

Cache Decision Making: The Effects of Competition on Cache Decisions in Merriam's Kangaroo Rat (*Dipodomys merriami*)

Stephanie D. Preston and Lucia F. Jacobs
University of California, Berkeley

Caching food is an economic, decision-making process that requires animals to take many factors into account, including the risk of pilferage. However, little is known about how food-storing animals determine the risk of pilferage. In this study, the authors examined the effect of a dominant competitor species on the caching and behavior of Merriam's kangaroo rat (*Dipodomys merriami*). The authors found that, as with conspecific competitors, kangaroo rats did not alter caching in response to the mere presence of a heterospecific competitor, but moved caches to an unpreferred area when the competitor's presence was paired with pilferage. These data suggest that Merriam's kangaroo rat assesses pilfer risk from actual pilferage by a competitor and adaptively alters cache strategy to minimize future risk.

Many species including birds, rodents, and humans cache food in order to ensure even access despite an uneven supply (Vander Wall, 1990). In order for this behavior to be effective, animals must take into account myriad factors such as when to cache, where to cache, how much to put in each cache, and whether to defend the cache. This makes caching a cognitive and economic decision. Because successful caching is crucial for the survival of many species, cache decisions must have played an important role in the evolution of decision making.

Generally, the greater the competition for the food (based on the availability of food and the number of competitors), the more effort animals put into caching—this means making more caches, farther from the source, with less food in each. However, it is largely unknown how animals assess the level of competition in their environment. For example, animals could indirectly assess competition from the number of other animals in the area or they could directly determine the level of competition from the proportion of caches lost to pilferage by other animals.

A significant literature in scatter-hoarding passerine birds from the family Paridae suggests that the mere presence of a conspecific observer affects cache decision making. Willow tits (*Parus montanus*) cache closer to the feeder when alone than when in the presence of conspecifics, and dominant individuals cache closer to the food source and more quickly than subordinates (Lahti et al., 1998). Black-capped chickadees (*Poecile atricapillus*) cache less when conspecifics are present than when they are alone (Stone & Baker, 1989). Coal tits (*Parus ater*) cache less when a neighbor is within 5 m (Brotons, 2000). Carolina chickadees (*Poecile carolinensis*) accumulate more mass over the day when in a flock compared to when alone (Pravosudov & Lucas, 2000).

Effects of being observed on caching have also been recorded in scatter-hoarding birds in the family Corvidae. Across multiple studies, these birds aborted caching in the presence of potential thieves (Burnell & Tombback, 1985; James & Verbeek, 1983; Kallander, 1978). Pinyon jays (*Gymnorhinus cyanocephalus*) ate more seeds before starting to cache in the presence of a conspecific observer, and began caching sooner if paired with a more dominant individual (Bednekoff & Balda, 1996). A recent study of Western scrub jays (*Aphelocoma californica*) uncovered a constellation of behavioral responses to being observed during caching, including increasing rates of recaching, caching in less preferred sites, and reducing the latency between caching and retrieval (Emery, Dally, & Clayton, 2004).

It may be adaptive to alter cache decisions in response to being observed if observation of the cache episode facilitates pilferage. In a series of comparative experiments, Pinyon jay observers remembered the area of their experimental partner's cache, and group-living Mexican jay (*Aphelocoma ultramarina*) observers retrieved caches as accurately as the cacher for up to 2 days; in contrast, solitary Clark's nutcracker (*Nucifraga columbiana*) observers only benefited from observation for 1 day after the cache event and even then were outperformed by the cachers. Thus, social living may increase information processing of observational information (Bednekoff & Balda, 1996).

The direct experience of pilferage also seems to change cache decisions in food-storing parid birds. Marsh tits (*Parus palustris*) decreased caching in locations where their seeds had been re-

Stephanie D. Preston and Lucia F. Jacobs, Department of Psychology, University of California, Berkeley.

This research was supported by a grant from the National Science Foundation (NSF IBN-9307317) and the University of California to Lucia F. Jacobs, and a spatial cognition training grant from the National Science Foundation to Stephanie D. Preston. Research was conducted under the authority of University of California at Berkeley Animal Care and Use Committee Protocol No. R188. All research was conducted in accord with the U.S. Public Health Service *Policy on Humane Care and Use of Laboratory Animals* and the National Institutes of Health *Guide to the Care and Use of Laboratory Animals*.

We thank Melissa Adams for technical assistance; Jan Randall for captive kangaroo rats; and Steve Jenkins, Martin Daly, Al Muth, Mark Fisher, and the Boyd Deep Canyon Desert Research Station for assistance in the field and facilitating our trapping expeditions. Eileen Lacey and Steve Glickman provided helpful comments on the manuscript.

Correspondence concerning this article should be addressed to Stephanie D. Preston, who is now at the University of Iowa Hospitals and Clinics, Department of Neurology–2RCP, 200 Hawkins Drive, Iowa City, IA 52242. E-mail: stephanie-d-preston@uiowa.edu

moved (Stevens, 1984). Black-capped chickadees (*Poecile atricapillus*) learned to avoid caching in spatial locations where previous caches were lost and reduced search times for caches in risky locations (Hampton & Sherry, 1994).

Despite the taxonomic divergence of birds and mammals, patterns of scatter hoarding are remarkably similar in these two groups, both in terms of behavior and in correlations with brain structure (Sherry, 1992; Sherry, Jacobs, & Gaulin, 1992). Both scatter-hoarding birds and scatter-hoarding mammals face the same economic decisions during scatter hoarding, decisions that are shaped in response to direct competition for food and caches. Comparing the cognitive and neural mechanisms of scatter hoarding in birds and mammals would yield important insights into the evolution of decision-making processes.

There is much less evidence on this topic in mammalian scatter hoarders; the existing evidence comes from a diverse range of rodent species. Laboratory rats cache less when in a group than when alone (Denenberg, 1952; Miller & Postman, 1946). Bank voles (*Clethrionomys glareolus*) redistribute their caches into the less preferred portion of the apparatus to avoid an introduced animal in the preferred portion, even though their nest is left in the preferred territory (Hansson, 1986). Gray squirrels (*Sciurus carolinensis*) have been observed to engage in more "false caching" (aborted attempts to cache) in the presence of an observer, which decreases the ability of a human observer to locate the cache (Steele, 2005).

