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Adaptations for Caching and Robbery in Two Sympatric Chipmunks

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Adaptations for Caching and Robbery in Two Sympatric Chipmunks

A Dissertation approved for the Department of Psychology

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Chapter 1

Indirect competition for cached food in two sympatric chipmunks

We captured least chipmunks (*Tamias minimus*) and eastern chipmunks (*T. striatus*) from co-existing populations and assessed their comparative success at heterospecific robbery in a naturalistic laboratory setting. The smaller species (*T. minimus*) found their competitors' caches quickly and with little effort. The value of pilfered caches for least chipmunks was magnified by their lower energetic demands and the bigger cache size of their larger competitor. We traced the comparative success of least chipmunks to searching tactics that targeted the vulnerabilities of eastern chipmunk caches, and a cache placement counter-strategy that protected their own food stores. We suggest that heterospecific robbery may be especially beneficial for *T. minimus* and other small mammals by allowing them to narrow the competitive gap they experience with larger competitors.

Sympatric rodent species exhibit a variety of adaptations that ease the pressure of interspecific competition. Variation in body size is common (Bowers & Brown, 1982), and can reduce competition by promoting resource partitioning (Bowers & Brown, 1982) and/or differential exploitation of similar resources (Basset, 1995). Desert rodent communities have been a particular focus of research because of extensive species overlap and limited resources (reviewed by Kotler & Brown, 1988; Randall, 1993). For instance, different-sized desert rodents may avoid direct competition by preferentially feeding upon different seed sizes (Dayan & Simberloff, 1994) or in structurally distinct microhabitats (e.g., Murray & Dickman, 1994; Price & Waser, 1985), or they may differ in their degree of patch specialization (Price, 1983).

On the other hand, community structures that appear to mitigate competition could actually be outcomes of ongoing competition, since seemingly distinct foraging patterns can change significantly when dominant species are absent (e.g., Ziv et al., 1993). Body size generally determines dominance (Kotler & Brown, 1988), so it is usually the smaller species that increase in number or shift foraging patterns upon the exclusion of larger competitors (Heske et al., 1994; Munger & Brown, 1981). Such findings suggest that "preferred" habitats and resources of smaller competitors are often enforced through subordination, not necessarily or wholly by adaptations for specific niches. This is consistent with other indirect evidence. For instance, assessment of harvest rates indicates that different sized rodents are best suited for similar, not different, foraging habitats (Price & Heinz, 1984). Thus, foraging differences may not be as distinct as once thought (reviewed by Randall, 1993), and

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ongoing competitive displacement of smaller species may account for much of the structure of rodent communities.

Many rodents scatter- and larder-hoard food for later consumption, thereby exploiting food bonanzas and protecting themselves against periods of scarcity. This foraging strategy is unique in that it opens the opportunity for pilfering, an indirect means of competition in which small body size may not be a disadvantage. Stockpiled food is principally for use by individual owners; nevertheless, pilfering rates are substantial in caching communities (e.g., Clark & Kramer, 1994; Daly et al., 1992; Vander Wall, 2000). Recent theoretical treatments of this issue suggest that cache exchange via robbery and scavenging may be high enough to promote coexistence of similar caching species (Price and Mittler, 2003), and that the benefits of such exchange may offset individual losses to pilfering victims (Vander Wall & Jenkins, 2003). Taking these models a step farther, we are interested in whether the competitive margin lost by smaller species in direct competition might be regained through pilferage.

There are some disadvantages to being a large hoarder. Larger animals may be unable to squeeze through narrow burrow entrances to steal larders of small animals (Jenkins & Breck, 1998), but their own burrows do not exclude entry by smaller species. Some have suggested that larger animals may predominately scatter-hoard to avoid such raids (Leaver & Daly, 2001; Price et al., 2000, but see Jenkins & Breck, 1998). To pay the costs of their greater mass, larger animals must ingest more food. They also make larger scatter-caches (Vander Wall et al., 1998, but see Jenkins & Breck, 1998) and store more seeds than would be predicted by metabolic rates

alone (Price et al., 2000). Of course the opposite is true of smaller animals, which creates a fundamental asymmetry in relation to cache-robbery: Larger animals have greater caloric needs, but robbing the caches of their small competitors returns comparatively little; smaller animals need less, but obtain more from the caches of larger competitors.   In general, then, smaller animals might be expected to devote more foraging effort to pilfering than to harvesting. There is little data bearing on this question, but recent work with heteromyid rodents is suggestive. Leaver & Daly (2001) report that pocket mice, compared to at least one of their larger competitors, were especially proficient robbers, raiding both conspecific and heterospecific food stores. Thus, we suggest that unless the scatter-hoards of larger animals are very carefully concealed, smaller competitors might be expected to exploit them and in this way contribute to their competitive stability of the community.

