Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy

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We investigated the effects of pilferage on caching behavior in the Merriam's kangaroo rat by manipulating two factors associated with pilferage: the presence of a conspecific, and the opportunity for pilferage. In one experiment we assessed animals in either "Stealer" or "Victim" roles and measured changes in caching, space use, and behavior after caches were pilfered. Victims shifted from a majority scatter-hoarding to a majority larder-hoarding strategy after their caches were pilfered by the Stealer. In Experiment 2, we measured changes after exposure to a conspecific when there was no pilferage, with or without prior exposure to pilferage from Experiment 1. Merriam's kangaroo rats were vigilant when a conspecific was present, but did not change cache strategy. Prior exposure did not have any major effect on caching or behavior. Food storage is an economic decision that is often made by a solitary forager. Our results suggest that social competition nonetheless influences such economic decisions, even in a nonsocial forager. *Key words:* anxiety, decision processes, *Dipodomys,* kangaroo rat, pilferage, scatter hoarding. *[Behav Ecol 12:517–523 (2001)]*

K angaroo rats larder hoard and defend their food supply in a single site, like a burrow, but Merriam's kangaroo rat, the smallest North American kangaroo rat species, primarily scatter hoards, storing food in multiple, undefended cache sites (Vander Wall, 1990). The actual proportion of scatter and larder hoarding in Merriam's kangaroo rat varies greatly (referred to hereafter as "cache strategy") (Jenkins and Breck, 1998), and the factors affecting this variation in cache strategy are unknown.

According to the "pilfering avoidance hypothesis" (Mac-Donald, 1976), cache strategy is determined by the likelihood of pilferage, which is in turn affected by the age, sex, reproductive status (Clarke and Kramer, 1994a, b) and dominance status of the food hoarder (Jenkins and Breck, 1998). For example, eastern chipmunks (*Tamias stiatus*) typically larder hoard their food in home burrows, but in a provisioning experiment, the females with young and the juveniles scatter hoarded (Clarke and Kramer, 1994a). Despite the fact that these animals defended some of their caches, approximately 46% of the scatter hoards were pilfered. Pilferage of scatter hoards is also likely to be a salient factor for Merriam's kangaroo rats. In one study, all of the nocturnal rodent species on the study site, including other Merriam's kangaroo rats, pilfered the caches made by an experimentally-provisioned animal (Daly et al., 1992).

How do animals detect the risk of pilferage? Because Merriam's kangaroo rats have overlapping home ranges (Behrends et al., 1986; Jones, 1989), pilfer risk may be correlated with the density or proximity of competitors in the area. This would allow animals to assess pilfer risk indirectly from the presence of competitors. Captive bank voles (*Clethrionomys glareolus*), for example, changed the location of their larder hoard when a conspecific was introduced to their arena (Hansson, 1986). Alternatively, kangaroo rats may assess pilfer risk directly after encountering emptied caches. In previous experiments with Merriam's kangaroo rats, subjects did not alter caching in response to pilferage by an experimenter (Jenkins, 1998) or to the scent cues of a conspecific in the same arena (Leaver and Daly, 1998). These experiments manipulated caching by isolating variables associated with pilferage scenarios, and it may be that kangaroo rats require the rich complexity of cues available to them in their natural habitat to detect and respond to pilferage.

The goal of this study was to determine if Merriam's kangaroo rats determine the risk of pilferage directly or indirectly, and how the detection of risk affects subsequent cache strategy. To provide a rich context of pilfer risk, a live conspecific was used to enact the actual pilfering. Experiment 1 tested the effects of pilferage on Merriam's kangaroo rat behavior and cache strategy. The purpose of Experiment 2 was to determine whether presence of a conspecific could affect cache strategy without pilferage, and to look for carry-over effects from the pilferage of Experiment 1.

Experiment 1

Experiment 1 tested the effects of pilferage on Merriam's kangaroo rat cache strategy and behavior and took place during the summer and fall of 1997. The study animals were 12 wild-caught male Merriam's kangaroo rats (seven trapped near Reno, Nevada, USA in 1996; two trapped near Palm Desert, California, USA in 1995, and five trapped in Portal, Arizona, USA, in 1991 and 1992). All were housed since capture at San Francisco State University and/or the University of California, Berkeley, USA. All animals had experience caching in experimental arenas. Experimental pairs were chosen randomly with the restriction that none were housed in adjacent cages in the main colony room. One animal was randomly assigned the role of "Victim," and the other became the "Stealer."