The Merriam's kangaroo rat (MK) is a mammalian scatter-hoarding species, a member of the rich guild of granivorous species in the Southwestern deserts of North America (J. H. Brown & Harney, 1993). It is the smallest species of *Dipodomys* (Rodentia: Heteromyidae), a genus of bipedal, nocturnal desert granivores (Valone & Brown, 1995). MK has a wide distribution and can be sympatric with up to eight species of granivorous rodent (J. H. Brown & Harney, 1993), making the risk of pilferage a salient factor in cache decisions (J. H. Brown & Harney, 1993). Competitors include other kangaroo rat species (e.g., chisel-toothed kangaroo rat [*Dipodomys microps*], banner-tailed kangaroo rat [*Dipodomys spectabilis*], Ord's kangaroo rat [*Dipodomys ordii*]), and other heteromyid species such as dark kangaroo mice (*Microdipodops megacephalus*), deer mice (*Peromyscus maniculatus*), and pocket mice (e.g., pocket mouse [*Perognathus parvus*], Arizona pocket mouse [*Perognathus amplus*], little pocket mouse [*Perognathus longimembris*], long-tailed pocket mice [*Chaetodipus formosus*]; J. H. Brown & Harney, 1993; J. S. Brown, 1988; Jenkins & Breck, 1998).

Because of their larger size, kangaroo rat species like *D. spectabilis*, *D. deserti*, and *D. microps* can defend a larder and are thus more likely to larder hoard than the smaller MK (Jenkins & Breck, 1998). MK does not defend its foraging ranges but instead uses its rapid locomotion (bipedal hopping) to traverse and scatter hoard seeds throughout its large home range, rotating residency among multiple burrow systems (Behrends, Daly, & Wilson, 1986a, 1986b), despite the fact that such wide-ranging activities significantly increase the risk of predation (Daly, Wilson, Behrends, & Jacobs, 1990) and may make MK especially vulnerable to competition from these sympatric species (Behrends et al., 1986b). The dependence of MK on scatter hoarding is accompanied by an accurate memory for the location of caches (Barkley & Jacobs, 1998; Jacobs, 1992) and a relatively larger hippocampus than other

Dipodomys species (Jacobs & Spencer, 1994). This is adaptive because it allows MK to make smaller, more widely dispersed caches that are less likely to be pilfered (Daly, Jacobs, Wilson, & Behrends, 1992), a pattern that MK intensifies for preferred seed types (Leaver & Daly, 1998).

A few field studies with MK have examined social effects on cache behavior. Correlative field data suggest that MK takes the presence of these species into account when foraging and caching (e.g., J. S. Brown, 1988; Jenkins & Ascanio, 1993; Jenkins & Breck, 1998; Jenkins & Peters, 1992; Jenkins, Rothstein, & Green, 1995). Despite this, fecal analysis in another study determined that all of the nocturnal rodent species on the study site pilfered the provisioned MK, and experimenters observed a cache observer immediately dig up the cache of a focal rat (Daly, Jacobs, et al., 1992). Hence, despite the solitary social system of MK, its economy of food storing is highly dependent on interactions with competitors. The ability to balance hoarding effort and risk of pilferage has no doubt evolved in light of the intense competition for seeds in this environment. However, it is not well understood how scatter hoarders, such as MK, assess and respond to a perceived risk of pilferage. Given a highly competitive environment, oversensitivity to signs of a competitor may be as disadvantageous for survival and fitness as undersensitivity. For example, scatter hoarders could assess the number of competitors (or the density of associated signs, such as feces), or assess the number of pilfered caches. To be useful, this information should also be encoded in space because microhabitat structure and competitor density make some areas inherently riskier than others.

The experimental examination of social caching decisions in mammals is thus a recent development that deserves more study. The goal of the present study was to continue our experimental examination of the cues MK uses to assess the level of risk in a particular environment. In our previous work, we found that cache strategy was not affected when 2 MKs were placed in close proximity with each other (Preston & Jacobs, 2001). When the subjects experienced pilferage from a proximate and familiar neighbor, however, cache strategy did change, but the change was only detectable the 1st day after pilferage (Preston & Jacobs, 2001). There were two important limitations to these earlier studies. First, the experiments were not designed to test for location-specific changes in caching, as the arenas were uniform and pilferage was not restricted. Yet, location-specific effects have been seen in other species of food-storing birds and mammals (Hampton & Sherry, 1994; Hansson, 1986; Stevens, 1984). Second, only conspecific competitors were used, although the smaller MK may in fact be more sensitive to the presence of larger, more dominant competitor species. The goal of the present study was thus to extend the experimental work in MK by examining location-specific changes in caching in response to a dominant competitor species. We chose the chisel-toothed kangaroo rat (CTK) as a competitor, that is, another individual who is competing for the same resources. CTK is a sympatric species that is larger, dominant to, and avoided by MK in the field (Kenagy, 1973). We measured the effect of the competitor's presence and pilferage on subjects' preferred cache side and behavior.

In both experiments, the arena was divided evenly into two distinct areas, designed to induce a preference for caching on one side. One half was dimly lit and decorated richly with landmarks (hereafter, the "rich" side); the other half was brightly lit and

contained no landmarks (hereafter, the “bare” side). Because MK relies on landmarks for memory (Barkley & Jacobs, 1998) and on darkness for cover from predators (Daly, Behrends, Wilson, & Jacobs, 1992), it was predicted that subjects would prefer to cache on the rich side. In a premanipulation trial, MK subjects established a preference for one side. In the subsequent manipulation trial, the relevant manipulation was introduced only on the preferred side of the area, only for experimental subjects. A final postmanipulation trial mimicked the premanipulation to determine whether changes would endure in a new cache trial. Experiment 1 was designed to determine whether the mere presence of CTK on the preferred side would affect cache side preference or behavior. Experiment 2 was designed to determine whether the combination of the presence of CTK with cache loss on the preferred side would affect cache location preference or behavior.

Experiment 1

Method

Study Animals

Subjects were 8, wild-caught, male MKs (*Dipodomys merriami*) that were tested in 1998 after varying lengths of residence in the lab. One male was trapped near Palm Desert, California, in 1995, 3 were trapped near Reno, Nevada, in 1996, and 4 were trapped in Palm Desert, California, in 1997. The heterospecific competitors were CTKs trapped in Reno, Nevada, in October 1996 and maintained in the same room with the same operating procedures as the MKs. All subjects had been housed at the University of California, Berkeley, since at least 1996. All subjects had experience caching in experimental arenas. None of the MKs had prior experimental

experience with CTK, but some had been trapped on the same study site and all were maintained in the same colony room as CTK, so they may have been familiar to each other as individuals, or as a species. Subjects were maintained on a reversed 12:12-hr light–dark cycle with lights off at 0900. As a means of motivating them to cache, subjects were food deprived in their home cages for 12 hr preceding the 1st day, with approximately 1.0 g of oats and 0.3 g of lettuce.