Little is known about how or if overlapping species differ in their cache-concealment and pilfering tactics. In view of the potential asymmetry in benefits to be gained by different sized pilferers, any such behavioral differences could have a pronounced impact on the competitive stability we have suggested. In the present study we set up caching and pilfering opportunities for two sympatric chipmunk species with the specific aims of determining 1) if the asymmetry we predict actually emerged, 2) if and to what extent the asymmetry was exploited to the competitive advantage of the smaller species, and 3) if either species used special searching or cache-concealment tactics that might permit or mitigate such exploitation.

As with previous studies that give close analysis to behavioral mechanisms (e.g., Emery et al., 2004; Jenkins & Breck, 1998; Preston & Jacobs, 2001; Vander

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Wall 1991), our study was carried out in a relatively controlled, but naturalistic, laboratory setting using wild-caught animals. The species selected satisfied three criteria—they exhibit natural sympatry (for stronger ecological inferences), are congeneric (for stronger comparative inferences), and show a marked size difference (the issue under consideration).

METHODS

Subjects

Our subjects were twenty eastern chipmunks and eighteen least chipmunks of both sexes captured from overlapping populations in the Seney National Wildlife Refuge located in Schoolcraft County in the upper peninsula of Michigan. Least chipmunks (*Tamias minimus*) and eastern chipmunks (*T. striatus*) show similar foraging behavior. Both species are diurnal, feeding primarily on seeds, but also fruits, nuts, berries, fungi, and invertebrates (Elliot, 1978; Verts & Caraway, 2000), and both are extensive scatter- and larder-hoarders (Criddle, 1943; Elliot, 1978). The two species tend to be found in somewhat different habitats, with *T. striatus* more common in hardwood forests and forest edges, and *T. minimus* more common along forest edges and more open areas near conifer forests (Forbes, 1966; Jackson, 1961). Nevertheless, the species overlap extensively in the upper Great Lakes area and surrounding states and provinces in the United States and Canada, sharing much of the same habitat throughout this region. Eastern chipmunks have a definite size advantage—their body mass is about twice that of least chipmunks (80-110 g vs. 30-50 g) and eastern chipmunks dominate in aggressive encounters (L. Devenport & J. Devenport, field observations).

Animals were trapped during the summers of 1999 and 2000 using procedures described in Devenport and Devenport (1994). After transport to the University of Oklahoma Animal Cognition Laboratory, each animal was implanted with a PIT (Pet Identification Tag), given distinctive fur markings, and housed with conspecifics in one of four large naturalistic enclosures (Devenport et al., 1998) under an LD 12:12 artificial light cycle. Both species were fed commercial rodent pellets, supplemented daily with fruits or vegetables. Tap water and minerals were continuously available.

Materials and procedures

Experimental caching areas consisted of two square 1.8 x 1.8 x 0.9 m translucent Plexiglas enclosures filled 6 cm deep with dry abrasion-grade sand. The two foraging areas were located in separate rooms. Within each area, we embedded four or five scattered landmarks—a tree stump with attached water bottle, logs, rocks, and a running wheel were typical. The walls and corners of the arena also served as fixed objects for all subjects. The starting configuration of objects remained the same across caching and recovery sessions, but was different for each set of animals. A video camera installed in the ceiling above each foraging area allowed for real-time monitoring and videotaping of experimental sessions from a separate control room equipped with dual VCRs and 13-inch monitors. This setup allowed us to observe pairs of animals simultaneously and to mark cache sites on-screen with a dry-erase pen to aid in locating them at the end of each session. More precise measurements were obtained later from videotape analysis.