We housed kangaroo rats individually in sand-filled (3 cm depth) plastic cages (48 cm × 27 cm × 20 cm high), each equipped with a home burrow (glass jar or plastic PVC pipe) and cotton bedding. They were fed 50 ml of commercial birdseed and two commercial rodent chow blocks once a week. One leaf of Romaine lettuce was provided three times a week as a water source. The colony was maintained on a reversed 12:12 light : dark cycle, with lights off at 0900 h.
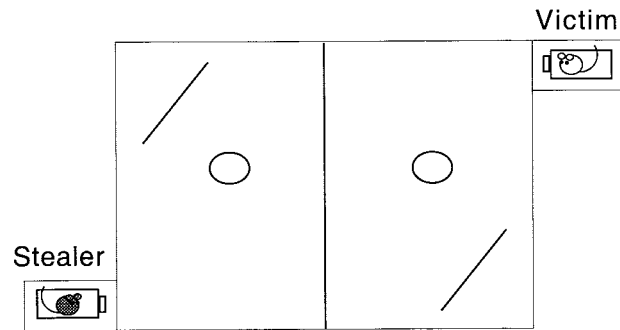
Apparatus
We conducted tests in a white acrylic arena (76 × 76 × 31 cm high) with two housing chambers (25 × 10 × 31 cm high)

A) The Arena

B) Sample Data

Day 1   Day 2   Day 3
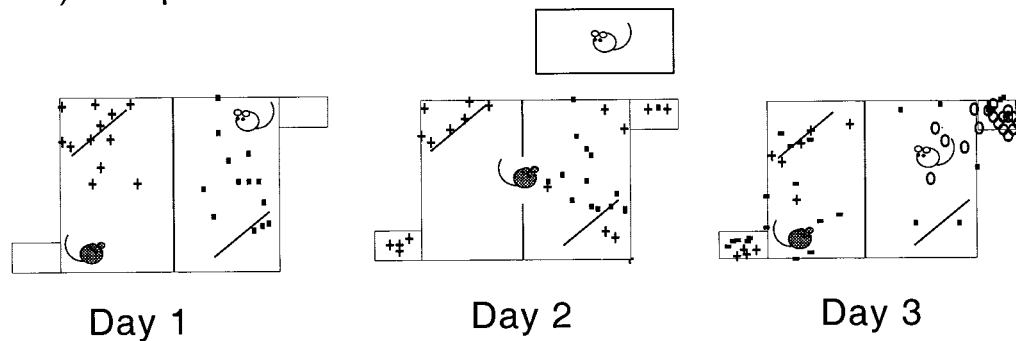
Figure 1
Schematic of Experiment 1. (A) Rectangles in the compartments adjacent to the arena represent home jars of the animals. Ovals in the center of each side represent feeding dishes from which seeds were dispensed. Diagonal lines on each side represent opaque barriers. (B) Sample data from one pair across the 3 days of the manipulation period. Filled animal symbols represent Stealers; open symbols represent Victims. The middle day shows the removal of the center portion of the center barrier, allowing access for the Stealer to the Victim's side of the arena while the Victim was in a separate holding cage (shown above the arena). Different seed colors for each role and day are represented by different shapes: the Stealer's seeds are represented by crosses on Day 1 and dashes on Day 3; the Victim's seeds are represented by filled squares on Day 1 and open circles on Day 3. Note the appearance of the Stealer's seeds (crosses) on the Victim's side on Day 2 and the increase in use of the home jar for larder hoarding by the Victim on Day 3.

attached to corners of the arena (Figure 1A). Each chamber contained the home burrow of one test subject. The main arena was divided in half by a wire-mesh screen barrier. The middle section of the barrier could be removed to allow animals access to both sides of the arena.