Apparatus

Tests were conducted in an arena composed of four white opaque acrylic walls (76.00 cm long \times 76.00 cm wide \times 31.00 cm high) with a clear Plexiglas top that left space along one edge for air. Two housing chambers (25.00 cm long \times 10.00 cm wide \times 31.00 cm high) were attached to diagonal corners of the arena for the competitor CTK (hereafter, the “competitor tunnel”). Entrance to the two tunnels was blocked with wire mesh to prevent larder hoarding and to provide a housing area for the CTK competitor. The main arena was divided evenly by a black opaque barrier (61.00 cm long \times 28.00 cm high \times 0.32 cm wide) that extended three fourths of the way across the arena, permitting subjects to move from one side of the arena to the other. A plastic food dish for seeds was placed at the space between the two sides. To facilitate a location preference, one side of the arena was richly decorated with a small bouquet of artificial flowers, two rocks, and a small pinecone. This rich side of the arena also had a low level of illumination provided by a 25-W red light bulb attached to the table on the side of the arena that shone through the opaque Plexiglas arena wall. The bare side of the arena did not contain any landmarks and was brightly lit with a 60-W white light bulb attached to the table on the opposite side of the arena in a similar fashion (see Figure 1).

The side of the arena designated rich or bare was counterbalanced between subjects. To eliminate odor cues across cache trials, the experimenter removed all sand from the arena and sifted it to remove nonsand

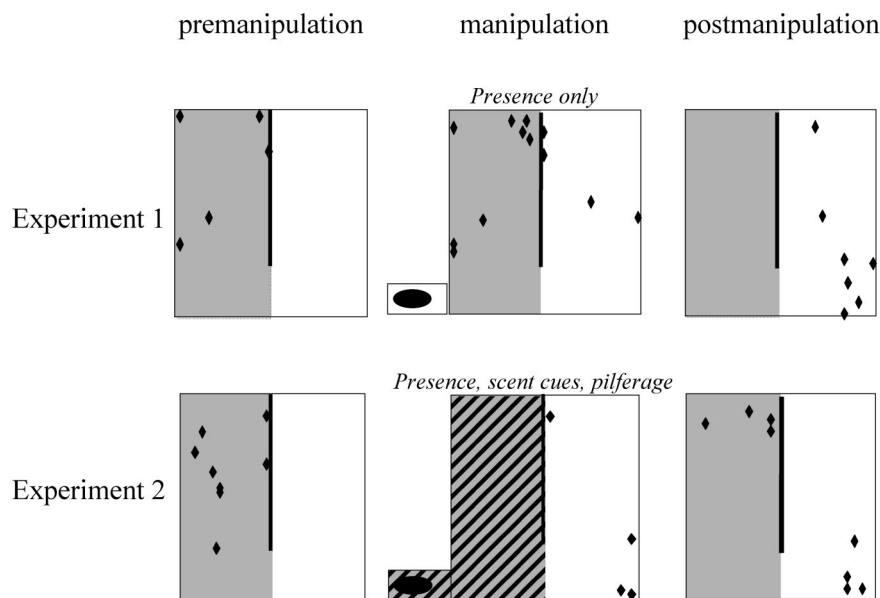


Figure 1. Schematic of Experiments 1 and 2 divided into the three trials (premanipulation, manipulation, and postmanipulation) with the experiment-specific manipulation described over each manipulation trial. The small black diamonds represent actual caches made by an experimental subject across the three trials. The heterospecific competitor is represented by a black oval in the competitor tunnel on the preferred side. In Experiment 2, hatched fill represents scent cues of the competitor spread on the sand. For control subjects, the three trials were the same, without any changes to the arena between trials (no competitor, no scent cues, no pilferage). Arenas are not drawn to scale.

particles, wiped down all parts of the arena (including the barrier and the landmarks) with alcohol, and allowed it to air dry.

Procedure

Each experiment consisted of three cache trials (premanipulation, manipulation, and postmanipulation), each separated by a 24-hr break (see Figure 1). During the 24-hr interval between experimental days, animals remained in home cages in the colony room on food deprivation (1.0 g oats, 0.3 g lettuce, per day). The first 4 subjects (2 control, 2 experimental) were given 2 hr to cache for each trial. Because virtually all caching was finished within 1 hr, the time allowed in the arena for the latter 4 subjects (2 control, 2 experimental) was reduced to 1 hr per condition.

Premanipulation. Each subject was given 100 shelled sunflower seeds to cache. The experimenter released each subject into the arena on a randomly determined side and left the room. After caching, the subject was removed and returned to the home cage with a new supply of oats and lettuce. The position of all seeds was recorded, and all seeds were replaced for the next trial. On the basis of these data, the cache side preference was determined, with more than 50% of caches located on one side considered indicative of a preference. The location side preference was determined from video analysis (described below), with more than 50% of the time spent on one side considered indicative of a preference.

Manipulation. Subjects were not given any new seeds, but all seeds from the premanipulation were available in their prior locations. Each subject was released into the arena on the side opposite that of the previous trial and given time to continue the cache session from the premanipulation. For experimental subjects only, a CTK was placed in the competitor tunnel on the preferred cache side before the subject entered the arena. After the allotted time (1 or 2 hr), the subject was removed and placed back into the home cage with a new supply of oats and lettuce.

Postmanipulation. The procedure was identical to the premanipulation, that is, all previous caches were removed, 100 new seeds were given to each subject, there was no competitor present, and the arena was cleaned to eliminate any cues from the competitor's prior presence. Subjects were placed in the arena on the opposite side as in the previous trial and given up to 1 hr to cache.

The postmanipulation was made to mimic the premanipulation for multiple reasons. Theoretically, if the final trial mimicked the first trial, rather than being an extension of the second, the pre- and postmanipulations could be directly compared to determine if experimental subjects would maintain their new cache side preference in the absence of the competitor or revert back to their original preference in an ostensibly new cache experience. Logistically, after 3 days in the arena, and especially after pilferage of experimental subjects' caches in the manipulation, there would not be enough seeds remaining for analysis without adding new seeds. These particular subjects were accustomed to two-episode cache trials (cache and retrieve); thus, they may not have been disturbed to find manipulation caches missing in the postmanipulation.

Measures

Cache data collection. After each cache episode, the exact location of each seed was recorded. The following measures were recorded: number and exact coordinate location (an area of 1 cm²) of seeds found in the arena but under the sand (scatter hoarded), number of seeds not found (eaten), number of seeds found in the arena above the sand (uncached), and total number of seeds not eaten (recovered). These data were used to calculate the percentage of cached seeds that were cached on the rich side versus the bare side in each trial.

Video coding of behavior. The behavioral data from each cache trial were videotaped and coded according to a behavioral ethogram (Preston, 1998) using the Event 3.02 program (Ha, 1996). Previous research had indicated that the most useful behavioral information was available in the

first 5 min of the trial (Preston, 1998). During the first 5 min, subjects explore the arena, displaying the most prominent reactions to the experimental conditions, and establish a resting place (i.e., where they stay while not active). After 5 min, we found that no new information was obtained from the video records; behavior was either unchanging or redundant with that of the first 5 min. All measures were collected as intervals, total time in seconds, and percent time of the first 5 min. Space use was divided into time spent in each side of the arena and at the food dish. Eating, chewing, sand bathing, rearing, and looking into the competitor tunnel were also recorded. Scratching, grooming, body shaking, and tail biting were recorded and analyzed collectively as "displacement behaviors."

