches. A sequential search pattern indicated that the bird had ceased using spatial memory to recover its own caches, and he had switched to searching his home range, possibly searching for the caches of others.

Cache-Removal Treatment: For four cache-recovery cycles jays cached in the presence of an observer (as above), then retrieved caches after witnessing cache pilferage by the

observer bird (Mote). After a caching session, I removed all birds from the holding cages, verified cache locations (as above), swept the room clean of any debris or surface cues, and counted and removed seeds remaining on the floor, ground, or feeder. I then placed the cacher bird in Mote's observer cage and released Mote into the room, allowing him to pilfer two seeds while the cacher was watching. I marked which caches Mote recovered, and summoned Mote back to the porthole by turning out the lights in the room. At this time birds were returned to their home cages.

I then removed 50% of the caches; if birds cached an odd number of seeds, I removed half the seeds + 1. To determine which of the remaining seeds would be removed, I flipped a coin for each cache site. If more than one seed was cached in a location chosen for pilferage (which sometimes occurred), then all seeds present in that cache site were removed. I chose to manually remove the majority of seeds since pinyon jays pilfer at an extremely rapid rate, and can be difficult to motivate and control, even in a laboratory setting. Using the same methods as above, I allowed the cacher bird to recover the remaining caches once they had returned to 90% ad-lib weight.

For the last (fifth) cache-recovery cycle, birds in this treatment underwent a caching cycle where Mote was not allowed to pilfer any of the caches nor did I remove any caches. Mote only served as a caged observer during caching. I included this trial as a probe in order to examine the immediate short-term effects due to the cache-removal treatment. Methods for this last cache-recovery cycle were identical to a control cache-recovery cycle.

Statistical Analyses: To determine if birds recovered caches more frequently than expected by chance, we used the hypergeometric probability distribution (as in Balda et al. 1986; Sokal & Rohlf 1995). We calculated the number of cache recoveries expected by chance given the number of correct and incorrect sites available and the number of recoveries that were attempted using Number Cruncher Statistical Systems™ 3.1 statistical and data analysis system (© J. Hintze, Kaysville, UT, www.ncss.com). We did not include revisits to holes within a trial, so recovery patterns could be modeled by sampling without replacement.

We used ANOVAs to compare behavior across cache-recovery cycles within a given treatment, and t-tests to compare overall means between treatments (if there were no differences across cycles within the treatment). For comparisons within birds that were involved in both the control and then the cache-removal treatment, we used paired t-tests to compare their behavioral responses. In order to compare birds receiving the control treatment with the birds receiving the cache-removal treatment, we used Wilcoxon t-tests since the treatment groups had unequal variances.

RESULTS

Habituation

Previous pilferers explored the room differently than birds who had not pilfered in the last experiment. All previous pilferers explored a novel object presented to them during habituation/training while only 3 of the previous cachers did so (exact binomial test, $P = 0.037$). Birds with recent pilfering experience were more likely to investigate the object repeatedly (3.00 ± 2.7 times) compared to cachers (0.57 ± 0.79 times) during the

course of habituation (exact binomial test, $P = 0.039$, Fig. 3.2). All birds ($N = 10$), regardless of previous history, habituated to the experimental room within similar amounts of time; previous catchers took $2.40 (\pm 0.51)$ sessions and previous pilferers took $2.00 (\pm 1.20)$ sessions ($t = 0.51$, $df = 8$, $P = 0.62$). During habituation to the room, the two sets of birds also probed a similar number of holes (previous catchers; 16.29 ± 11.86 , previous pilferers; 12.67 ± 8.15 , $t = 1.7$, $df = 8$, $P = 0.10$).

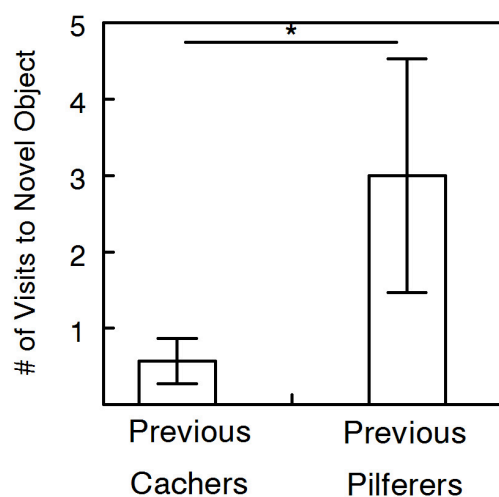


Figure 3.2. Individuals with recent experience pilfering visited the novel object (a flower-patterned metal water dish) introduced during the habituation sessions more frequently than those individuals who had recent experience as catchers (exact binomial test, $P = 0.039$).

Once birds had begun to handle food, I also measured how they approached and interacted with seeds. One of the most notable behavioral differences between birds was that some assessed seed quality with a bill-weighing technique, while others did not. Bill-weighing is a learned behavior used to assess seed weight (and possibly composition); jays select a seed and hold it in the middle portion of their bill for a brief amount of time, discarding seeds that feel overly-light and therefore may be rotten (Ligon & Martin

1974). During all habituation sessions six out of seven birds without experience pilfering exhibited bill-weighing, whereas none of the previous pilferers ever bill-weighed.

The same individuals that weighed seeds using the bill-weighing technique consumed fewer seeds overall. Birds without pilferage experience 17.4 (± 8.2) seeds, while those with recent experience pilfering other's caches ($N = 3$) ate an average of 27.2 ($\pm 5.9 = SD$) seeds per habituation session ($N = 10$, $t = -2.46$, $P = 0.023$, Fig. 3.3).

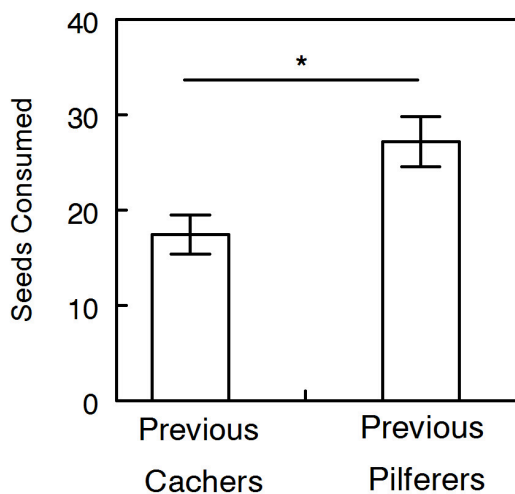


Figure 3.3. Jays with recent experience as pilferers ate more seeds during habituation to the experimental room than birds with recent experience as cachers (Welsh's t-test, $t = -2.49$, $P = 0.023$).

Summary of General Behavior during Caching Sessions

All caching sessions were completed within 37.0 (± 12.6) m, and birds did not make their first cache until 13.9 (± 8.6) m into the session. Birds ate seeds and occasionally socialized with the observer before they began caching. All birds vocalized to the observer (a male, Mote), making contact calls before and during caching. These calls included *racks*, *nears*, *multiple racks*, and *kaws* (as described in Marzluff & Balda

1992). Only two birds (both female) ever *rattled* or gave a *piping rattle*. Whenever these vocalizations were given, they were performed while observing Mote pilfering and consuming seeds. As Marzluff and Balda predict, the *rattle* preceded the *piping rattle* both times we observed the *piping rattle*.

Birds usually recovered seeds at levels significantly above chance during recovery cycles of control and cache-removal treatments (chance levels were calculated using the hypergeometric distribution, see Fig. 3.4 and Fig. 3.5, respectively). Birds 765 and 43770 could not be tested for cache recovery during the 4th cache-recovery cycle of the cache-removal treatment because they did not cache during this cycle.

Effects of Previous History on Caching Behavior

During the control treatment of the study, birds with experience pilfering behaved similarly to birds that lacked such history. There was a near-significant trend for previous pilferers to probe more often around the room, probing $53.70 (\pm 6.81)$ times per caching opportunity, compared to previous cachers who probed $22.89 (\pm 2.01)$ times ($F_{1,48} = 5.78, P = 0.070$). There were no differences between previous pilferers and cachers for the other behavioral metrics we measured.

During the cache-removal treatment, however, birds with experience pilfering did behave differently from birds lacking such experience. During the cache-removal treatment, jays without pilferage experience probed 23.18 ± 3.41 times but birds that had recently pilfered probed $104.48 (\pm 14.01)$ times ($F_{1,41} = 150.71, P < 0.0001, \text{Fig. 3.4a}$). Previous cachers probed in $12.07 (\pm 1.29)$ unique sites, which was comparable to their performance in the control treatment. But previous pilferers cached in more than twice as

many unique sites, averaging $35.92 (\pm 2.58)$ locations per caching bout ($F_{1,41} = 30.09$, $P < 0.0001$, Fig. 3.4b). We found a tendency approaching significance for previous pilferers to false cache (or abort caching attempts) more often than previous cachers (previous pilferers: 1.41 ± 0.51 , previous cachers: 0.42 ± 0.13 , $F_{1,41} = 4.91$, $P = 0.057$).