The arena floor was composed of four identical caching plates. There were two plates on each side of the arena. Each plate consisted of a 26 × 26 cm styrene grid, composed of 1 × 1 × 1.24 cm deep squares, yielding a total of 676 square cells in each plate and 2704 in the whole arena. The bottom of the plate was covered in wire-mesh screen. The entire plate was covered with sand for a total depth of approximately 2 cm. This design allowed us to locate caches by lifting the plates, draining the sand and visually inspecting caches. We placed a small (15 × 31 cm) white acrylic barrier and three crumpled paper balls on each side of the barrier to add structural complexity. Seeds were available in a plastic dish (10 cm diameter weigh boat), placed in the center of each side at the beginning of each period. Numerous extra-apparatus cues were visible in the room (e.g., recording equipment, wall attachments).

Procedure
Before the experiment, partners were given 24 h exposure to each other. Experiment 1 had three periods, each lasting for 3 days: "premanipulation control," "manipulation," and "postmanipulation control," in that order. Each period was

separated by approximately 1 month, during which time animals remained in home cages in the colony room.

On Day 1 of each period, each subject of an experimental pair was placed in the arena on his side of the barrier. On Day 2 of each period, the Victim was removed from the arena to a holding cage identical to its colony cage, while the Stealer remained in the arena. On Day 3 of each period, the Victim was returned to the arena. On Day 2 of both Control periods, the barrier remained intact so that the Stealer could not access the caches made by the removed Victim. But on Day 2 of the manipulation period, the middle section of the center barrier was removed, giving the Stealer full access to the Victim's side, including its home burrow (Figure 1A, B).

On Days 1 and 3 of all periods, each Merriam's kangaroo rat was provided with 100 shelled sunflower seeds in the food dish. Seeds were dyed with food color to identify the day and the individual to whom the seeds were given; seed colors were counterbalanced for experimental condition and role. Lettuce was available *ad libitum* throughout testing. To eliminate differences in hunger between Stealer and Victim on Day 2, the Victim was given approximately 150 undyed sunflower seeds in the holding cage.

The control-manipulation-control design allowed us to control for order effects by comparing behavior in the manipulation period with behavior in the Control periods, where the Victim was also removed on Day 2 but the barrier remained impermeable. In addition, the postmanipulation control pe-

riod allowed us to look for changes in behavior between the roles, as a result of the manipulation. For example, Stealers spent 9 days in the arena, with only 1 day of pilfering. This may have engendered habituation. The Victims had a more diverse experience and may have been conditioned to expect pilferage in the postmanipulation control.

Data collection

Cache placement. Seeds were censused each day during the last hour of the light phase. We recorded the following measures: number and color of seeds found in home burrow (larder hoarded), number and color of seeds found in the arena but under the sand (scatter hoarded), number of seeds in each scatter hoard (cache size), number of seeds not found (eaten), and number of seeds found in the arena, above the sand (uncached).

For scatter hoards, we recorded the cell coordinates (an area of 1 cm²) and the general location of each scatter hoard (along an edge, behind the barrier, in open arena). After censusing, the seeds were returned to their exact cell location at an intermediate depth. All feces were returned to the surface of the sand so that some original odors remained.

Overt behaviors. The first 5 min of each day were coded and analyzed according to a behavioral ethogram (Preston, 1999). Space-use was divided into time spent in the arena, behind the opaque barrier, in the burrow, and at the food dish. Vigilance was operationalized as the amount of time an animal spent at the center barrier, with his head directed towards the opposite side. The frequency of scratching, grooming, body shaking and tail biting were also recorded and analyzed collectively as "self-directed behaviors." The first 12 hours of each day were recorded during both the premanipulation control and the manipulation for later analysis. In the postmanipulation control, only 3 hours were recorded: the first, fourth, and last hour of the dark cycle. Day 2 of each period was not coded as only the Stealer was in the arena.

Analysis

Data were analyzed, except where noted, in a 2 × 3 × 2 design, using repeated measures ANOVA. Day (1 or 3, i.e., before or after the Victim was removed), period (premanipulation control, manipulation, postmanipulation control) and role (Stealer or Victim, the between-subject factor) were the independent variables. Except where noted, the alpha level was .05. Subjects with missing video data were eliminated from all analyses that required this data. We arcsine transformed all percent data.