Analysis

The binomial test was first used to determine whether subjects' preference for the rich side in the premanipulation was random or nonrandom. To analyze changes in the percentage of seeds cached on the rich and bare sides across trials, we used repeated measures analysis of variance with a three-level within-subjects factor (trial: premanipulation, manipulation, postmanipulation) and a two-level between-subjects factor (condition: control or experimental). These results were followed up with nonparametric tests for their greater power at low sample sizes. Data were recoded discretely (1 or 0, respectively) as to whether subjects changed their side preference across pairs of days (i.e., premanipulation to manipulation, manipulation to postmanipulation, and premanipulation to postmanipulation), whether they simply increased their use of the bare side from the premanipulation to the manipulation, and whether they kept the same side preference across all 3 days. Control and experimental subjects were compared on these values with two-tailed tests of Pearson's chi-square. The alpha level was .05 for all comparisons; *p* values less than or equal to .10 are reported as statistical trends.

Results

Cache Data

The majority of subjects preferred to cache on the rich side of the arena in the premanipulation (7/8, or 88%; Binomial test for nonrandomness: *p* = .07). There was an increase in caching on the bare side across trials (sample data included in Figure 1, mean performance graphed in Figure 2). On average, subjects cached 14% (*SD* = 21%) of their seeds on the bare side in the premanipulation, 33% (*SD* = 33%) in the manipulation, and 56% (*SD* = 48%) in the postmanipulation, $F(2, 12) = 4.77$, *p* = .03 (see Figure 2). This increase in caching on the bare side did not differ between control and experimental subjects: interaction, $F(2, 12) = 0.54$, *ns*.

Control and experimental subjects were equally likely to change their cache side preference from the premanipulation to the manipulation, $\chi^2(1, N = 8) = 0.53$, *p* = .47; from the manipulation to the postmanipulation, $\chi^2(1, N = 8) = 0.53$, *p* = .47; and from the premanipulation to the postmanipulation, $\chi^2(1, N = 14) = 0.00$, *p* = 1.00. Both groups were also equally likely to simply increase caching on the unpreferred side from the premanipulation to the manipulation, $\chi^2(1, N = 8) = 0.53$, *p* = .47, and to keep the same cache side preference across all three trials, $\chi^2(1, N = 14) = 0.00$, *p* = 1.00.

Behavioral Data

Location side preference was strongly correlated with cache side preference (*r* = .519, *p* = .009). The majority of subjects preferred to be on the rich side of the arena in the premanipulation (7/8, or

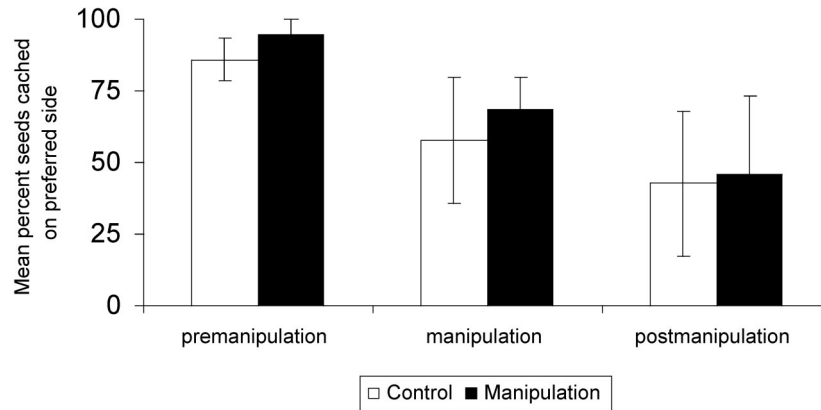


Figure 2. Cache side preference in Experiment 1, expressed as the mean (\pm SEM) percentage of seeds placed on the preferred side in each trial. Preference is based on Trial 1 preferences, where preference is defined as greater than 50% use.

88%; binomial test for nonrandomness: $p = .07$). On average, subjects spent 25% ($SD = 19\%$) of their time on the bare side in the premanipulation, 33% ($SD = 27\%$) in the manipulation, and 57% ($SD = 37\%$) in the postmanipulation. This increase in time spent on the bare side was not significant, $F(2, 12) = 2.19$, $p = .16$, and did not differ between control and experimental subjects: interaction, $F(2, 12) = 0.01$, *ns*. There were no other significant differences in behavior between experimental and control subjects, $F(2, 12) < 0.02$, *ns*, although there was a trend for experimental subjects to spend more time looking into the competitor's tunnel, $F(1, 6) = 5.80$, $p = .05$, and for all subjects to decrease displacement behaviors as the experiment progressed, $F(2, 12) = 3.15$, $p = .08$.

Experimental subjects were more likely than control subjects to switch their location side preference from the premanipulation to the manipulation, $\chi^2(1, N = 8) = 4.80$, $p = .03$, but there was no difference in the likelihood of control and experimental subjects to change their location side preference from the manipulation to the postmanipulation, $\chi^2(1, N = 8) = 0.53$, $p = .47$, or from the premanipulation to the postmanipulation, $\chi^2(1, N = 14) = 0.00$, $p = 1.00$. Both groups were equally likely to simply increase time spent on the unpreferred side from the premanipulation to the manipulation, $\chi^2(1, N = 14) = 0.00$, $p = 1.00$, but there was a trend for control subjects to stay on the same side of the arena across all 3 days of the experiment, more so than experimental subjects, $\chi^2(1, N = 8) = 2.67$, $p = .10$.

Discussion

The addition of CTK to an adjacent compartment of the arena did not affect the cache side preference of MK. Although it is possible that data from 8 subjects do not offer enough statistical power to test the hypothesis, none of the cache measures showed trends or indications that the presence of the heterospecific affected the cache preference of the experimental subjects, or that caching differed between experimental and control subjects. So, although observation may indeed increase pilferage in this species, in the present experiment, the mere presence of the heterospecific competitor was not sufficient to cause experimental subjects to move their caches to the unpreferred part of the arena.

It is not the case that the experimental subjects simply did not notice the CTK presence manipulation, because they did tend to look into the tunnel more than control subjects, only during the manipulation trial. In addition, the experimental subjects seemed to avoid the competitor because they spent more time in the previously unpreferred area than control subjects during the manipulation trial when the competitor was placed on their preferred cache side. The ineffectiveness of the heterospecific presence manipulation may have been due to the habituation of MK to the presence of CTK from previous experience in the laboratory colony room or the field, or to their recognition that the CTK was innocuous as a competitor and potential pilferer because it was secured behind the solid wire mesh.