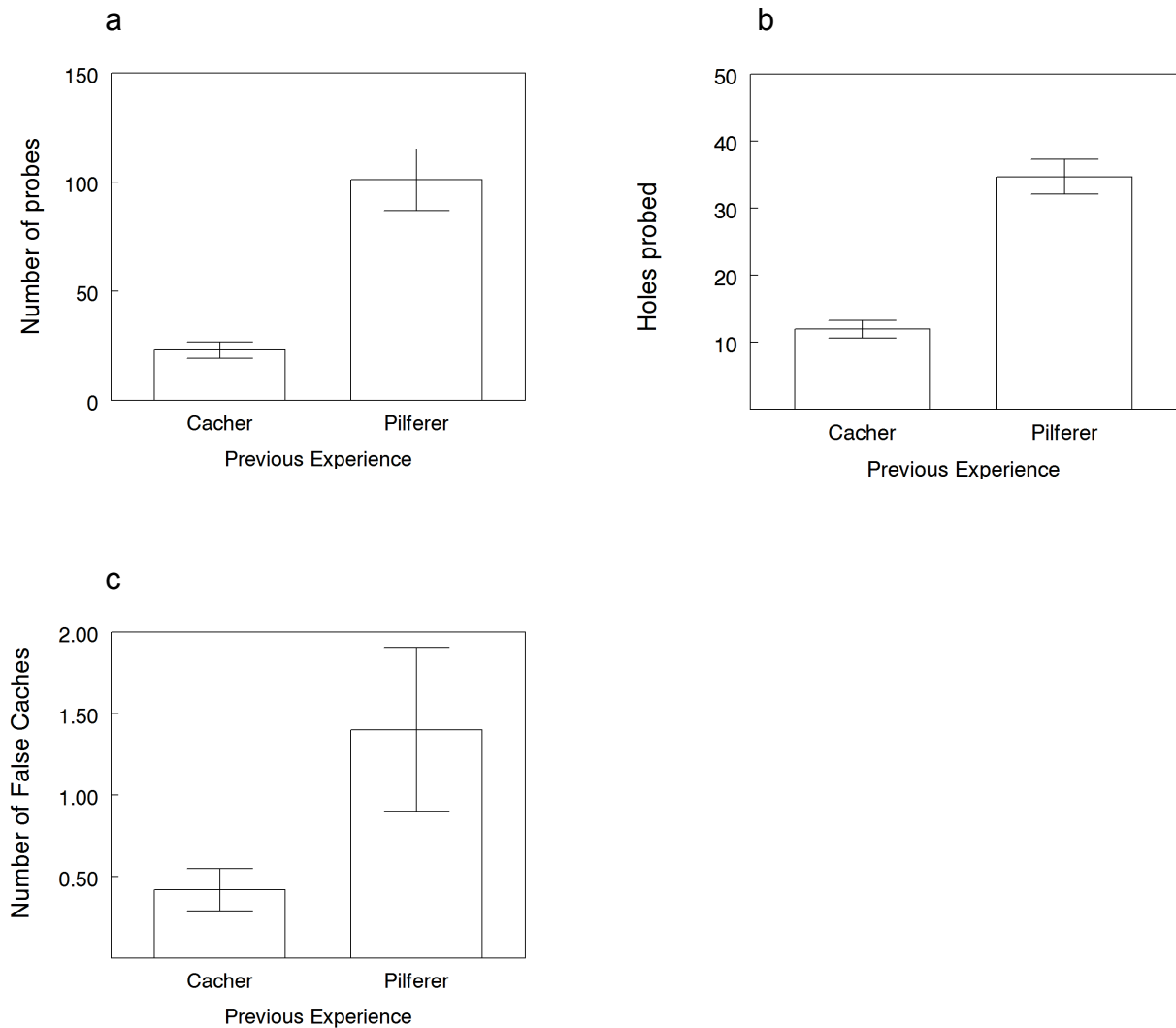


Figure 3.4. Birds with previous experience pilfering reacted differently to cache-removal than birds who had acted as cachers in the last study. During the cache-removal treatment, birds with previous experience caching (A) probed more often ($F_{1,41} = 150.71$, $P < 0.00001$) in (B) more locations ($F_{1,41} = 30.09$, $P = 0.0006$) around the room, and (C) tended to create more false-caches ($F_{1,41} = 4.9$, $P = 0.057$).

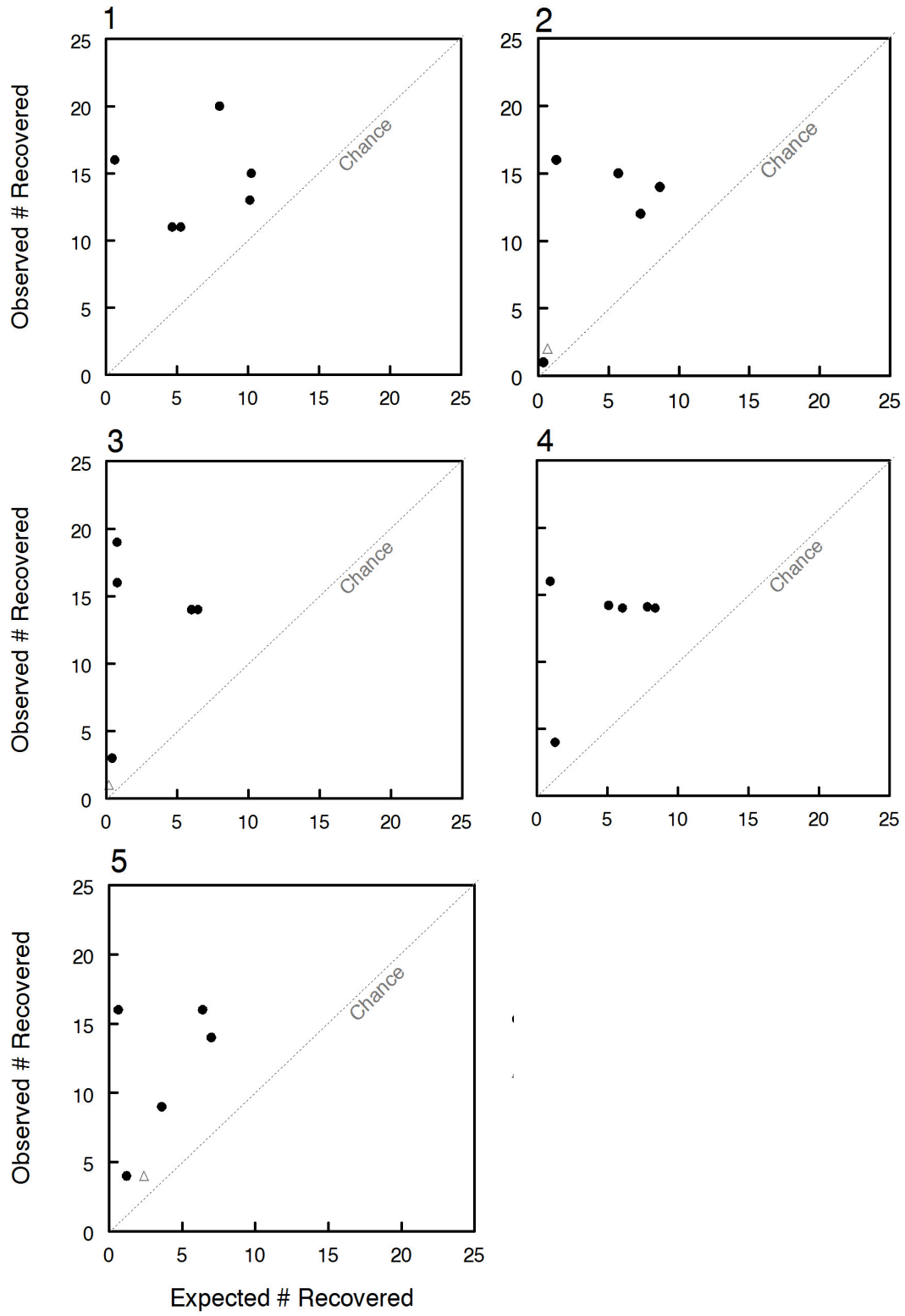


Figure 3.5. Number of caches recovered by each bird in each cache-recovery session (1-5) compared to those expected by chance for the control treatment. Jays generally recovered cached seeds at levels significantly above chance (represented by ●, $P < 0.05$). The only birds that didn't recover their cached seeds better than chance (represented by △) were female jays that had previously served as pilferers. We calculated recovery accuracy via hypergeometric analyses using the number of caches recovered (X), and holes probed (R) out of 51 open holes (N) by each bird in each trial in the control condition.