RESULTS

In 89% of trials, kangaroo rats entered the arena from their starting location in the home burrow within the first 10 min of the experiment. Inspection of the other side usually took place shortly thereafter with 95% (80/84) of inspections within 20 min. The majority of subjects interacted with their partner at the barrier within 2 h (56%, 27/48); 78% (21/27) of these interacted within the first 20 min.

Across all days that the animals were supplied with new seeds (Day 1 and Day 3 of each period), animals cached (scatter or larder hoarded) on average 57% (SE = 3.12) of the seeds, ate 27% (SE = 1.57) and left 16% (SE = 3.09) in the dish. Of all of the seeds cached, 67% (SE = 2.79) were scatter hoarded and 32% (SE = 3.84) were larder hoarded. There were no average differences between Stealers and Victims in these proportions (percent scatter hoarded: $F_{(1,82)} = 0.08$, ns). On average, animals only left 1.84 (SE = 0.41) of 11.29 (SE = 1.24) caches in place when allowed to re-cache. An
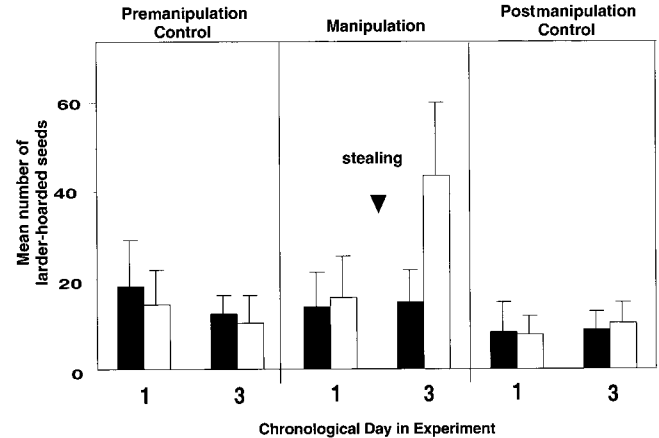

Figure 2
Larder hoarding in Experiment 1. Bars height is the mean (+ SE) number of larder-hoarded seeds for Stealers (filled) and Victims (open). Data from Day 2 of each period is not included since only the Stealers were in the arena.

example of cache placement by one pair across the 3 days of the manipulation period is shown in Figure 1B.

All Stealers stole from the Victim on Day 2 of the manipulation and ate or re-cached the seeds. An average of 75% of caches were stolen (SE = 14.38). Generally, the Stealer re-cached seeds across the whole arena, using both his original side and the Victim's side. At the end of Day 2, an average of 76% (SE = 28.62) of the caches on the Stealer's side and 69% (SE = 26.18) of the caches on the Victim's side were new. Stealers also larder hoarded seeds in the home burrows of the Victim and were occasionally found there at the end of Day 2.

Changes in caching

The only qualitative changes in cache strategy were by Victims after being pilfered. The mean number of seeds larder hoarded was higher for Victims, but not Stealers, when comparing Day 3 of the manipulation, to the same day in the two control periods ($F_{(2,12)} = 3.75$, $p = .05$; Figure 2). Quantitatively, there was an effect of period ($F_{(2,24)} = 9.90$, $p = .001$) and day ($F_{(1,12)} = 17.02$, $p = .001$) for the number of scatter hoards, due to an increasing number of scatter hoards across days ($R^2 = .22$; $F_{(1, 82)} = 22.53$, $p < .001$).

Changes in overt behavior

There was a significant main effect of day for the percent time in the arena spent inspecting the opposite side ($F_{(1,8)} = 6.18$, $p = .038$; Figure 3). On average, there was more inspecting on Day 3 of each period when the animals were reunited, a trend more noticeable for the Stealers. The increase in the average percent time the Stealers spent inspecting the opposite side from Day 1 (0.05, SE = 0.02) to Day 3 (0.29, SE = 0.11) of the manipulation, approached significance ($F_{(1,6)} = 4.37$, $p = .08$). This increase did not correlate with the number of seeds the Stealer had cached on the opposite side ($R^2 = .16$; $F_{(1, 5)} = 0.96$, ns).