This finding is in contrast to previous experiments with food-storing birds in which scatter-hoarding species did cache differently in the mere presence of an observer (Bednekoff & Balda, 1996; Brotons, 2000; Burnell & Tomback, 1985; Denenberg, 1952; James & Verbeek, 1983; Lahti et al., 1998; Miller & Postman, 1946; Stone & Baker, 1989); however, many of these experiments were done with highly social bird species such as chickadees and jays, which scatter hoard while foraging in flocks. MK, like other *Dipodomys* species, is generally solitary (Randall, 1993), although experimenters have seen them pilfering observed caches in the field (Daly, Jacobs, et al., 1992). Our subjects also performed differently than herbivorous bank voles (*Clethrionomys glareolus*), which, in a similar study, did move food into a less preferred area when an observer vole was introduced in the preferred portion, though this behavior varied by population, only occurring in North Swedish cyclic voles and not in their southern, noncyclic counterparts (Hansson, 1986).

Our findings do agree with previous experiments in MK using a conspecific competitor. In these experiments, the mere presence of the competitor did not affect cache strategy, but subjects changed their cache strategy after the MK competitor was allowed to pilfer their caches (Preston & Jacobs, 2001). The goal of Experiment 2 was to test the hypothesis that, as with a conspecific competitor, MK will change cache behavior only after actual pilferage in association with the heterospecific competitor.

Our results are also consistent with optimal cache placement theory (Clarkson, Eden, Sutherland, & Houston, 1986; Tinbergen, Impeken, & Franck, 1967), as subjects in both the control and experimental conditions gradually started to use the bare side across days of the experiment. This suggests that the difference between the rich and the bare side was large enough to establish a consistent initial preference, but not large enough to prevent caching on the bare side. It is logical that the use of the bare side would increase across days of the experiment as subjects became familiar with the arena without experiencing any direct signs of predation risk or pilferage.

The experimental design may have also contributed to the increased use of the bare side, because all of the subjects' seeds were removed between the manipulation and postmanipulation, which may have been perceived as pilferage. However, the data do not support this explanation because subjects began using the unpreferred side from the premanipulation to the manipulation, when there was no seed loss, and did so in a graded and linear fashion, with an average of 20% change in cache side preference and 23% in location side preference per trial. Thus, given the gradual increase in use of the unpreferred side across all three trials for both groups, it is most likely that the change was due to the fact that the difference between the preferred and unpreferred side was not great enough to prevent the rats from engaging in optimal cache placement, a factor known to reduce pilferage in MK (Daly, Jacobs, et al., 1992; Leaver & Daly, 2001).

The protocol of Experiment 2 was designed to address factors that could have contributed to a null result in Experiment 1. To address the potential problem of sample size, we trapped a new cohort of rats in 2001, thereby almost doubling the previous sample size. We also increased the effect size of the manipulation in Experiment 2 by both decreasing the within-group variance and increasing the between-groups variance. We decreased the within-group variance by making the rich and bare sides more distinct from each other, thereby increasing the preference for the rich side. We made the rich side darker by removing the dim 25-W lighting and made the rich side safer by adding a small opaque elbow of plastic plumbing pipe (Acrylonitrile-Butadiene-Styrene [ABS] tubing). We also made the bare side brighter by putting the 60-W light bulb closer to the outside wall of the arena. We increased the between-groups difference by augmenting the manipulation in multiple ways. In addition to the presence of the CTK in the competitor tunnel, we pilfered half of the caches of the experimental subjects before the trial and placed the lost seeds in the competitor tunnel against the wire mesh where the subject could see and smell but not access them. We also added feces and chunks of urine mixed with sand from the home cage of the CTK to the competitor tunnel and to the preferred side of the arena. We predicted that, as in Experiment 1, subjects would again prefer to cache on the rich side, but should shift to the bare side after caches on the preferred side were pilfered in association with the heterospecific competitor.

Experiment 2

Method

Methods were identical to that of Experiment 1, except as specified otherwise.

Study Animals

Experiment 2 was run at two different times, with samples from two different populations. All 14 subjects were wild-caught male MKs housed at the University of California, Berkeley; all were tested during their dark (active) phase; and all had prior experience caching in experimental arenas. The first 8 subjects were the same rats as in Experiment 1, tested in the fall of 1998, 1 month after Experiment 1, while maintained on a reversed 12:12-hr light–dark cycle with lights off at 0900. The last 6 subjects were trapped in Palm Desert and Palm Springs, CA in 2000 and tested in the spring of 2001 while maintained on a 12:12-hr light–dark cycle with lights off at 1600.

Trapping location was not expected to affect the results of the experiment because the majority of rats in both populations were trapped from the same general area (Palm Desert/Palm Springs, CA), and all rats were from the same habitat type. Season and the cycle of lighting in the laboratory were not expected to affect the results of the experiment because all subjects were habituated to constant, controlled laboratory conditions without seasonal variation. Most important, half of the rats from each population (1998 and 2001) were assigned to the control condition, and the other half were assigned to the experimental condition; thus, any effects of population would only increase within-group variance and the possibility of a Type II error but would not produce spurious results.

Procedure

Figure 1 summarizes the changes in the protocol from Experiment 1 to Experiment 2. For experimental subjects only, during the manipulation trial there was a CTK in the competitor tunnel on the preferred side. There were also feces and soiled sand from the competitor's cage spread on the surface of the competitor tunnel and of the preferred side. In addition, half of the caches were removed from the preferred cache side. If there was an odd number of caches, the larger number was removed, but a minimum of 30 seeds were left in the arena so that there would be enough seeds after the trial for statistical analysis. The removed seeds were placed with a CTK in the competitor tunnel where the subject could see and smell but not access them.

To minimize the time needed to run each subject in Experiment 2, the experimenter checked each subject in the premanipulation after 30 min. If there were no seeds in the plastic dish at this time, the subject was removed and given the same amount of time to cache in the remaining trials. If seeds still remained in the dish, the subject was given additional blocks of 30 min to cache, up to 2 hr. If after 2 hr the subject still had not cached, he was removed and given another opportunity later in the day or the next day. In subsequent trials, all subjects were left in the arena for the time they required in the premanipulation, up to 2 hr.

Results

Cache Data

The majority of subjects preferred to cache on the rich side of the arena in the premanipulation (12/14 or 86%, binomial test for nonrandomness: $p = .01$). One control subject cached only on the bare side; the other control subject cached marginally more on the bare side than on the rich side. Of all the caches from the remaining 12 subjects, only one cache was placed on the bare side.

On average, subjects cached 13% ($SD = 32\%$) of their seeds on the bare side in the premanipulation, 25% ($SD = 31\%$) in the manipulation, and 30% ($SD = 38\%$) in the postmanipulation, which is not a significant change in caching on the bare side across days, $F(2, 24) = 2.24$, $p = .13$. However, only experimental subjects significantly increased caching on the bare side after the manipulation, from 2% of seeds on the bare side in the prema-

nipulation, to 36% in the manipulation and postmanipulation: interaction, $F(2, 24) = 4.19$, $p = .03$ (sample data included in Figure 1, mean performance graphed in Figure 3).