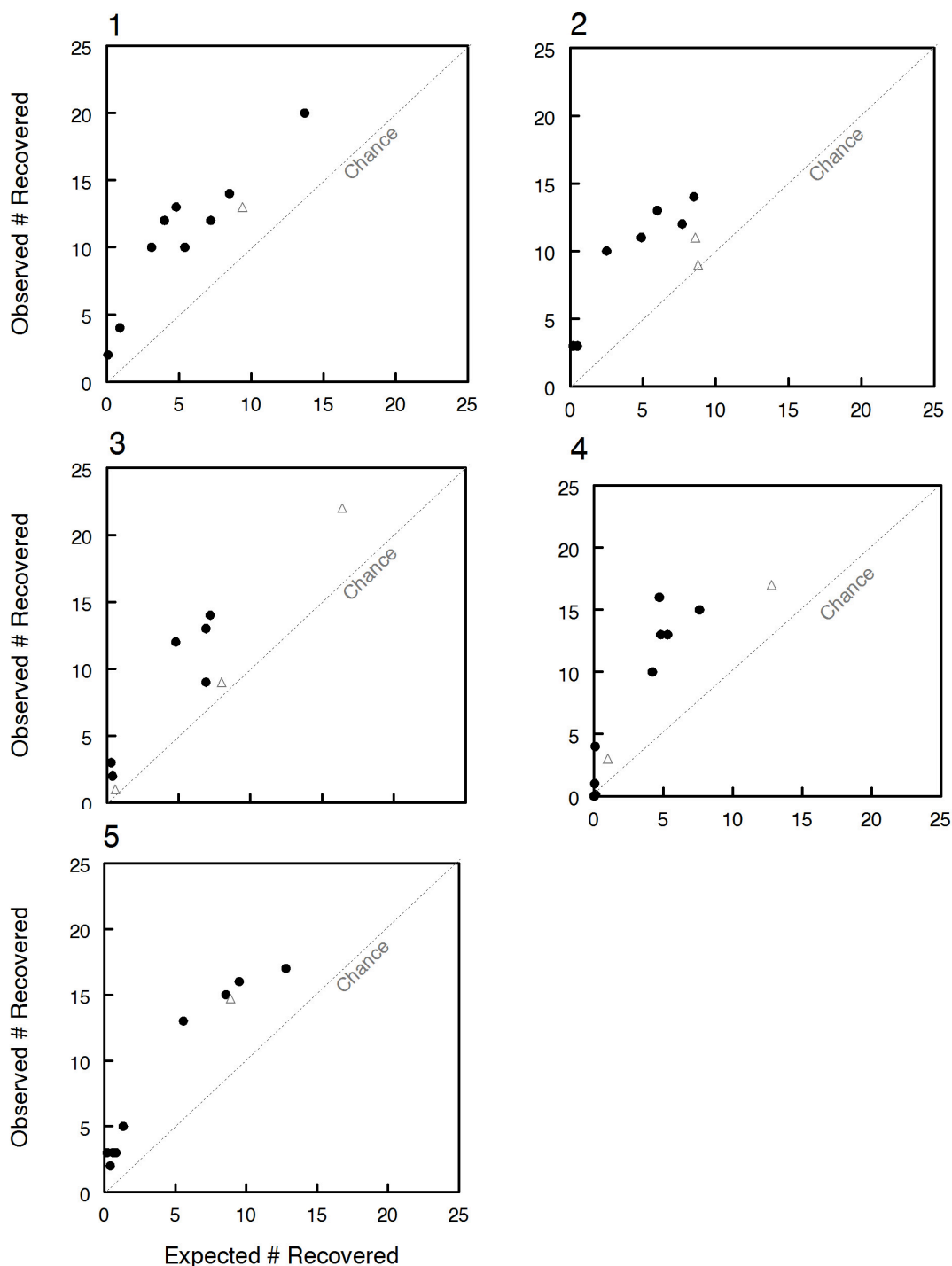


Figure 3.6. Number of caches recovered by each bird in each cache-recovery session (1-5) compared to those expected by chance for the cache-removal treatments. Jays generally recovered cached seeds at levels significantly above chance (represented by ●, $P < 0.05$). The only birds that didn't recover their cached seeds better than chance (represented by △) were female jays that had previously served as pilferers with the addition of one male "previous cacher" in cache-recovery cycle 3. We calculated recovery accuracy by hypergeometric analyses using the number of caches recovered (X), and holes probed (R) out of 51 open holes (N) by each bird in each trial.

As in habituation, the same six birds with experience as cachers continued to weigh seeds using the bill-weighing behavior. None of the birds with previous experience as pilferers performed this behavior in any of the cache-recovery cycles of either treatment.

Comparing Treatments

To examine the effect of repeated cache-removal on pinyon jay caching behavior I first compared the mean of behaviors between the control and the cache-removal groups for the last cache-recovery cycle (cycle 5) using between subjects ANOVAs. I did not find any effects on behaviors (see Appendix, Part A). I then used mixed model ANOVAs with groups as a between-subject effect and cycles as a within-subject effect to examine the effects of treatment across all 5 cache-recovery cycles.

Jays in the experimental treatment ate fewer seeds than birds in the non-pilferage treatment, resulting in a significant effect of cache-removal on seed consumption over the 5 cache-recovery cycles (Fig. 3.7, $F_{1,54} = 7.83$, $P = 0.0081$).

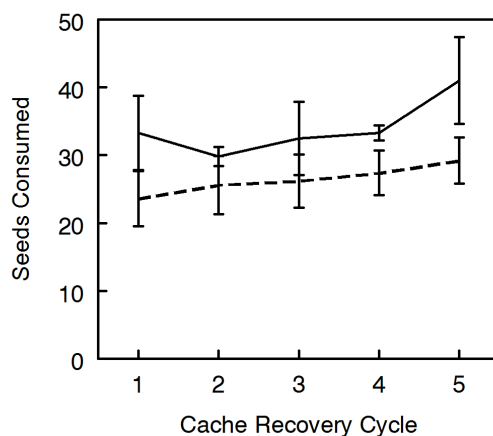


Fig 3.7. Jays in the cache-removal treatment (dotted line) ate fewer seeds throughout the study than birds in the control treatment (solid line, $F_{1,54} = 7.8$, $P = 0.0081$).

I also found a non-significant effect of cache-removal on the number of seeds cached over the course of the study (Fig. 3.8a, $F_{1,54} = 3.044$, $P = 0.091$). Birds in the cache-removal treatment hid a greater proportion of their seeds behind shielding landmarks than birds in the control treatment (Fig. 3.8b, $F_{1,54} = 5.66$, $P = 0.023$). I found no effect of cache-removal on latency to first cache, overall session time, number of holes probed or frequency of probes, re-caches, or false caches (see Appendix, Part B).

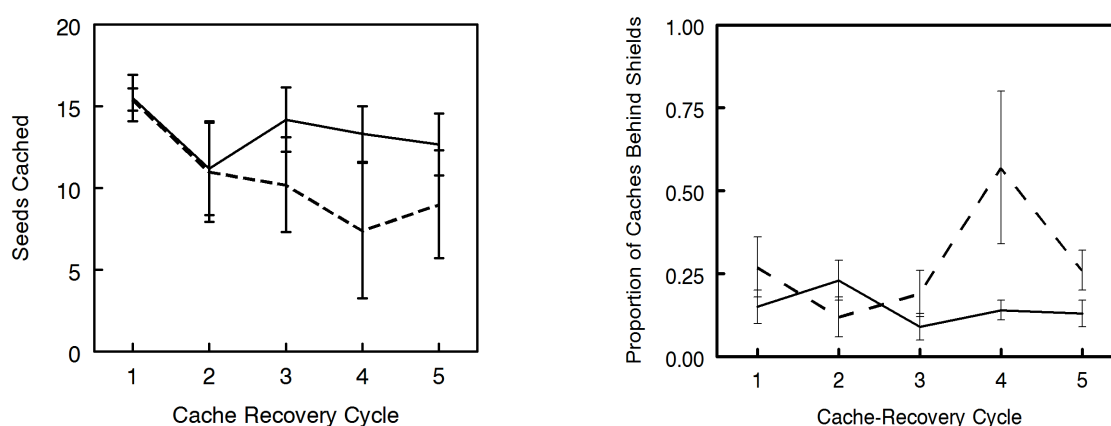


Figure 3.8. (A) There was a trend for birds in the cache-removal group to cache fewer seeds compared to birds in the control treatment ($F_{1,54} = 3.04$, $P = 0.09$). (B) Birds in the cache-removal treatment hid a greater proportion of the seeds that they did cache behind shielding landmarks ($F_{1,54} = 5.66$, $P = 0.02$).