There was a period-by-role interaction for the percent time spent in the arena and the percent of arena time behind the barrier, when comparing Day 3 of the postmanipulation to the same day in the premanipulation control ($F_{(1,10)} = 8.34$, $p = .016$; $F_{(1,10)} = 5.11$, $p = .047$, respectively; Figure 4A,B).

There was an effect of day ($F_{(1,8)} = 5.43$, $p < .05$), a period-by-role interaction ($F_{(2,16)} = 4.37$, $p = .03$) and a peri-
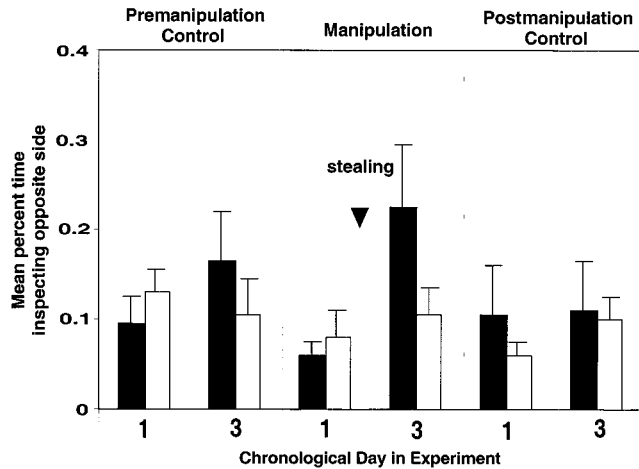
Figure 3
Time in the arena spent inspecting the opposite side in Experiment 1. Bars height is the mean (+ SE) time for Stealers (filled) and Victims (open). Data from Day 2 of each period is not included since only the Stealers were in the arena.

Figure 4
(A) Average percent time spent in the arena in Experiment 1. (B) Average percent time in the arena spent behind the barrier in Experiment 1. Bars height is the mean (+ SE) percent for Stealers (filled) and Victims (open). Data from Day 2 of each period is not included since only the Stealers were in the arena.

od-by-day-by-role interaction ($F(2,16) = 3.99$, $p = .04$) for the number of self-directed behaviors (scratching, grooming, body shaking, and tail biting) (Figure 5). On average, the reuniting on Day 3 was associated with more self-directed behaviors than Day 1; this was true of all periods. Also, Victims significantly increased the number of self-directed behaviors from Day 1 to Day 3 of the postmanipulation control relative to Day 3 in the premanipulation control, producing a significant day-by-role interaction ($F(1,10) = 12.48$; $p = .005$). Using a corrected alpha of .0085 for post-hoc comparisons, the difference between roles was significantly different on Day 3 of the postmanipulation control ($F(1,10) = 19.50$; $p = .001$), but on no other day ($F(1,12) < 5.75$; $p > .034$).

DISCUSSION

Our results are consistent with the interpretation that pilferage caused Victims to switch from a scatter-hoarding strategy to a larder-hoarding strategy. Although scatter hoarding is usually considered the strategy that minimizes the risk of catastrophic loss (MacDonald, 1976), larder hoarding may have been appropriate in this context because cache movement was catastrophic (almost all caches were moved by the Stealers) but incomplete (the Stealers re-cached many of the seeds on the Victim's side). Victims may respond differently to area-restricted or complete seed loss, as in studies by Stevens (1984) and Hampton and Sherry (1994). Our unpublished data suggest that Merriam's kangaroo rats will move scatter hoards if they experience an area-restricted loss of caches (Preston SD and Jacobs LF, unpublished data).

In previous studies, Merriam's kangaroo rats did not change cache strategy in response to the cues of a conspecific without pilferage (Leaver and Daly, 1998) or in response to pilferage without the cues of a conspecific (Jenkins, 1998). In contrast, our experiment produced a change in cache strategy in response to the cues of a conspecific with pilferage. However, the presence of a live, familiar conspecific without pilferage may also lead to changes in cache strategy, especially once an animal has experienced pilferage. We tested this hypothesis in Experiment 2.