Experiment 1: Heterospecific Pilfering

Caching Phase

Approximately two days before the start of caching sessions, pairs of heterospecifics were transported to their respective foraging areas and allowed to habituate for 24-48 h. During this time the animals were given standard food rations, but no seeds. Following the habituation period, they were each given a bowl of unshelled sunflower seeds and allowed to scatter-cache. To obtain roughly the same number of caches from both individuals in a pair, we frequently varied the length of an animal's caching session (between 1-3 h), depending upon its caching rate. At the end of this caching session, animals were transferred to individual, sterilized polycarbonate cages, where they remained until the start of the pilfering phase. Each cage contained hardwood chips, cotton bedding, a nest bottle, fresh water, and rodent pellets. Throughout all experimental sessions, animals were kept on an LD 12:12 h light cycle matching that of their group living areas.

Pilfering Phase

Foraging areas were exchanged for the members of each heterospecific pair 1-2 d after caching sessions. They were now allowed to search for and pilfer seeds during sessions that lasted 1-2 h. For most animals, more caches were available than could be consumed, re-cached, or found in one test session, so they were given up to two additional sessions over consecutive days to find as many caches as possible until they gave up searching. Whenever time was extended for one member of a pair, it was extended for both. The animals were returned to their individual cages between sessions. Pilfering sessions ended when both individuals had refused to search, dig, or otherwise explore for an extended time (usually about 1 h). We returned animals to their group living quarters immediately following the end of the pilfering phase and

removed undiscovered caches, disposed of soiled sand, redistributed landmarks, and sifted and raked the sand.

Experiment 2: Conspecific Pilfering

To determine if least chipmunks might be specializing on eastern chipmunk caches, we assessed least and eastern chipmunks' success at pilfering conspecific caches. Such comparisons would allow us to determine the extent to which any interspecific differences in pilfering behavior from Study 1 were attributable to superior pilfering strategies by one species and/or to poor cache placement by another. Furthermore, we could determine if any vulnerability to heterospecific pilferage detected in Experiment 1 held for conspecific competitors as well. For this experiment, we conducted caching and pilfering sessions as described for Study 1, but did so with pairs of same-species chipmunks. Therefore, during pilfering sessions, animals searched for caches made by conspecific instead of heterospecific animals.

Data Collection and Analysis

Following the caching phase, we obtained measurements of cache construction by relocating individual caches and measuring each for size (number of seeds) and depth (distance from the surface of the sand to the top of the cache). We then restored each cache as closely as possible to its original condition. At the end of the pilfering phase, we again relocated all caches (along with any new caches) and recorded the number of seeds in each. We wore disposable, unscented latex gloves when taking measurements or performing other manipulations in the foraging arenas.

Videotape recordings were used to independently confirm real time observations and to obtain precise distance measurements. To assess how each cache was situated

with respect to local objects, we recorded the distance of each cache to the nearest- and next-nearest object, as well as the distance between the two nearest objects (inter-object distance) as explained in Devenport et al. (2000). To assess cache dispersion, we calculated mean nearest-neighbor distance for each animal's set of caches.

Digging behavior during pilfering sessions was timed and categorized into time spent in exploratory searching and time spent extracting seeds from caches already found. We further separated exploratory digging into that occurring near (within 5 cm) and away from objects, in order to detect any directed searching. Dig times were recorded until animals found all available caches, or gave up, whichever came first.

Upon finding a cache, animals were observed to remove the seeds and eat them, cache them elsewhere, eat some and cache some, or leave them in place (sometimes re-burying them, sometimes not). To simplify, we divided these outcomes into cache "finds" (discovered but not taken) and "removals" (found and taken). To the extent that energy can be considered a commodity in caching communities (Price & Mittler 2003; Vander Wall 2003), we were interested how kilocalories, in the form of sunflower seeds, moved between and/or among the two chipmunk species. Therefore, using only seed "removal" data, we calculated the gains (kilocalories) obtained through pilfering by each species, based on the reported caloric value of our commercial sunflower seeds. Because of body weight disparity, caloric gains alone are not meaningful for interspecific comparisons. Furthermore, calculating caloric gains per gram of body weight is also not appropriate since larger animals are metabolically more efficient than smaller ones. Therefore, for valid interspecific comparisons, we used the exponential scaling reported for rodents by Nagy et al.

(1999) (body weight [kg] $^{0.71}$) to standardize energetic gains for species of different body mass.