As an additional treatment, birds from the control treatment underwent a cache-removal treatment. Once again, I compared the mean of each behavior between the cache removal treatment and the control treatment for cycle five. There were no significant effects in any of these analyses (see Appendix, Part C).

I then compared the behavior of the birds in the control treatment with their behavior in the subsequent cache-removal treatment across all five cycles using repeated measures ANOVAs. Jays tended to cache more of their seeds behind shielding landmarks

during the cache-removal treatment compared to their behavior during the control ($F_{1,54} = 4.68$, $P = 0.081$, Fig. 3.9). This effect was only apparent during the fourth cycle of the cache-removal treatment birds cached more of their seeds behind shielding landmarks ($F_{1,54} = 8.69$, $P = 0.00083$, Fig. 3.9). The cache-removal treatment had no other effects on the birds' behaviors once they had already been subjected to a control treatment (see Appendix, section D.)

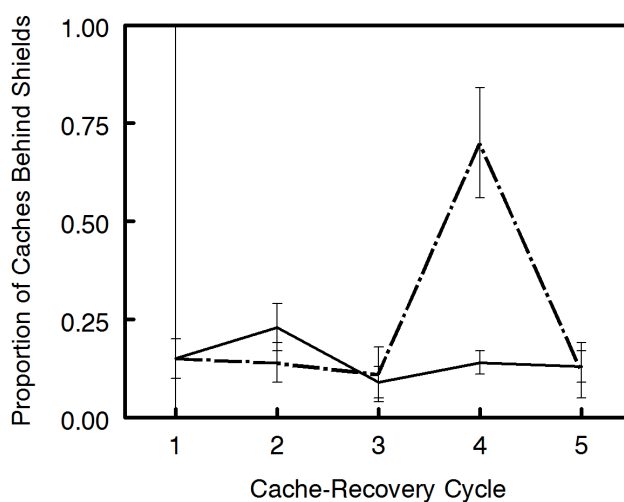


Figure 3.9. We found a significant interaction effect between treatment and cache-recovery cycle on the proportion of seeds that were cached behind shielding landmarks ($F_{1,54} = 8.69$, $P = 0.00083$). Control treatment is represented by solid line.

To compare behaviors between birds that participated in both treatments to birds that participated only in a cache-removal treatment, I used mixed model ANOVAs. My models included treatment as a between-group factor and cycle as a within-group factor. Pinyon jays that participated in both a control and a cache-removal treatment ate more seeds than birds subjected to only a cache-removal treatment ($F_{1,49} = 6.33$, $P = 0.016$, Fig. 3.10).

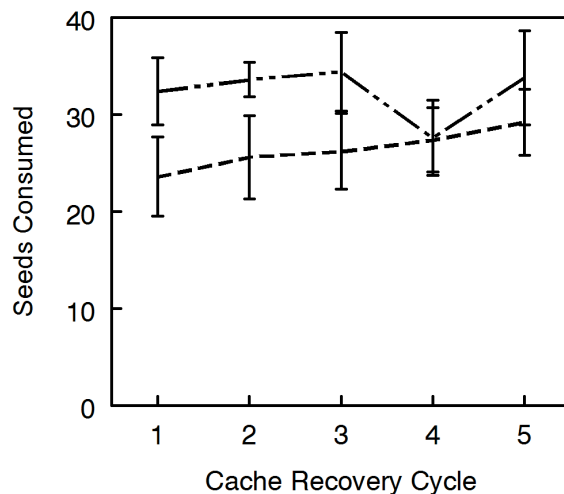


Figure 3.10. Pinyon jays that participated in both a control and a cache-removal treatment (dotted-dashed line) ate more seeds during the removal treatment when compared to birds subjected to only the cache removal treatment (dotted line, $F_{1,49} = 6.33$, $P = 0.016$).

I also found that birds that participated in both treatments cached more seeds than birds that participated in only the cache-removal treatment ($F_{1,49} = 8.37$, $P = 0.0062$, Fig. 3.11).

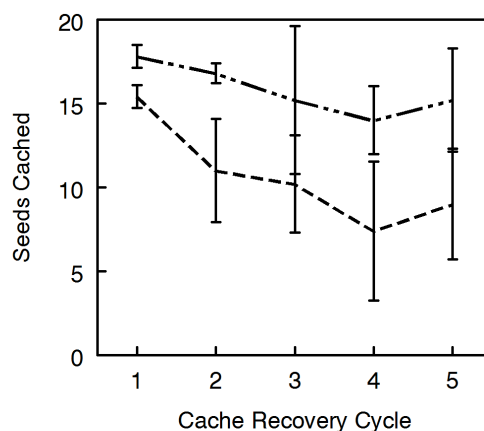


Figure 3.11. Birds that participated in both treatments (dotted-dashed line) cached more seeds during the removal treatment compared to birds that participated in only a cache-removal treatment (dotted line, $F_{1,49} = 8.37$, $P = 0.0062$). Jays in the cache-removal treatment cached significantly fewer seeds throughout the course of the study, whereas birds receiving the control treatment before the cache-removal treatment did not share this adjustment in caching behavior.

DISCUSSION

The suite of behaviors that comprise pinyon jay cache management strategies are flexible. Jays that were given the cache-removal treatment adjusted their cache-protection strategies from those involving false- and re-caching in the first experiment (and the beginning of this one), to one primarily dependent upon hiding caches behind shielding landmarks. Birds that received the control treatment followed by a cache-removal treatment did not make the same behavioral modifications, but instead maintained re-caching, false-caching, and out-of-sight caching behaviors at the same levels as in the control treatment.

General Behavior

All birds in the second study shared certain patterns of behavior, no matter which treatment or experimental histories they experienced. Jays took about the same amount of time to begin caching (latency to first cache) and to complete caching sessions. As in the previous experiment, all jays recovered caches with a high degree of accuracy. Finally, all birds communicated with the observer/companion birds using similar basic communication calls, though as I will discuss some birds demonstrated a greater variety of calls than others.

Latency to First Cache: None of the jays modified the amount of time they took to begin caching. If birds were maintained at a consistent motivational state, they should have been regularly hungry for pine nuts when they entered the room. Pinyon pine nuts have a relatively uniform handling time since they are fairly uniform in shape and size (Balda &

Kamil 2006, also see Chapter 2). It follows that jays would consume the same amount of seeds each time before caching, and spend about the same amount of time handling their food before caching were their motivational states controlled. The unchanging latencies indicate that efforts to control motivational state were successful. Latency to first cache remained constant since the majority of jays' pre-caching time was occupied by feeding, rather than room-exploration, perching, preening, or socialization.

Studies that found changes in latencies (Stone & Baker 1989, Heinrich & Pepper 1998, Bednekoff & Balda 1996) differed from this one in one major way—birds in those studies did not consume nearly as many seeds (or handle as many food items, in the case of ravens who handled frozen meat) per caching bout. The average number of seeds consumed in this study was 30 seeds per caching session, while birds in the above studies ate an order of magnitude fewer seeds (ranging from 2-4 seeds for chickadees, and 3-4 seeds for pinyon jays). These birds did not receive any pine nuts outside of the experiment, whereas during ad libitum feeding they received 4 seeds per day (= 28 seeds per week). Since birds were tested between once and twice a week, eating 30 seeds per session seems reasonable given their usual feeding regime. The aforementioned studies found responses in overall session time, latency to first cache, and caching rate (defined as # caches / session time – latency to first cache). The differences between the current study and previous ones can be accounted for given the variation in food-handling and feeding time.

Recovery Accuracy: Other studies have demonstrated that pinyon jays can accurately recover caches using spatial memory (e.g. Bednekoff et al. 1997, Dunlap et al. 2006,

Stafford et al. 2006). It was still important to confirm that pinyon jays could perform cache recovery in this experimental setting. Jays in this study were wild-caught and therefore particularly sensitive to conditions within the experimental room. Jays will not cache without a conspecific companion in vocal communication (Balda & Kamil 1989). Test birds are also slow to habituate if there are too few landmarks, or if the landmarks are not spaced throughout the entire room.

Jays retrieved caches with accuracies well above chance levels. Of the 80 recovery trials, there were only 12 occasions (representing 15% of all recovery bouts) in which jays did not recover caches at levels significantly above chance (see Figures 3.5 & 3.6). All but one (representing 92%) of these at-chance recovery bouts were performed by female pinyon jays who had also served as pilferers in the previous study.