Subjects tested in 1998 used the bare side more than subjects tested in 2001 (36% and 5%, respectively), $F(1, 12) = 6.10$, $p = .03$. However, planned comparisons did not change when testing date was added as a second between-subjects factor: effect of day, $F(2, 20) = 2.20$, *ns*; Day \times Condition interaction, $F(2, 20) = 3.43$, $p = .05$, and there were no new interactions with testing date, $F(2, 20) < 1.07$, *ns*.

Experimental subjects, but not control subjects, tended to change their cache side preference from the premanipulation to the manipulation, $\chi^2(1, N = 14) = 3.82$, $p = .05$, and from the premanipulation to postmanipulation, $\chi^2(1, N = 14) = 3.82$, $p = .05$, but there were no changes from the manipulation to the postmanipulation, $\chi^2(1, N = 14) = 2.33$, $p = .13$. In addition, only experimental subjects increased caching on the unpreferred side from the premanipulation to the manipulation, $\chi^2(1, N = 14) = 4.67$, $p = .03$ (Figure 3), whereas control, but not experimental, subjects cached only on one side for all three trials, $\chi^2(1, N = 14) = 5.60$, $p = .02$.

Behavioral Data

As a result of technical problems, video data were not collected for some subjects, disproportionately affecting subjects from the 2001 cohort. Premanipulation data were available for 11 subjects, 5 control (4 from 1998, 1 from 2001) and 6 experimental (4 from 1998, 2 from 2001); data for all three trials were available for 8 subjects, 4 control (all from 1998) and 4 experimental (3 from 1998, 1 from 2001).

In the premanipulation, location side preference was strongly correlated with cache side preference ($r = .77$, $p = .006$), and the majority of subjects preferred to stay on the rich side of the arena (8/11, or 73%; binomial test for nonrandomness: *ns*). On average, subjects spent 38% ($SD = 38\%$) of their time on the bare side in the premanipulation, 24% ($SD = 27\%$) in the manipulation, and 40% ($SD = 37\%$) in the postmanipulation. These changes in the

time spent on the bare side were not significant, $F(2, 12) = 1.53$, *ns*, and did not differ between control and experimental subjects: interaction, $F(2, 12) = 0.63$, *ns*. There were no other significant differences in behavior between experimental and control subjects, $F(2, 12) < 0.15$, *ns*, although there was a trend for experimental subjects to spend more time looking into the competitor's tunnel, $F(1, 6) = 4.13$, $p = .09$, and to spend more time secluded in their refuge, the opaque ABS tube, $F(1, 6) = 4.49$, $p = .08$.

Control and experimental subjects were equally likely to change their location side preference between trials, whether from the premanipulation to the manipulation, $\chi^2(1, N = 8) = 0.03$, *ns*; from the manipulation to the postmanipulation, $\chi^2(1, N = 8) = 0.03$, *ns*; or from the premanipulation to the postmanipulation, $\chi^2(1, N = 8) = 0.90$, *ns*. Both groups were also equally likely to simply increase time spent on the unpreferred side from the premanipulation to the manipulation, $\chi^2(1, N = 8) = 2.06$, *ns*, and to stay on the same side of the arena across all 3 days of the experiment, $\chi^2(1, N = 8) = 0.24$, *ns*.

Discussion

Whereas the single-variable manipulation of Experiment 1 had no perceptible effect on the subjects, there was a striking effect when multiple cues were used in combination. Only the experimental subjects increased caching on the unpreferred side when the manipulation was introduced, and they maintained this use of the unpreferred side for caching in the postmanipulation, in the absence of the heterospecific competitor. Control subjects, in contrast, maintained their original cache side preference throughout the three trials. These findings replicate those of our previous investigations using a conspecific competitor, in which pilferage was required to elicit a change in cache strategy (Preston & Jacobs, 2001). They also accord with findings from food-storing birds such as marsh tits (Stevens, 1984) and black-capped chickadees (Hampton & Sherry, 1994).

The change in cache side preference by experimental subjects suggests that the changes in the protocol made to further distinguish the rich side from the bare side succeeded in making the

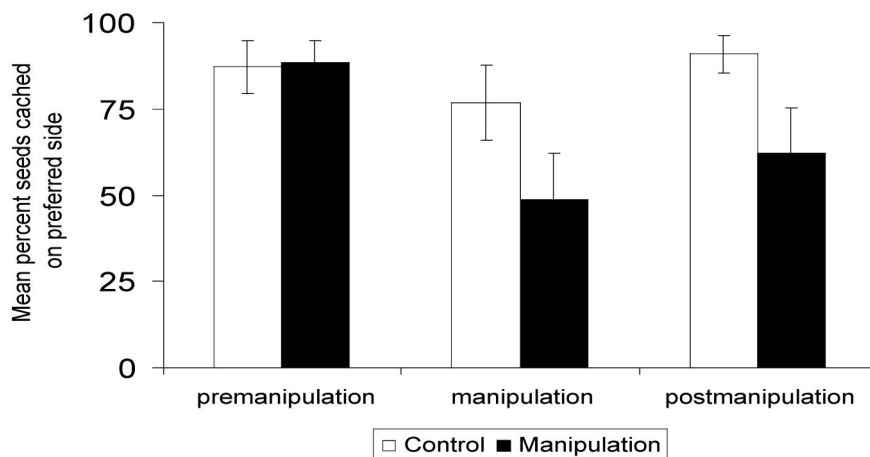


Figure 3. Cache side preference in Experiment 2, expressed as the mean (\pm SEM) percentage of seeds placed on the preferred side in each trial. Preference is based on Trial 1 preferences, where preference is defined as greater than 50% use.

preference for the rich side stronger (effectively decreasing within-group variance). For example, in contrast to Experiment 1, in Experiment 2 control subjects did not increase their caching on the bare side across trials, and none of the subjects increased their time spent on the bare side across trials. Thus, the kangaroo rats' preference for the rich side was perhaps strong enough in Experiment 2 to curtail their natural tendency for optimal caching, in which caches are dispersed more widely over time.

The behavioral data again indicated that the experimental subjects noticed the heterospecific competitor, with increased time spent looking into the competitor's tunnel compared with that of control subjects. In addition, experimental subjects spent more time in the new refuge (ABS tube) than control subjects. This may have been an indication of avoidance by the experimental subjects, who had experienced not only the competitor, but also its scent cues in the arena.