Time engaged in active searching indexed the principal foraging cost in this experiment, and therefore was compared with intake as our indicator of pilfering success. We first estimated rates of cache discovery for each animal by calculating the number of caches found per minute of exploratory digging. To assess how efficiently animals foraged, we calculated standardized rates of gains and losses. To assess gains, we calculated each subject's standardized caloric gains from pilfering per each minute of exploratory digging. Likewise, losses were calculated by dividing each subject's standardized caloric losses to robbery by their heterospecific pilferer's searching time.

When appropriate, multiple data points taken from the same subject were averaged to avoid pseudo-replication. Since heterospecific pairs were run in parallel, most measurements of pilfering success in Experiment 1 were analyzed using paired Wilcoxon Z tests. Measurements of cache placement in both experiments were analyzed using independent Mann-Whitney U tests, as were measurements of conspecific pilfering success in Experiment 1. Difference scores were computed for each experiment to compare results between Experiment 1 and 2. Pooled or adjusted data were occasionally used, and for some analyses we used truncated data sets to adjust for opportunity and other statistical artefacts. The use of these procedures are noted and explained as they appear in the Results and Discussion section. Data are reported as medians and interquartile ranges since means and standard errors are inappropriate for nonparametric comparisons.

RESULTS AND DISCUSSION

Experiment 1: Heterospecific Pilfering

Cache Construction and Placement

The physical characteristics and distribution of scatter-caches differed

between species in several reliable ways. *T. minimus* buried fewer seeds per cache

than did *T. striatus* (4.08 [2.11, 6.21] vs. 17.0 [13.84, 21.95]; Mann-Whitney *U* test:

U=0, *N*=18, *P*<0.001), resulting in an overall difference in median total seeds cached

per animal (36.00 [12.0, 67.50] vs. 172.0 [130.5, 266.5]; *U*=3, *N*=18, *P*< 0.001) for *T.*

minimus and *T. striatus*, respectively. No differences were expected in the number of

caches made, and none were found: the median number of caches for the species

combined was 10.5 (5.0, 13.0). As explained in Methods, we tried to hold this

variable constant so that the opportunity to find heterospecific caches would be

similar for the two species.

Eastern chipmunk caches were buried at a statistically equivalent depth

compared to those of least chipmunks (1.82 cm [1.21, 2.44] vs. 1.33 cm [1.19, 1.90],

respectively; Mann-Whitney *U* test: *U*=28, *N*=18, P=0.27). The largest caches of

both species tended to be closer to the surface (*T. striatus*: *r*=-0.42, *N*=98, *P*<0.001;

T. minimus: *r*=-0.29, *N*=81, *P*<0.01). Apparently chipmunks prepare their caches by

digging to a more or less constant depth, and the volume of seeds deposited

determines how far the cache rises toward the surface.

The horizontal distribution of caches across the substrate differed between

species. Eastern chipmunks cached near objects, but least chipmunks usually kept

their caches about twice as far away. Average distances, however, fail to give a full

account of cache distribution in relation to objects. For instance, if an animal were attempting to avoid caching near objects, then the distance a cache could be placed away from one object would be constrained by other objects in the arena, which the cacher would also need to avoid. On the other hand, for animals preferring to bury their food stores near objects, local object density would have little influence.

We therefore determined the relationship between cache-object distance in relation to local inter-object distance (after Devenport et al., 2000, see methods). To avoid over-representation of animals that made more caches, we used the first three caches from each animal to perform our analyses (an unbiased method of data-pooling as long as sample sizes are equal; Leger & Didrichsons 1994). As shown in Fig. 1, *T. minimus* took advantage of the available space as inter-object distance increased by placing their caches progressively further away from objects. In contrast, eastern chipmunks continued to target objects with little regard for the amount of open space available. The slopes of these regression lines are also significantly different (t_{15}=2.91, N=54, P<0.01). The way caches are placed in relation to objects in the environment is important because there are indications that pilferers perform directed searches around objects (Clarke & Kramer, 1994; Daly et al., 1992; Vander Wall, 1982; Vander Wall, 1991). To the extent that potential robbers search strategically (see below), the caches of eastern chipmunks would be in jeopardy.