There are several reasons as to why pilferers may have recovered fewer caches. Natural history predicts that female pinyon jays should have inferior spatial memory for caches since they create caches then rely on their mates to recover them later in the season while they incubate the nest (Balda et al. 1996). The females in this study behaved similarly to mated females in a study conducted by Dunlap et al. (2006), where mated females demonstrated low recovery accuracy, while unmated females recovered at similar levels to males. Differences may have been due to a decrease in recovery activity (the number of probes were not tallied), but could have also been due to memory loss. A facultative loss of memory in mated females would imply that retaining the memory of cache location carries a cost to the female. The females that recovered at chance levels in this study had all recently performed as pilferers, and therefore could recover food without having to create long term memories of where food was cached. If these females

had become familiar with the high pay-offs and low costs of pilfering, it might take time for these individuals to re-adopt a more costly strategy involving long-term memory for cache location. Of course, an alternative explanation exists that the birds that did not perform accurately may have not been properly motivated to accurately recover all caches.

Pinyon jays responded to the staged pilferage event, even though up to 9 days passed between pilfering and a subsequent caching opportunity. Between one pilferage event and the next opportunity for a jay to react to that event, time passed as the cacher returned to 90% of ad lib weight for the recovery session, recovered seeds, then return to 90% ad lib weight again. This cycle usually took between 3-5 days. If a second recovery session was needed because the cacher had not recovered all his seeds in the first recovery bout, then the time between pilferage and the next caching round could be even longer (up to 9 days). In other studies that have examined pinyon jay response to pilferage, intervals were much shorter during testing (e.g. Balda & Kamil 2006, Bednekoff et al. 1997). In the field, however, retention intervals could reasonably be expected to vary. Pinyon jays tolerate a degree of (sometimes immediate) cache pilferage by Stellar's jays (Marzluff & Balda 1992), while other caches might not be discovered lost until a subsequent caching bout days or even weeks later (Stotz & Balda 1995). In view of these considerations, the time intervals between cache-removal and subsequent test sessions were realistic.

Vocal Communication: All birds vocalized to the companion/observer bird. Calls included contact and identification calls, such as *racks*, *kaws*, *multiple racks*, and *nears*,

all of which are typically heard during feeding, seed harvesting, and before the flock moves to or from a caching site. Further descriptions of these calls and how they are used in social contexts are discussed elsewhere (Berger & Ligon 1977, Marzluff & Balda 1992).

Perhaps the most interesting vocalizations the pinyon jays gave during the study were performed by female pinyon jays. *Female* pinyon jays are known to *trill*, *rattle*, and *piping rattle* during the mating season when undesired males approach too closely; these calls will immobilize the male (Marzluff & Balda 1992). Males do not perform these calls, and do not have equivalent calls in their repertoire--differences in communication between males and females are common within this species (Dahlin et al. 2005).

The three calls are similar in their underlying structures though *rattles* have additional notes compared to *trills*, and *piping rattles* have high-pitched notes added on to those. Given that *piping rattles* always follow *rattles* in the context of male/female interactions, Marzluff and Balda interpret these calls together as a graded aggressive response. These calls are particularly interesting because they appear to be a case of a signal being used flexibly in a novel context. During the current experiment, I witnessed two different females *rattle*, then *piping rattle* towards Mote (a male) as they witnessed him pilfer their seeds. On both occasions, females were leaning out between the bars of the observer cage in the direction of the male pilferer, Mote. As in the context of courtship, calls seemed to represent increasing levels of aggression by the female.

Effects of Previous History on Behavior

Previous experience influenced how birds explored the room, interacted with seeds, and reacted to cache removal. Previous pilferers exhibited less neophobia during habituation, readily exploring a novel object. These birds also probed holes more often in more unique locations during the cache-removal treatment of the experiment (though there was a non-significant trend towards this behavior during the control treatment.) Finally, jays that had acted as pilferers were also more likely to quickly consume seeds without bill-clicking or bill-weighing (behaviors used to assess seed composition and quality).

Exploratory Behavior: Birds with recent experience pilfering were more exploratory; during the cache-removal treatment they probed two times as many holes within the room, probed four times more often during a visit to the room, and during habituation were more likely to explore a novel object (both initially and repeatedly) compared to birds that had acted as cachers in the first experiment.

These results were as expected, since birds acting as pilferers were rewarded for exploratory behavior in the first experiment. Observer/pilferer jays received pine seeds during the first experiment only if they recovered them using observational memory. When released into the room to recover food, all surface cues (e.g. disturbed sand, remnant shells from opened seeds, etc.) had been removed, so a room stocked with caches looked identical to the caching room in the context of this experiment. Since trials only stopped after 6 incorrect nearest-neighbor searches, pilferers could have been further encouraged to probe holes for food.

Seed Assessment: Jays that had experience as pilferers never bill-clicked or bill-weighed their seeds during habituation or any of the treatments (for a total of 10 to 12 feeding opportunities in the room, depending upon how long they took to habituate). These individuals ate 10 more seeds on average during the habituation session, but there were no differences in how many seeds they ate during any of the other treatments.

Comparing Treatments

There was an overall trend for birds in the cadre which received the control followed by the cache-removal treatments to be less responsive to cache-removal compared to birds who received cache-removal immediately after habituation. One of two processes are most likely to explain this pattern. (1) If the control treatment further reinforced the rule that “conspecific presence \neq pilferage,” five cycles of cache-removal in the subsequent treatment may not have been sufficient for jays to learn the new rule “conspecific presence \Rightarrow pilferage.” Jays became desensitized/habituated to the observer as the experiment progressed. (2) jays responded to cache-removal, but with a shallower learning curve. If the birds were not allowed enough cache recovery cycles to fully adjust management tactics, a change in behavior could not be detected. Here, I consider each cache protection measure in light of these alternative processes.

Caching Behind Shielding Landmarks: Cache removal evoked a change in pinyon jays’ caching strategies. While the birds had primarily relied on false- and re-caching to protect their caches (see Chapter 2), pinyon jays receiving the cache-removal treatment responded by hiding a greater proportion of their seeds behind shielding landmarks.

Pinyon jays appeared to learn to adjust their caching behaviors when subjected to a more competitive caching environment. These results support lab and semi-naturalistic studies conducted with mountain chickadees (Pravosudov 2008, Pravosudov et al. 2010), scrub jays (Dally et al. 2005b) and ravens (Bugnyar & Kortschal 2002), where individuals preferably cached behind shielding landmarks when observers were present.

There is limited field data supporting the notion that animals cache food out-of-sight from other observers. To date, no field studies have specifically addressed whether scatter-hoarders cache behind shielding landmarks. Part of the difficulty in addressing this question lies in the fact that observers in the wild often surround the cacher, so controlling the point-of-view of all observers would prove exceptionally challenging, if not impossible. One observational study on Eastern grey squirrels did demonstrate that cachers shielded their caches from conspecific observers by turning their backs on the observer while caching (Leaver et al. 2007). In this case, the authors argued that the squirrels' backs served as the visual barrier between the observer and the cache.

There are several non-exclusive explanations as to why jays, along with the other cachers mentioned above, could be caching out-of-sight from the observer. They may be caching behind barriers to reduce stress (Steele 2008), or they could use shielding landmarks to restrict visual information about the cache location as predicted by the pilferage avoidance hypothesis (Vander Wall 2003). Since the point-of-view of our observer was constrained to the observer cage, caching behind shielding landmarks would be an effective method of reducing information about cache location to the observer. This would be a viable cache protection strategy, especially considering that

pinyon jays are able to remember the location of caches they have observed being created (Bednekoff et al. 1996, this study, Chapter 2).

Whether jays are caching behind landmarks to reduce stress or to reduce visual information to an observer is impossible to determine with the data we currently possess. Others have speculated as to the “intentionality” behind withholding cache location information (Bugnyar & Kortschal 2002, Dally et al. 2005), but these actions could simply be a result of stimulus association or the formation of simple rules (i.e. “if there is another bird in the room, then cache near large landmarks”, or “if I can’t see you, you can’t see me”) rather than higher-order cognition.

Birds that received the control treatment and then the cache-removal treatment did not increase the proportion of caches they placed behind shielding landmarks across cycles of the cache-removal treatment (see Fig. 3.9). This could be the result of carry-over effects from the control treatment, in which cachers repeatedly associated the room with food and high recovery rates. Since the same bird that pilfered was present in the control treatment (where pilferage did not happen), the birds may have learned that the observer was not a threat to caching. Thus birds that participated in both control and cache removal treatments were slow to associate him with pilferage. Had I extended the study or used a different observer, birds may have exhibited the same behaviors seen in the experimental treatment.

False-caching: Birds receiving only the cache-removal treatment false-cached less than birds in the control treatment. Again, these findings support the hypothesis that pinyon jays employ a variety of flexible cache protection strategies. Jays may have learned to

switch from false-caching as a strategy since they continued to experience cache loss despite initial use of false-caching as a cache protection method. False-caching could be also viewed as an aborted caching attempt; perhaps jays subjected to cache removal become more decisive with their choice of cache locations as a product of increased pressure to get caches hidden quickly. In making more decisive caching movements, the number of interrupted cache attempts would decrease. One could test whether this was the case by limiting the number of probes allowed to the cacher, then determining how birds allocate those probes amongst caches and cache-protection behaviors, including false-caches.