Subjects tested in 1998 in both the experimental and control groups were more likely than 2001 subjects to cache on the bare side, across all three trials. Most likely, this cohort difference is due to the fact that the 1998 subjects had already participated in Experiment 1 one month previous, and thus had already been accustomed to the bare side and may have been less intimidated by it. Experimental subjects from the 1998 cohort were also more likely than those from the 2001 cohort to switch their cache side preference entirely after experiencing the manipulation. This greater impact of the manipulation is also likely due to their prior participation in Experiment 1, which may have primed the subjects for risk associated with the heterospecific competitor. The 1998 cohort was housed in the same colony room as the CTKs, and the communication of odors in the colony room may have further primed their perception of the competitor. Moreover, the 2001 cohort may have been less primed to react to the heterospecific competitor because these rats had not experienced CTKs under natural conditions. Because half of each cohort was assigned to each condition (control and experimental), these cohort differences could not have produced the effect of Experiment 2, but they do invite future research into the amount of prior experience required to classify another animal as a competitor.

General Discussion

Scatter hoarding is a foraging strategy that requires animals to possess a greater facility for encoding spatial locations in comparison with closely related species that do not scatter hoard (Biegler, McGregor, Krebs, & Healy, 2001; Olson, Kamil, Balda, & Nims, 1995). What has not been appreciated until recently is that this behavior may also require unique decision-making processes because of the economics of caching and pilfering. Even with the advantages of reciprocal pilferage (Vander Wall & Jenkins, 2003), each scatter hoarder faces hundreds to thousands of cache decisions each year, and each decision may require an estimation of the risk of pilferage. Moreover, this process appears to be similar in birds and mammals and is likely to be similar in humans (Preston, 2001), which therefore offers a unique opportunity for comparative studies of decision-making processes.

The goal of the current study was to examine how cache decision making in MK is changed by heterospecific competition from a larger, more dominant kangaroo rat species. In our previous studies, we found that the presence of a conspecific individual was

not enough to induce MK subjects to alter their cache strategy. When the conspecific pilfered subjects' caches, however, they changed their cache strategy from predominantly scatter hoarding to predominantly larder hoarding (Preston & Jacobs, 2001). These effects were replicated in the current investigation with a heterospecific competitor. Once again, MK subjects did not alter their cache side preference in response to the mere presence of the CTK competitor, but did so when there was evidence that the competitor had pilfered their preferred caches.

These results, from a scatter-hoarding mammal, differ from the robust effects of observers on caching decisions seen in birds (Bednekoff & Balda, 1996; Brotons, 2000; Lahti et al., 1998; Pravosudov & Lucas, 2000; Stone & Baker, 1989), and even in other food-storing rodents (Denenberg, 1952). Several factors may contribute to this difference. First, observer effects are most commonly studied in social species that may have evolved better observation and memory skills in order to take advantage of the higher probability of observing and accessing others' caches (e.g., Bednekoff & Balda, 1996). Second, the effects may be found only in more subtle measures of caching such as the latency to cache (Bednekoff & Balda, 1996; Lahti et al., 1998), the amount cached versus amount eaten (Bednekoff & Balda, 1996; Pravosudov & Lucas, 2000), the distance of caches from the feeder (Lahti et al., 1998), or the probability of caching at all (Brotons, 2000; Denenberg, 1952; Miller & Postman, 1946; Stone & Baker, 1989). These and other measures in future studies might yield similar results in a mammalian scatter hoarder; for reasons of experimental design, these measures were not taken in the present study (e.g., trials had to last until all seeds were cached so that there would be a sufficient number of caches to examine side preferences).

Another factor underlying the response to competitors in MK may be the social milieu of caching. Under natural conditions, MK competes within the large and diverse desert granivore community, consisting not only of granivorous rodent species, but also granivorous birds and seed-harvesting ants (J. H. Brown, Reichman, & Davidson, 1979). Responding to the mere presence of any one competitor may result in poor cache decisions because MK may collect direct evidence for the presence of numerous sympatric competitors on its daily foraging trips. In this environment of intense competition for resources, MK may instead have a higher threshold for the presence of competitors than scatter-hoarding birds, only responding when there is direct evidence of pilferage. This ecological difference would result in the observed differences in response to competitors between MK and scatter-hoarding birds.

In addition, direct evidence of pilferage may be easier for a mammal to ascertain than a bird, because of the inherent difference between avian and mammalian sensory abilities. Olfactory-based pilfering is widespread in mammals (see review in Vander Wall & Jenkins, 2003), yet birds appear unable to use olfaction to detect food caches. This taxonomic difference would contribute to a higher threshold for changing cache strategy in mammals, because a mammal can theoretically detect not only the fact that pilferage occurred, but also who did the pilfering.

In our studies, MK showed the same pattern of response to both conspecific and heterospecific competitors: It ignored the mere presence of the competitor but responded rapidly to cues that the competitor was associated with cache loss. Such cues included the competitor's unique olfactory signature on feces in the area where caches were pilfered. Thus, a kangaroo rat may derive information

about the risk of pilferage from a particular individual, and learn to ignore the presence of individuals not associated with an actual cache pilferage event. If so, MK may allocate changes in caching (e.g., caching in less preferred areas) only in response to those individuals whose odors have been directly associated with a pilfered cache, which may result in the increased tolerance of the presence of competitors, similar to the *dear enemy* effect seen in territorial species (Randall, 1991; Temeles, 1994; Yoerg, 1999).

In conclusion, our results suggest that MK use a conservative rule to assess the risk of future pilferage: They require the occurrence of actual pilferage by an animal known to be present, whether heterospecific or conspecific. These results suggest that decision-making processes in scatter hoarders, both birds and mammals, are complex yet adaptable, with the actual rules and decisions varying with conditions.

Our results raise several questions for future research on the comparative analysis of decision making. For example, might there be a nonlinear relationship between prior experience with and response to a competitor such that some experience is necessary to prime the perception of risk, but high levels of experience lead to tolerance? Also, do scatter hoarders alter cache strategy on the basis of a simple heuristic, such as the presence of a competitor plus pilferage, or do they dynamically assess each situation on the basis of a variety of factors, including overall number of competitors and food availability? The answers to these questions would have significance not only for the comparative study of decision-making processes in birds and mammals, but also for the cognitive mechanisms underlying species interactions in ecological communities.