Contrary to our hypothesis, many of the behavioral effects took place in the postmanipulation control (time in arena, time and caching behind the barrier, self-directed behaviors).
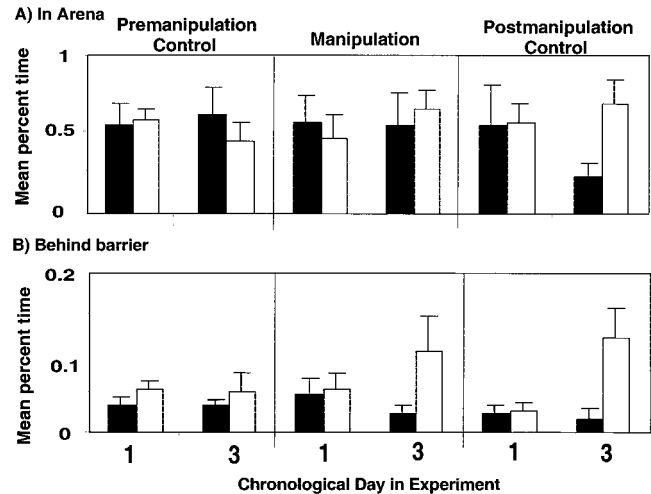
From Day 1 to Day 3 of this period, these behaviors tended to increase in Victims and decrease in Stealers. These behavioral differences are likely due to the differences in their experience. The Stealers were in the arena on Day 2 of the postmanipulation control and thus knew that there was no pilferage. The Victims, however, having been removed on Day 2 of this period, could not have known that stealing did not take place again. Thus, the Stealers may have habituated to the context, with activity levels that decreased or remained the same while the Victims continued to be active, with activity levels that increased or remained high. Differences in self-directed behaviors particularly suggest such a divergence as these "displacement behaviors" are considered behavioral indicators of anxiety (e.g., Armstrong, 1952; Fentress, 1968; Maestripieri et al., 1996; Tinbergen, 1952).

Experiment 2

Experiment 2 was designed to determine whether presence of a conspecific without pilferage could affect cache strategy.
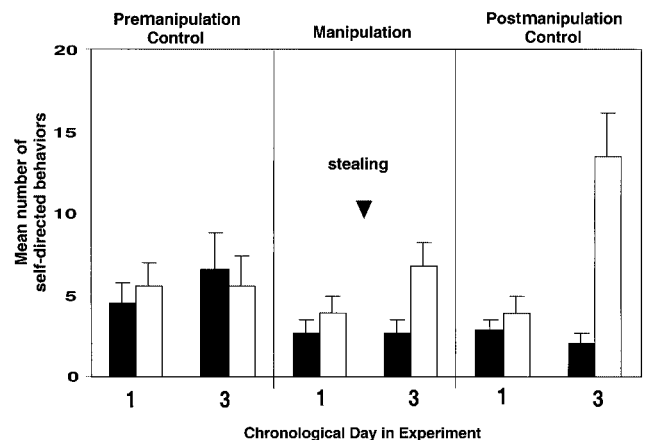

Figure 5
Mean number of self-directed behaviors in Experiment 1. Bars height is the mean (+ SE) number for Stealers (filled) and Victims (open). Data from Day 2 of each period is not included since only the Stealers were in the arena.

We also compared animals from Experiment 1 to naive animals to determine if prior experience with pilferage affects the perception of risk.

Study animals

Subjects were compared in a 2×2 design that manipulated prior experience (Experiment 1 or naive) and presence of conspecific (paired or unpaired on Day 2). There were six pairs of experienced animals ($N = 12$), five of which were original pairings from Experiment 1. There were five pairs of naive animals ($N = 10$), trapped in Palm Desert, California, USA in 1997 and maintained in the laboratory under the same conditions as noted in the General Methods. Experiment 2 took place in the fall of 1998.

Apparatus

Animals were placed into a plastic, sand-filled arena (51 cm $\times$ 41 cm $\times$ 20 cm high), divided lengthwise with a wire-mesh barrier, sequestering one Merriam's kangaroo rat on each side. Each arena was equipped with the individual's home burrow (glass jar or plastic pipe) and an *ad libitum* supply of lettuce.