Studies with other food-caching corvids found false-caching might have been a more effective cache protection method compared to other pilferage avoidance strategies. Both ravens (Bugnyar & Heinrich 2002) and scrub jays (Dally et al. 2005) increased their false-caching rates when in the presence of a competitor. However, in neither case was the opportunity to cache in a concealed location available to cachers.

Throughout the experiment, false-caches were the least common of all cache protection behaviors performed by birds in any treatment group. Unlike birds that received only the cache removal treatment, jays that participated in both a control and a cache-removal treatment did not alter their frequency of false-caches. Even if false-caching really is a less effective cache protection tactic than cache site selection or re-caching (as suggested above, and by Dally et al. 2005b), one still might expect false-caches to persist at low rates in a population where alternative cache protection behaviors are less effective, less of an option, or more costly.

Re-caching: Pinyon jays had re-cached as a cache-management strategy in the first experiment, yet re-caching rates were considerably lower throughout the later cycles of the cache-removal treatment. At the start of this experiment (cache-recovery cycle 1) I found no difference between re-caching rates of the first experiment and the control of this experiment. However, all but one jay had stopped re-caching by the last (fifth) caching cycle in the cache-removal treatment.

Jays may not have used re-caching as a cache management strategy if they had an alternative (and more effective) means of cache protection available to them, namely the option of caching out-of-sight. In a series of experiments controlling the point-of-view of the observer and the caching options available to the cacher, Dally et al. (2005) also found that when cachers had shielding landmarks available to them, they did not re-cache during caching but instead cached behind shielding landmarks, just as our birds did. When not given shielding landmarks, their scrub jays primarily used alternate cache-management strategies, including re-caching (see also Chapter 2).

Re-caching rates were relatively low for most of the birds throughout both experiments although one individual re-cached at exceptionally high rates. This is consistent with some field data. Stotz & Balda (1995) report that pinyon jays do not recache during caching. Field studies of black-capped chickadees also indicate that these birds do not re-cache (Stone & Baker 1989). Pinyon jays, like black-capped chickadees do not have territories, and cache in a flock. Re-caching at the time of caching could be costly, especially in a species with observational memory. The act of digging up a cache could draw an observer's attention to the food, and increase the risk of detection. The studies that have found frequent re-caching usually involved more solitary scatter

hoarders, such as grey jays (Waite & Reeve 1995), scrub jays (Degange et al. 1989), robins (Burns & Van Horik 2007), and eastern and yellow pine chipmunks (Clarke & Kramer 1994, Vander Wall & Joyner 1998). In these studies, food was re-sequestered only when conspecific competitors were out of sight. Our jays did not re-cache once the observer was removed from the room (during the recovery sessions). Instead, our jays consumed the majority of seeds, or left seeds for later consumption.

Seeds Consumed: Birds in the cache-removal group ate fewer seeds than birds in the control group. Individuals that received both the control treatment and the cache removal treatment did not decrease the number of seeds they consumed in the removal treatment. It is unclear why one group of birds responded by consuming fewer seeds, and the other did not. It is possible that jays exposed only to repeated cache removal reduced the number of seeds they consumed as a result of increased stress. Other studies have found that birds increased the number of seeds they consumed when in the presence of increased competition (Bednekoff & Balda 1996, Lahti 1998). However, stressed individuals with high levels of cortisol tend to eat less food (for birds; Virden et al. 2007, for other taxa, see review in Davidson 1997). Birds that received the control treatment first may have had comparatively lower stress levels, since they had the benefit of a stress-free environment during the control treatment before receiving the removal treatment. Considering this groups' lack of reaction (or possibly delayed reaction) to cache-removal (see above) it would therefore seem likely that these birds were not stressed by the removal treatment. It would therefore be reasonable to expect them to continue to eat heartily.

Determining whether or not this was the case will require further study. A cortisol test of jays' fecal samples (according to the methods outlined in Kortschal 1998) would be sufficient to determine relative stress levels between individuals. Pinyon jays routinely defecate in the experimental chamber while caching, so obtaining a sample from the floor would not be difficult. Further collections taken from the home cages could determine an individual's cortisol levels throughout the week for a measurement of each individuals' baseline stress fluctuations/range.

Number of Seeds Cached: Jays subjected to cache removal did not respond to the treatment by modifying the number of seeds they cached though there was a trend to cache fewer seeds throughout the study. This could have occurred because birds had to cache 15 seeds to meet criterion in the previous study. Birds were not allowed to leave the room until they had cached all 15 seeds. In this study, I allowed the number of seeds cached per session to vary so that a change in the number of seeds cached could be detected. However, it is possible that the previous experience limited the ability of the birds to adjust the number of seeds they cached during each bout. The number of seeds birds cached is consistent with this idea; the group that received the removal treatment significantly reduced the number of seeds they ate. The cadre that received the control treatment and then the cache-removal treatment also reduced the number of seeds they consumed, but to a far lesser extent (see Fig. 3.10).

Conclusions

These findings indicate that the behaviors comprising pinyon jay cache management strategies are not fixed. Pinyon jays exhibited plasticity in their selection of specific cache-management strategies in response to cache removal. Some changed their cache-protection strategies from those involving false- and re-caching in our first study (see Chapter 2) to one primarily dependant upon hiding caches behind shielding landmarks, while others forewent such a change. Birds that participated in a control treatment before being subjected to cache removal appeared to be less sensitive to cache removal stimulus and forewent a change in behavioral tactics.

Previous experience also influenced how jays behaved during the experiment. Jays with experience as pilferers were less neophobic and more exploratory. They were also quicker to consume seeds (instead of measuring them first), and cached a greater proportion of the seeds that they handled—though they cached fewer seeds overall. A particularly intriguing follow-up study would be to examine the interaction effects of previous experience and treatment on the various metrics of caching behavior. Our sample size was constrained since we used birds from a previous study—ideally we would have included more birds with previous experience as observers and pilferers within the lab. It does appear that such an experiment would be warranted, especially given the indications of treatment order effects. Effects of previous experience have also been found in caching behavior in scrub jays (Emery & Clayton 2001), and in nesting behavior in pinyon jays (Marzluff 1988).

I anticipated that order effects would be present if birds were conditioned by having their caches removed; however I did not predict a delay in behavioral adjustments due to the control treatment being administered first. Although the comparison is flawed

(confounded with all the variables associated with time, order effects, and increasing age) it suggests some intriguing possibilities for future study. Repeating the experiment with a complete Latin square design would allow one to confirm the effects of treatment order on learning.

REFERENCES

- Balda, R. P. & Bateman, G. C.** 1971. Flocking and annual cycle of the pinon jay, *Gymnorhinus cyanocephalus*. *The Condor*, 73, 287-302.
- Balda, R. P. & Kamil, A. C.** 2006. The Ecology and Life History of Seed Caching Corvids.
- Balda, R. P. & Kamil, A. C.** 1998. The Ecology and Evolution of Spatial Memory in Corvids of the Southwestern USA: The Perplexing Pinyon Jay. In: *Animal Cognition in Nature: The Convergence of Psychology and Biology in Laboratory and Field* (Ed. by Balda, R. P., Pepperberg, I. M. & Kamil, A. C.), pp. 29-64. San Diego: Academic Press.
- Balda, R. P., Kamil, A. C. & Grim, K.** 1986. Revisits to emptied cache sites by Clark's nutcrackers (*Nucifraga columbiana*). *Animal Behavior*, 34, 1289-1298.
- Bednekoff, P. A. & Balda, R. P.** 1996. Observational spatial memory in Clark's nutcrackers and Mexican jays. *Animal Behaviour*, 52, 833-839.
- Bednekoff, P. A., Balda, R. P., Kamil, A. C. & Hile, A. G.** 1997. Long-term spatial memory in four seed-caching corvid species. *Animal Behaviour*, 53, 335-341.
- Bugnyar, T. & Heinrich, B.** 2005. Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proceedings of the Royal Society B-Biological Sciences*, 272, 1641-1646.
- Bugnyar, T. & Kotrschal, K.** 2002. Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? *Animal Behaviour*, 64, 185-195.
- Burns, K. C. & Steer, J.** 2006. Dominance rank influences food hoarding in New Zealand robins *Petroica australis*. *Ibis*, 148, 266-272.
- Clarke, M. F. & Kramer, D. L.** 1994. The placement, recovery, and loss of scatter hoards by eastern chipmunks, *Tamias striatus*. *Behavioral Ecology*, 5, 353-361.
- Dahlin, C. R., Balda, R. P. & Slobodchikoff, C.** 2005. Food, audience and sex effects on pinyon jay (*Gymnorhinus cyanocephalus*) communication. *Behavioural Processes*, 68, 25-39.
- Dally, J. M., Emery, N. J. & Clayton, N. S.** 2005. The social suppression of caching in western scrub-jays (*Aphelocoma californica*). *Behaviour*, 142, 961-977.
- Dally, J. M., Emery, N. J. & Clayton, N. S.** 2005. Cache protection strategies by western scrub-jays, *Aphelocoma californica*: implications for social cognition.