References

- Barkley, C. L., & Jacobs, L. F. (1998). Visual environment and delay affect cache retrieval accuracy in a food-storing rodent. *Animal Learning & Behavior*, 26, 439–447.
- Bednekoff, P. A., & Balda, R. P. (1996). Social caching and observational spatial memory in pinyon jays. *Behaviour*, 133, 807–826.
- Behrends, P., Daly, M., & Wilson, M. I. (1986a). Aboveground activity of Merriam's kangaroo rats (*Dipodomys merriami*) in relation to sex and reproduction. *Behaviour*, 96, 210–226.
- Behrends, P., Daly, M., & Wilson, M. I. (1986b). Range use patterns and spatial relationships of Merriam's kangaroo rats (*Dipodomys merriami*). *Behaviour*, 96, 187–209.
- Biegler, R., McGregor, A., Krebs, J. R., & Healy, S. D. (2001). A larger hippocampus is associated with longer-lasting spatial memory. *Proceedings of the National Academy of Sciences, USA*, 98, 6941–6944.
- Brotans, L. (2000). Individual food-hoarding decisions in a nonterritorial coal tit population: The role of social context. *Animal Behaviour*, 60, 395–402.
- Brown, J. H., & Harney, B. A. (1993). Population and community ecology of heteromyid rodents in temperate habitats. In H. H. Genoways & J. H. Brown (Eds.), *Biology of the Heteromyidae* [Special Publication No. 10] (Vol. 10, pp. 618–651). Provo, UT: American Society of Mammalogists.
- Brown, J. H., Reichman, O. J., & Davidson, D. W. (1979). Granivory in desert ecosystems. *Annual Review of Ecology and Systematics*, 10, 201–227.
- Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, 22, 37–47.
- Burnell, K. L., & Tomback, D. F. (1985). Steller's jays steal grey jay caches: Field and laboratory observations. *Auk*, 102, 417–419.
- Clarkson, K., Eden, S. F., Sutherland, W. J., & Houston, A. I. (1986). Density dependence and magpie food hoarding. *Journal of Animal Ecology*, 55, 111–121.
- Daly, M., Behrends, P. R., Wilson, M. I., & Jacobs, L. F. (1992). Behavioural modulation of predation risk: Moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Animal Behaviour*, 44, 1–9.
- Daly, M., Jacobs, L. F., Wilson, M. I., & Behrends, P. R. (1992). Scatter hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. *Behavioral Ecology*, 3, 102–111.
- Daly, M., Wilson, M., Behrends, P. R., & Jacobs, L. F. (1990). Characteristics of kangaroo rats, *Dipodomys merriami*, associated with differential predation risk. *Animal Behaviour*, 40, 380–389.
- Denenberg, V. H. (1952). Hoarding in the white rat under isolation and group conditions. *Journal of Comparative and Physiological Psychology*, 45, 497–503.
- Emery, N. J., Dally, J., & Clayton, N. S. (2004). Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. *Animal Cognition*, 7, 37–43.
- Ha, J. (1996). Event (Version 3.02) [Computer software]. Seattle: Department of Psychology, University of Washington.
- 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.
- Hansson, L. (1986). Geographic differences in the sociability of voles in relation to cyclicity. *Animal Behaviour*, 34, 1215–1221.
- Jacobs, L. F. (1992). Memory for cache locations in Merriam's kangaroo rats. *Animal Behaviour*, 43, 585–593.
- Jacobs, L. F., & Spencer, W. D. (1994). Natural space-use patterns and hippocampal size in kangaroo rats. *Brain Behavior and Evolution*, 44, 125–132.
- James, P. C., & Verbeek, N. A. M. (1983). The food storage behavior of the northwestern crow. *Behaviour*, 85, 276–291.
- Jenkins, S. H., & Ascanio, R. (1993). A potential nutritional basis for resource partitioning by desert rodents. *American Midland Naturalist*, 130, 164–172.
- Jenkins, S. H., & Breck, S. W. (1998). Differences in food hoarding among six species of heteromyid rodents. *Journal of Mammalogy*, 79, 1221–1233.
- 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 hypothesis. *Ecology*, 76, 2470–2481.
- Kallander, H. (1978). Hoarding in the rook, *Corvus frugilegus*. *Anser Supplement*, 3, 124–128.
- Kenagy, G. J. (1973). Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology*, 54, 1201–1219.
- 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., & Daly, M. (1998). Effects of food preference on scatter-hoarding by kangaroo rats (*Dipodomys merriami*). *Behaviour*, 135, 823–832.
- Leaver, L. A., & Daly, M. (2001). Food caching and differential cache pilferage: A field study of coexistence of sympatric kangaroo rats and pocket mice. *Oecologia*, 128, 577–584.
- Miller, G. A., & Postman, L. (1946). Individual and group hoarding in rats. *American Journal of Psychology*, 59, 652–668.
- Olson, D. J., Kamil, A. C., Balda, R. P., & Nims, P. J. (1995). Performance of four seed-caching corvid species in operant tests of nonspatial and spatial memory. *Journal of Comparative Psychology*, 109, 173–181.
- Pravosudov, 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.
- Preston, S. D. (1998). *Effects of conspecific pilferage on caching, space use and displacement behaviors in the Merriam's kangaroo rat (Dipodomys merriami)*. Unpublished master's thesis, University of California, Berkeley.
- Preston, S. D. (2001). *Effects of stress on decision making in the Merriam's kangaroo rat (Dipodomys merriami)*. Unpublished doctoral dissertation, University of California, Berkeley.
- Preston, S. D., & Jacobs, L. F. (2001). Conspecific pilferage but not presence affects cache strategy in Merriam's kangaroo rats. *Behavioral Ecology*, 12, 517–523.
- Randall, J. A. (1991). Sandbathing to establish familiarity in the Merriam's kangaroo rat, *Dipodomys merriami*. *Animal Behaviour*, 41, 267–275.
- Randall, J. A. (1993). Behavioural adaptations of desert rodents (Heteromyidae). *Animal Behaviour*, 45, 263–287.
- Sherry, D. F. (1992). Memory, the hippocampus, and natural selection: Studies of food-storing birds. In L. R. Squire & N. Butters (Eds.), *Neuropsychology of memory* (2nd ed., pp. xvii, 620). New York: Guilford Press.
- Sherry, D. F., Jacobs, L. F., & Gaulin, S. J. (1992). Spatial memory and adaptive specialization of the hippocampus. *Trends in Neurosciences*, 15, 298–303.
- Steele, M. (2005). *The audience effect in grey squirrels (Sciurus niger)*. Manuscript in preparation.
- Stevens, A. (1984). *The food storage behavior of marsh tits and shrikes*. Unpublished doctoral dissertation, Oxford University, Oxford, England.
- Stone, E. R., & Baker, M. C. (1989). The effects of conspecifics on food caching black-capped chickadees. *Condor*, 91, 886–890.
- Temeles, E. J. (1994). The role of neighbors in territorial systems: When are they 'dear enemies'? *Animal Behaviour*, 47, 339–350.
- Tinbergen, N., Impeken, M., & Franck, D. (1967). An experiment on spacing-out as a defence against predation. *Behaviour*, 28, 307–321.
- Valone, T. J., & Brown, J. H. (1995, February 10). Effects of competition, colonization, and extinction on rodent species diversity. *Science*, 267, 880–883.
- Vander Wall, S. B. (1990). *Food hoarding in animals*. Chicago: University of Chicago Press.
- Vander Wall, S. B., & Jenkins, S. H. (2003). Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology*, 14, 656–667.
- Yoerg, S. I. (1999). Solitary is not asocial: Effects of social contact in kangaroo rats (*Heteromyidae: Dipodomys heermanni*). *Ethology*, 105, 317–333.

Received March 19, 2004

Revision received August 27, 2004

Accepted October 16, 2004 ■