Procedure

There were three testing days, each separated by approximately 10 days. On each test day, subjects were given 100 shelled sunflower seeds. On Day 1, all animals ($N = 22$) were placed in the arena alone on one side of the arena; both sides of the arena contained a jar and feeding dish. After 24 h, subjects were returned to their home colony cages for 10 days. When they returned for Day 2 in the experimental apparatus, subjects were placed on the same side of the small arena as in Day 1. Half of the subjects were again alone in their small arenas ($N = 4$ for naive; $N = 6$ for experienced), while the other half were placed with their experimental partner on the opposite side ($N = 6$ for naive; $N = 6$ for experienced). After 10 days, kangaroo rats returned to the small arenas for Day 3. On this day, all subjects were again alone.

Data collection

Caches were checked as in Experiment 1, but were removed from the arena after each experimental day. Subjects were videotaped for the first 2 h of each 24-h period. Behavior was measured as in Experiment 1. Due to technical problems, there were not enough data from the naive pairs for video analysis. Data from one experienced pair on Day 2 were also lost; these subjects were eliminated from any analyses that required these data.

RESULTS

Cache strategy in response to proximity

The pattern of caching was similar to Experiment 1. On average, animals cached 66% (SE = 1.76) of the seeds, ate 32% (SE = 1.19) and left 2% (SE = 1.46) in the dish. There were no qualitative changes in the percent of seeds scatter hoarded and larder hoarded associated with the presence of a conspecific ($F(2,42) < 0.87$, $p > .42$; Table 1). Across all days and conditions, 85% (SE = .035) of the seeds cached were scatter hoarded and 15% (SE = .035) were larder hoarded.

The only changes in caching were quantitative and related to the amount of time that animals spent in arenas. There was a main effect of day on the percent of seeds scatter hoarded ($F(2,42) = 4.79$, $p = .014$; Table 1). The percent was greater on Day 3 than on either Day 1 or 2. On average, naive animals increased the percent of scatter hoarding more than experienced animals, for an interaction that approached signifi-

Table 1

Percent of cached seeds scatter hoarded each day of Experiment 2

Condition		Day 1 (SE)	Day 2 (SE)	Day 3 (SE)
Experienced	alone	0.77 (0.16)	0.77 (0.16)	0.99 (0.01)
	paired	0.92 (0.08)	0.86 (0.12)	0.93 (0.06)
Naive	alone	0.66 (0.24)	0.90 (0.07)	0.94 (0.06)
	paired	0.78 (0.15)	0.70 (0.19)	0.97 (0.02)

cance ($F(2,36) = 2.34$, $p = .11$). This seems due to the fact that experienced subjects began Experiment 2 with a higher proportion of scatter hoarding ($F(1,20) = 3.13$, $p = .092$; Table 1). Conversely, all subjects decreased their larder hoarding, an effect approaching significance ($F(2,42) = 2.77$, $p = .07$). There was a main effect of general cache location by day ($F(2,36) = 6.91$, $p = .003$), due to an increasing number of scatter hoards along the inside barrier across days ($R^2 = .15$; $F(1,64) = 11.32$, $p = .001$).

Changes in overt behavior in response to proximity

Among experienced pairs, there was no difference across days in the proportion of time spent in the arena versus the burrow ($F(2, 16) = 0.24$, ns). There was a day-by-condition effect for time inspecting the opposite side that approached significance ($F(2,16) = 3.36$, $p = .06$), due to the fact that paired subjects spent more time inspecting the opposite side than unpaired subjects on Day 2 ($F(1,8) = 5.65$, $p = .045$). There were no differences in self-directed behaviors due to pairing or to the number of days in the arena ($F(2,16) < 1.86$, ns).

DISCUSSION

In Experiment 2, the presence of a conspecific was again correlated with an increase in vigilance, but it was not correlated with a change in cache strategy. Paired animals increased the percent time spent inspecting the opposite side of the arena, but the proportion of scatter and larder hoarding did not differ between paired and unpaired animals. These results support the conclusion from Experiment 1 that pilferage is necessary to elicit a change in cache strategy. The presence of the barrier may have inhibited the perception of risk; although, previous research suggests otherwise. In a similar experiment with voles, the location of food storage was altered even though the competitor was restricted to a net cage (Hansson, 1986).