Animal Behaviour, 70, 1251-1263.

- Davidson, W.** 1997. The effects of exercise on teleost fish, a review of recent literature. *Comparative Biochemistry and Physiology Part A: Physiology*, 117, 67-75.
- DeGange, A. R., Fitzpatrick, J. W., Layne, J. N. & Woolfenden, G. E.** 1989. Acorn harvesting by Florida scrub jays. *Ecology*, 70, 348-356.
- Dunlap, A. S., Chen, B. B., Bednekoff, P. A., Greene, T. M. & Balda, R. P.** 2006. A state-dependent sex difference in spatial memory in pinyon jays, *Gymnorhinus cyanocephalus*: mated females forget as predicted by natural history. *Animal Behaviour*, 72, 401-411.
- Emery, N. J. & Clayton, N. S.** 2001. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, 414, 443-446.
- Hampton, R. R. & Sherry, D. F.** 1994. The effects of cache loss on choice of cache sites in black-capped chickadees. *Behavioral Ecology*, 5, 44-50.
- Heinrich, B. & Pepper, J. W.** 1998. Influence of competitors on caching behaviour in the common raven, *Corvus corax*. *Animal Behaviour*, 56, 1083-1090.
- Kotrschal, K., Hirschenhauser, K. & Mostl, E.** 1998. The relationship between social stress and dominance is seasonal in greylag geese. *Animal Behaviour*, 55, 171-176.
- Lahti, K., Koivula, K., Rytkonen, S., Mustonen, T., Welling, P., Pravosudov, V. V. & Orell, M.** 1998. Social influences on food caching in willow tits: A field experiment. *Behavioral Ecology*, 9, 122-129.
- Leaver, L. A., Hopewell, L., Caldwell, C. & Mallarky, L.** 2007. Audience effects on food caching in grey squirrels (*Sciurus carolinensis*): evidence for pilferage avoidance strategies. *Animal Cognition*, 10, 23-27.
- Lewis, J.** 2005. Interference effects in the spatial memory of seed caching corvids, University of Nebraska.
- Ligon, J. D. & Martin, D. J.** 1974. Piñon seed assessment by the piñon jay, *Gymnorhinus cyanocephalus*. *Animal Behavior*, 22, 421-429.
- Marzluff, J. M. & Balda, R. P.** 1988. Pairing patterns and fitness in a free-ranging population of pinyon jays: what do they reveal about mate choice? *Condor*, 90, 201-213.
- Marzluff, J. M.** 1988. Do pinyon jays alter nest placement based on prior experience? *Animal Behavior*, 36, 1-10.

- Pravusodov, V. V.** 2008. Mountain chickadees discriminate between potential cache pilferers and non-pilferers. *Proceedings of the Royal Society B-Biological Sciences*, 275, 55-61.
- Pravusodov, V. V. & Clayton, N. S.** 2001. Effects of demanding foraging conditions on cache retrieval accuracy in food-caching mountain chickadees (*Poecile gambeli*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268, 363-368.
- Pravusodov, V. V., Roth, T. C. & LaDage, L. D.** 2010. Chickadees are selfish group members when it comes to food caching. *Animal Behavior*, 80, 175-180.
- Sokal, R. R. & Rohlf, F. J.** 1995. *Biometry*, 3rd. edn. New York: W.H. Freedman & Co.
- Stafford, B. L., Balda, R. P. & Kamil, A. C.** 2006. Does seed-caching experience affect spatial memory performance by pinyon jays? *Ethology*, 112, 1202-1208.
- Steele, M. A., Halkin, S. L., Smallwood, P. D., Mckenna, T. J., Mitsopoulos, K. & Beam, M.** 2008. Cache protection strategies of a scatter-hoarding rodent: do tree squirrels engage in behavioural deception? *Animal Behaviour*, 75, 705-714.
- Stone, E. R. & Baker, M. C.** 1989. The Effects of Conspecifics on Food Caching by Black-Capped Chickadees. *Condor*, 91, 886-890.
- Stotz, N. & Balda, J.** 1995. Cache and recovery behavior of wild pinyon jays in Northern Arizona. *The Southwestern Naturalist*, 40, 180-184.
- Vander Wall, S. B. & Jenkins, S. H.** 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology*, 14, 656-667.
- Vander Wall, S. B. & Joyner, J. W.** 1998. Secondary wind dispersal of winged pine seeds. *American Midland Naturalist*, 139, 365-373.
- Viriden, W. S., Thaxton, J. P., Corzo, A., Dozier, W. A. I. & Kidd, M. T.** 2007. Evaluation of models using corticosterone and adrenocorticotropin to induce conditions mimicking physiological stress in commercial broilers. *Poultry Science*, 86, 2485-2491.
- Waite, T. A. & Reeve, H. K.** 1995. Source-use decisions by hoarding Gray Jays: effects of local cache density and food value. *Journal of Avian Biology*, 26, 59-66.

CHAPTER 4: CONCLUSIONS

Cachers

These studies have revealed several key insights into how pinyon jays make cache management decisions. Pinyon jays do not use social context to assess cache threat during caching. For a bird such as the pinyon jay that harvests, transports, and caches in the presence of dozens-to-hundreds of conspecifics, the presence of an observer is not an exceptional or particularly informative event. Since jays are constantly surrounded by conspecifics, social environment will not be a useful proxy for pilferage threat. Noting the presence of a conspecific without knowing the relative dominance of the observer (dominant or subordinate) may not yield useful information about the threat to caches posed by conspecifics. Instead we find jays used cues from an actual pilferage event (cache removal + the presence of a conspecific) along with cache survival to signal whether they should modify caching behaviors. Pinyon jays responded by consuming fewer seeds and switching from false caching tactics to placing caches behind shielding landmarks. Other studies have also found that cachers directly assess the threat of pilferage by monitoring cache survival. Cache-recovery studies performed with marsh tits (Stevens 1984), black-capped chickadees (Hampton & Sherry 1994), mountain chickadees (Pravosudov 2001), as well as other caching mammals (Preston 2001, 2005) have all found that the presence of an observer combined with the experience of cache removal was required to elicit a response in caching-related strategies. In the studies above, like the studies outlined here, the presence of an observer *per se* did not cause a response in cache management.

Many other scatter-hoarding species appear to be more sensitive to the social climate during caching than pinyon jays (see Chapter 1). Not only do many of these species respond to the presence of conspecifics (e.g. Dally et al. 2006, Bugnyar & Kortschal 2004, see Chapter 1), but some respond to heterospecific (Bugnyar & Kortschal 2002, Pravusodov 2008) or even human (Bugnyar & Kortschal 2002) observers. It could be costly for pinyon jays to react to stimuli that do not accurately predict an increase in pilferage threat. These costs could manifest in several ways. If jays returned to their caches to re-cache, observers could determine the new cache location, or cachers could suffer from memory interference. Unnecessary false caching would result in time lost for feeding, attending young or potential mates. Hypersensitivity to conspecific presence would also be costly if jays cached further away since an increase in transport time would reduce caching efficiency and expose lone jays to predation. If jays chose to place caches to restrict visual information, this might compromise microhabitat selection, and therefore seed preservation. Jays must therefore accurately assess the competitive climate when weighing caching decisions.

Pinyon jays did not require all the cues of an actual pilferage event to modify their caching strategies. Thus I have used “direct” evaluation of pilferage as a relative term. The salient features available to birds for monitoring cache-survival were reduced to information transferred during cache-creation and observation of the pilferage event. I left no disturbance surface cues after the removal of a cache, and I always cleaned and re-set the room between sessions. Although cachers and pilferers were able to watch and vocalize to each other, our cachers never interacted physically with the pilferer due to IACUC regulations. Despite the fact that birds lacked the extra cues they would have had

in the wild during an “authentic” pilferage experience, jays still responded to cache-removal by shifting cache-management strategies. This indicates that direct aggression may not be a salient or useful category of behaviors (for pilfering or cache-defense). The low degree of overall aggression within a pinyon jay flock is well-documented within the field (Marzluff & Balda 1992, Balda 2002, Wiggins 2005).