Density of cache distribution did not differ between *T. minimus* and *T. striatus*: median nearest neighbor distance was almost identical (34.69 cm vs. 34.40 cm, respectively).

Searching Behavior

In some respects, searching behavior was similar between species, and much like that described for yellow pine chipmunks (Vander Wall, 1991)—relatively shallow digging followed by rapid, short distance movements and more digging. Sometimes slower forward locomotion was accompanied by digging, resulting in a shallow trench. The searching was periodically interrupted when a likely cache site was partially uncovered, presumably as cued by the release of an olfactory signal. Vigorous excavation followed and if no cache was found, the search pattern resumed. Frequently, caches were detected in the absence of digging, when animals ran over a site. This was especially true for *T. minimus* and was likely due to olfactory cues.

Although both species actively foraged for caches, eastern chipmunks spent much more time engaged in exploratory digging (*T. striatus*: 6.7 [2.0, 32.8] min; *T. minimus*: 0.9 [0.4, 2.3] min, N=18, P<0.05), an important measure of foraging costs, a point to which I will return later.

To determine if either species employed directed random searches when pilfering, we divided exploratory dig time into two categories: digging near or away from objects, as explained in Methods. If searches were carried out randomly, the distribution of digging effort would be proportional to the amount of space available in each of the two categories (about 20% near objects and 80% away from objects). Any significant bias toward objects would imply an area-restricted search, which, for the purposes of the present study will be referred to as object-directed searching.

Figure 2 shows that both species divided their exploratory digging very unevenly, with a decided concentration in the area immediately surrounding objects

in the arena (Wilcoxon signed-ranks test: *T. minimus*: $Z=2.38$, $n=9$, $P<0.02$; *T. striatus*: $Z=2.55$, $n=9$, $P<0.02$). Thus, when allowed to forage for caches in our naturalistic enclosures, *T. minimus* and *T. striatus* behaved as systematic pilferers who concentrated their efforts in predictable places. Although the two species both searched near objects, Fig. 2 also shows that eastern chipmunks engaged in over ten times more near-object searching than *T. minimus* (Mann-Whitney *U* test: $U=12.0$, $P<0.02$, $N=18$). This difference in search effort is to be expected, since most of the least chipmunk caches were not located near objects, thus prolonging the efforts of eastern chipmunks.

Pilfering Success

Least chipmunks discovered more eastern chipmunk caches and did so more quickly. Least chipmunks found all heterospecific caches (100% [92%, 100%]), over 20% more caches than they lost to eastern chipmunks (78% [36.5%, 97.1%]; Wilcoxon signed-ranks test: $Z=2.24$, $n=9$, $P<0.025$). Because we allowed animals to forage until they stopped exploring and became inactive, this comparison represents the best each species could do when unconstrained. In terms of seeds discovered (uncovered), *T. minimus* found a median of 172 (125.0, 250.0) seeds compared to 20 (2.0, 63.5) seeds found by *T. striatus*, a significant difference (Mann-Whitney *U* test: $U=2$, $N=18$, $P<0.01$). This difference is to be expected given the larger cache size of eastern chipmunks. Least chipmunks physically removed (consumed or re-cached) more seeds (66 [26.5, 92.0], $n=9$) than eastern chipmunks (32 [1.0, 63.5], $n=9$), a difference that is smaller and not statistically significant, and suggests that least chipmunks became satiated earlier in the observation period, explaining why they

stopped removing seeds from the caches. Yellow pine chipmunks are reported to display the same pattern of searching for, but not removing, seeds from uncovered caches as they become increasingly satiated (Vander Wall, 1991). This interpretation seems especially likely in view of the small size of least chipmunks and the large caches they found. To explore this possibility, we corrected for metabolic rate (see methods for complete details) and found that least chipmunks obtained more than three times the energy gained by eastern chipmunks (*T. minimus*: 70.24 [30.33, 112.43] Kcal/Kg$^{0.71}$ vs. *T. striatus*: 22.23 [0.68, 47.71] Kcal/Kg$^{0.71}$; *U*=13; *P*<0.02).