Caching did change quantitatively across the 3 days of the experiment; animals used more scatter hoarding and less larder hoarding and increased caching along the inside barrier wall. The effect of day on scatter hoarding seemed to generalize across experiments. Naive animals increased scatter hoarding across Experiment 2 as the experienced animals had done in Experiment 1. The experienced animals, however, employed a high level of scatter hoarding from the beginning of Experiment 2 and remained stable.

General discussion

Though Merriam's kangaroo rat is a solitary species (Randall, 1994), our study indicates that this scatter-hoarding rodent is sensitive to its social environment, and uses this information when making cache decisions. In both experiments, animals increased vigilance when they were paired with a conspecific, even a familiar one; but pairing per se did not affect cache strategy. Animals changed cache strategy after caches were pilfered, from a majority scatter-hoarding strategy to a majority larder-hoarding strategy.

Under natural conditions, this may be an adaptive strategy. Although the risk of pilferage is usually correlated with competitor density (Clarkson et al., 1986; Daly M, Jacobs LF and Wilson MI, unpublished data), there are instances when they are dissociated. For example, they are dissociated when food is super-abundant, as it was in this experiment. Therefore, it may not have been necessary to change cache strategy in response to mere proximity of a conspecific.

Much experimental evidence points to the notion that animals change caching in the presence of a competitor. Captive bank voles move caches into an unpreferred portion of an arena to avoid an introduced animal in the preferred portion, even though their nest remains in the preferred territory (Hansson, 1986). Willow tits (*Parus montanus*) cache closer to the feeder when alone than in the presence of conspecifics (Lahti et al., 1998).

These effects of competitor presence on caching may be due to the fact that cache observation facilitates pilferage. In experiments with the social, scatter-hoarding Pinyon jay, observer jays remember the area of their partner's cache (Bednekoff and Balda, 1996a). Group-living Mexican jays (*Aphelocoma ultramarina*) retrieve caches with the same accuracy as the cacher for 2 days after observing a cache episode (Bednekoff and Balda, 1996b). Even the solitary Clark's nutcracker (*Nucifraga columbiana*) benefits from observing a cache episode for a day after observation (Bednekoff and Balda, 1996b). In Merriam's kangaroo rats, there is an anecdotal report of an observer immediately digging up the caches of a focal conspecific (Daly et al., 1992). Therefore, observational information can be useful for pilferage at short intervals, even in solitary species such as the Clark's nutcracker and the Merriam's kangaroo rat. In accordance, many bird species abort caching in the presence of potential thieves (Burnell and Tomback, 1985; James and Verbeek, 1993, Kallender, 1978), and grey squirrels (*Sciurus carolinensis*) make more false caches when a conspecific observer is nearby (Steele, in preparation).

Thus, evidence exists from many species that a competitor can more easily retrieve caches after observing the cache episode, and for this reason, animals may alter cache behavior or location in the presence of a competitor. Yet, even with well-documented variation in cache strategy in Merriam's kangaroo rats (Jenkins and Breck, 1998), laboratory experiments have been unable to produce changes in cache strategy in response to cues of a competitor (Leaver and Daly, 1998) or to pilferage without a competitor (Jenkins, 1998). In this experiment, animals may have restricted caching to times when the neighbor was in the burrow and out of sight; however, the proportion of scatter and larder hoarding did not change in response to the presence of a conspecific, only to the raiding of caches.

Thus, it seems that Merriam's kangaroo rats need all the cues of an actual pilferage event (a live competitor present and cache disturbance) to change strategy. If this were the case, only the combination of factors in Experiment 1 would have provided enough cues to elicit the response. It could also be that cache disturbance is enough to affect cache strategy in the field, but that laboratory conditions extinguish or mitigate this natural response. Caches made in the laboratory are often lost when cages are changed or experiments end, and thus laboratory animals may be habituated to this phenomenon.

The differences between Stealers and Victims in Experiment 1 indicate that caching in the Merriam's kangaroo rat could be a productive paradigm for studying the relationship between emotion, memory, and decision-making in rodents. In the future, our protocol could be refined to yield more natural and generalizable tests of these phenomena than are currently available with electric shock and water maze protocols. Understanding the forces that shape behavior and the behavioral malleability in response to changes is essential to our ability to understand the evolution of behavioral and cognitive mechanisms.

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