Pilferers

Unmated pinyon jays of either sex were consistently able to recover observed caches with a high degree of accuracy. Previous studies have demonstrated that males can recover observed caches more reliably than females at both short (48 h) and long (1 wk – 4 mo) retention intervals (Dunlap et al. 2006). One possible reason for the difference in results may be that the experimental design outlined here allowed pilferers to recover caches after shorter intervals of 30m - 1h (depending on how long it took to reset the room). Observational memory in both sexes appears to function at ecologically-relevant timescales. Since jays cache side-by side for a period of one to several hours (Marzluff & Balda 1992), jays of both sexes could pilfer each other’s food during a flock’s caching bout in the wild. Cache pilferage should therefore be an efficient short-term strategy for individuals, though it could also translate to a long-term strategy if pilferers re-cache recovered seeds as new caches (which should be easier for them to remember). It would be interesting to study whether there are trade-offs in resource allocation and spatial memory: do efficient pilferers cache fewer seeds? Do they recover their own seeds as well as individuals that don’t pilfer many seeds? Are overall recovery levels related to dominance or sex? How do these metrics relate to cache protection

behaviors? Each of these questions could be answered by tracking the caching and recovery patterns of birds of known sex and dominance ranking. If all jays were given the opportunity to act as cachers and pilferers, one could examine whether there were trade-offs in memory, links between dominance rank and behavioral strategies, etc.

Pilferers in this study recovered caches at levels significantly above chance whether cachers used cache protection behaviors or not. However pilferers were more likely to visit false-cache sites than holes that were not visited by cachers. In other words, false-caching could reduce pilferer efficiency if time or access to cache sites were restricted, as would be expected in a real-life scenario. Though false-caching occurred at relatively low rates, false caching may be used as an effective cache protection method in the wild. For every false cache site a pilferer visits, the pilferer incurs costs including time locating the site, digging through substrate, and most likely digging in adjacent locations as birds are observed to do in laboratory and field settings (Balda & Kamil 1998).

Birds with experience acting as pilferers in the first experiment subsequently behaved differently from birds lacking such experience. Throughout the second study, these birds exhibited more exploratory behaviors and a lower degree of neophobia. These birds never exhibited the characteristic measuring behaviors *bill clicking* and *bill weighing* typically associated with seed caching corvids. Individuals with experience as pilferers ate significantly more seeds during habituation, but never exhibited key measuring behaviors that would indicate they were weighing seeds for fat and moisture content, indicating they were trading quantity for quality.

Experiences from the past as well as information from current situations effect how pinyon jays act in to ensure cache survival. Significantly, jays are desensitized to irrelevant information: since they are surrounded by conspecifics virtually all of the time, it does not benefit them to respond to the presence of a single observer. Instead, they garner direct information about cache-survival to determine whether they should modify caching behaviors. The experiments described in this thesis revealed that jays perform different behavioral strategies, but it is likely that in the wild these approaches to cache protection complement each other. Pinyon jays are likely to integrate past experiences with pilferage to inform them of future caching decisions while they continue to monitor the survival of their caches through time.

REFERENCES

- Balda, R. P. & Kamil, A. C.** 1998. The Ecology and Evolution of Spatial Memory in Corvids of the Southwestern USA: The Perplexing Pinyon Jay . In: *Animal Cognition in Nature: The Convergence of Psychology and Biology in Laboratory and Field* (Ed. by Balda, R. P., Pepperberg, I. M. & Kamil, A. C.), pp. 29-64. San Diego: Academic Press.
- Bugnyar, T. & Kotrschal, K.** 2002. Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? *Animal Behaviour*, 64, 185-195.
- Bugnyar, T. & Kotrschal, K.** 2004. Leading a conspecific away from food in ravens (*Corvus corax*)? *Animal Cognition*, 7, 69-76.
- Dunlap, A. S., Chen, B. B., Bednekoff, P. A., Greene, T. M. & Balda, R. P.** 2006. A state-dependent sex difference in spatial memory in pinyon jays, *Gymnorhinus cyanocephalus*: mated females forget as predicted by natural history. *Animal Behaviour*, 72, 401-411.
- Dally, J. M., Clayton, N. S. & Emery, N. J.** 2006. The behaviour and evolution of cache protection and pilferage. *Animal Behaviour*, 72, 13-23.
- Hampton, R. R. & Sherry, D. F.** 1994. The effects of cache loss on choice of cache sites in black-capped chickadees. *Behavioral Ecology*, 5, 44-50.
- Marzluff, J. M. & Balda, R. P.** 1992. *The Pinyon Jay: Behavioral ecology of a colonial and cooperative corvid*. London: T & AD Poyser.
- Pravosudov, V. V. & Clayton, N. S.** 2001. Effects of demanding foraging conditions on cache retrieval accuracy in food-caching mountain chickadees (*Poecile gambeli*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268, 363-368.
- Pravosudov, V. V.** 2008. Mountain chickadees discriminate between potential cache pilferers and non-pilferers. *Proceedings of the Royal Society B-Biological Sciences*, 275, 55-61.
- Preston, S. D. & Jacobs, L. F.** 2001. Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy. *Behavioral Ecology*, 12, 517-523.
- Preston, S. D. & Jacobs, L. F.** 2005. Cache decision making: the effects of competition on cache decisions in merriam's kangaroo rat (*dipodomys merriami*). *Journal of Comparative Psychology*, 119, 187-196.
- Stevens, T. A.** 1984. Food storing by marsh tits and shrikes, Oxford University.

Turney, P. D. 2002. Myths and Legends of the Baldwin Effect *Proceedings of the 13th International Conference on Machine Learning, Workshop on Evolutionary Computation and Machine Learning*.

APPENDIX

Part A: To examine the effect of repeated cache-removal on pinyon jay caching behavior I compared the mean of behaviors between the control and the cache-removal groups at the very end of the experiment (cache-recovery cycle 5). To perform these comparisons, I used between subjects ANOVAs.

There was no effect of the cache-removal treatment on how many seeds birds cached ($F_{1,9} = 1.01$, $P = 0.34$), consumed ($F_{1,9} = 2.36$, $P = 0.16$), how many times they false-cached ($F_{1,9} = 3.14$, $P = 0.11$), re-cached ($F_{1,9} = 1.16$, $P = 0.31$), or cached behind shielding landmarks ($F_{1,9} = 3.41$, $P = 0.10$). Jays were also uniform in the timing and style of caching behaviors (latency to first cache: $F_{1,9} = 0.51$, $P = 0.49$, session time: $F_{1,9} = 0.29$, $P = 0.60$, number of probes: $F_{1,9} = 0.24$, $P = 0.63$, holes probed: $F_{1,9} = 0.35$, $P = 0.57$).

Part B: I used mixed model ANOVAs with groups as a between-subject effect and cycles as a within-subject effect to examine the effects of heavy cache-removal across all 5 cache-recovery cycles on behavior. There was no effect of cache-removal on latency to first cache ($F_{1,54} = 0.3$, $P = 0.58$), overall session time ($F_{1,54} = 0.24$, $P = 0.63$), number of holes probed ($F_{1,54} = 1.28$, $P = 0.26$) or frequency of probes ($F_{1,54} = 0.01$, $P = 0.91$) and re-caches ($F_{1,54} = 1.26$, $P = 0.28$).

Part C: As an additional treatment, birds from the control treatment also underwent a cache-removal treatment (see Fig. 3.1). Once again, we compared the mean of each behavior between the cache removal treatment and the control treatment for cycle five.

There was no effect of the subsequent cache-removal treatment on how many seeds birds cached ($F_{1,8} = 1.89$, $P = 0.21$), consumed ($F_{1,8} = 0.61$, $P = 0.46$), how many times they false-cached ($F_{1,8} = 0.40$, $P = 0.55$), re-cached ($F_{1,8} = 0.87$, $P = 0.38$), or cached behind shielding landmarks ($F_{1,8} = 2.16$, $P = 0.18$). Jays were also uniform in the timing and frequency of their caching behaviors (latency to first cache: $F_{1,8} = 0.09$, $P = 0.77$, session time: $F_{1,8} = 0.11$, $P = 0.75$, number of probes: $F_{1,8} = 0.28$, $P = 0.61$, holes probed: $F_{1,8} = 0.57$, $P = 0.47$).

Part D: Jays from the control treatment also participated in a cache-removal treatment.

Once again, I compared the mean of each behavior between the cache removal treatment and the control treatment for cycle five. Birds did not adjust the number of seeds they cached ($F_{1,54} = 1.48$, $P = 0.26$) or consumed ($F_{1,54} = 0$, $P = 1$) between the first and second treatments. Nor did they adjust some of their cache protection behaviors, including reaching ($F_{1,54} = 0.42$, $P = 0.54$), and false caching ($F_{1,54} = 2.28$, $P = 0.19$).