Least chipmunks found eastern chipmunk caches at more than ten times the rate of their counterparts (*T. minimus*: 6.88 [4.74, 14.51] caches/min exploratory digging vs. *T.striatus*: 0.53 [0.15, 1.47] caches/min; Wilcoxon signed-ranks test: *Z*=2.52, *n*=9, *P*<0.02). However, this difference does not take into account actual energy extracted from pilfered caches, nor does it take into account body weight, which discounts the value of each item obtained. To address these limitations, and because the movement of energy between and among caching species was a central focus of this study, we therefore analyzed the rate at which energy was gained or lost by interspecific theft. Thus, for this analysis, we were not concerned with the overall energy budgets of the chipmunks; rather, we were interested in how a single source of energy, in the form of cached sunflower seeds, was displaced between the two species. Digging time, a principal foraging cost in our study, was used to calculate the rate at which energy, in the form of seeds, was gained and lost. As can be seen in Fig. 3, the differences are dramatic. Compared to eastern chipmunks, least chipmunks obtained size-corrected energy units more than 100 times faster than eastern

chipmunks (Mann-Whitney U test: $U=2.0$, $N=18$, $P<0.001$), and the rate at which

least chipmunks inflicted energetic losses to eastern chipmunks was more than 15

times that of the losses they, themselves, incurred ($U=12$, $N=18$, $P<0.05$). Thus, least

chipmunks experienced considerable success relatively quickly while experiencing

only a small rate of loss.

Experiment 2: Conspecific Pilfering

Given the interspecific differences in cache placement and searching

strategies reported for heterospecific pilfering comparisons in Study 1, we were

interested in the extent to which both species succeeded in finding conspecific caches.

In particular, we predicted that eastern chipmunks, who, in Experiment 1

concentrated their pilfering efforts near objects, would fare much better in a search

for conspecific caches. Furthermore, a comparison of conspecific pilfering would

verify the extent to which the differences seen in Experiment 1 could be attributed to

species differences in caching behavior, searching strategies, or both.

Cache Construction and Placement

Most of the interspecific differences in caching behavior reported earlier were

also observed in Experiment 2. Eastern chipmunks buried seeds in similar quantities,

at similar depths, and at similar distances from objects ($P>0.05$ for all three

comparisons). Least chipmunks buried seeds at the same depth, and continued to

cache in open areas ($P>0.05$ for both comparison), but made somewhat larger caches

in the current experiment (13.7 [8.8, 18.1] seeds/cache), and therefore did not differ

significantly from eastern chipmunks (19.3 [14.1, 31.3] seeds/cache; $P>0.05$).

Searching Behavior

In Experiment 1, eastern chipmunks engaged in more than six times the amount of exploratory digging by least chipmunks. However, analysis of digging behavior in the current experiment revealed no species differences (*T. striatus*: 2.0 [0.9, 6.1] min; *T. minimus*: 2.0 [1.5, 4.3] min, $N=18$, $P>0.05$). To compare the current results to those from Experiment 1, we computed difference scores from the digging times of interspecific pairs in both experiments, and statistically compared the two sets of difference scores. We found that the interspecific differences in searching behavior seen earlier for heterospecific pilfering disappeared when animals searched for conspecific caches (Experiment 1: Median Diff=-4.8 [-25.0, -1.6]; Experiment 2: 0.4 [-1.1, 3.2], $N=18$, $U=12$, $P<0.02$).

Pilfering Success

The conspecific pilfering success of both species differed from their success at heterospecific pilfering reported for Experiment 1. When searching for conspecific caches, *T. minimus* and *T. striatus* did not differ significantly in the percentage of caches found (88.8% [77.5, 100.0] vs. 87.5% [71.4, 100.0] respectively, $N=20$, $U=41.5$, $P>0.05$) or the rate of cache discovery (3.3 [1.2, 5.7] vs. 2.9 [1.0, 7.6] caches found per minute of exploratory digging, respectively, $N=20$, $U=47.0$, $P=0.45$). As described above, we used difference scores to compare our findings from Experiment 1 and 2. We found that the interspecific differences in pilfering success reported for Experiment 1 disappeared when animals searched for their own species' caches in Experiment 2, as measured by the percentage of caches found (Experiment 1: Median Diff=0.22 [2.9, 5.8]; Experiment 2: Median Diff=0.00 [-0.1, 0.1], $N=18$, $U=16$,

P<0.03) and the rate of cache discovery (Experiment 1: Median Diff=6.20 [3.2, 14.1];

Experiment 2: 0.24 [-5.3, 3.2], *N*=17, *U*=5, *P*<0.01).

Further comparisons between the two experiments indicate that eastern

chipmunks are especially vulnerable to robbery. Least chipmunks found a higher

percentage of eastern caches (100%) than they did their own (88.8%; *N*=18, *U*=18.0,

P<0.05), and both species found eastern chipmunk caches at a higher rate than they

uncovered least chipmunk caches (*T. minimus*: 6.8 caches/min [Experiment 1] vs. 3.3

[Experiment 2], *N*=18, *U*=15.0, *P*<0.05 *U*; *T. striatus*: 2.9 caches/min [Experiment 2]

vs. 0.5 [Experiment 1], *N*=20, *U*=16.0, *P*<0.01).

Least chipmunks, on the other hand, are especially good at robbery. In

addition to excelling at heterospecific robbery (Experiment 1), they also stole other

least chipmunks caches with less effort than eastern chipmunks expended, finding

other *T. minimus* caches (Experiment 2) at a rate more than five times that of eastern

chipmunks (in Experiment 1) (*T. minimus*: (3.3 [1.2, 5.7] caches/min [Experiment 2]

vs. *T. striatus*: 0.5 [0.1, 1.4] cache/min [Experiment 1], *N*=18, *U*=16, *P*<0.05). Least

and eastern chipmunks did not differ statistically in their success at robbing *T. striatus*

caches (*T. minimus*: 6.8 [4.7, 14.5] caches/min [Experiment 1]; *T. striatus*: 2.9 [1.0,

7.6] caches/min [Experiment 2], *U*=25, *N*= 19, *P*>0.05).

GENERAL DISCUSSION

We modeled interspecific pilferage in a laboratory setting to determine if

smaller species that cannot succeed in direct competition could recoup at least some

of their losses through indirect competition. The possibility seemed likely because of

the known advantage of small body size—a magnified energetic value per given food item. Using the standard body weight correction for interspecific comparisons (Klieber 1947), we found that food items had twice the energetic value for the smaller species in this study. These benefits were magnified by the positive relationship between cache size and body mass (Jenkins & Breck, 1998; Price et al., 2000; Vander Wall et al., 1998), a trend that held in the current study, where the larger species filled their caches with about four times as many items. Therefore, the overall energetic value of a single eastern chipmunk cache was eight times greater to the smaller pilferer than to its owner. Of course, the value of the smaller least chipmunk cache was discounted by the eastern chipmunks' greater body mass, making the relative profitability of pilfering between these species even more disparate. Given the magnitude of the difference, it is reasonable to expect that at least a qualitatively similar asymmetry exists among naturally overlapping populations of chipmunks. Both are known to scatter-cache in natural settings and such caches are usually undefended, opening an opportunity for least chipmunks to narrow or close the overall competitive margin between the two species.

In Experiment 1, we set out to determine if and to what extent least chipmunks exploited this small-animal advantage, and whether or not either species employed tactics that mitigated the advantage. For this, we examined cache placement behaviors that might deter or invite robbery as well as search strategies that might improve or diminish the chances of robbery. We found that least chipmunks did exploit the potential advantage. They found all available eastern caches and did so quickly. The actual rate of standardized energetic gain was two

orders of magnitude greater than that observed for the larger species. While least

chipmunks were obviously adept at robbing their natural competitor, a major

behavioral reason for their comparative success lay in cache-placement and searching

tactics. We found that the smaller chipmunk species thoroughly exploited the

vulnerabilities of the larger species' cache-placement and construction tactics, but

that they, themselves, avoided such vulnerabilities.

Eastern chipmunks buried seeds in predictable places—around objects—but

T. minimus did not. Caching near prominent objects has been shown or suggested by

others to increase vulnerability to theft. Kangaroo rats (*Dipodomys merriami)* are

known to pilfer caches near small bushes and logs (Daly et al., 1992), and birds and

other mammals reportedly search near landmarks (e.g., Clarke & Kramer, 1994;

Vander Wall, 1982; Vander Wall, 1991) and arena walls (Jenkins & Breck, 1998;

Vander Wall, 1991) when foraging for conspecific caches. The object-directed

searching of least chipmunks in the present study is consistent with these reports.

Targeting the area surrounding objects readily led them to *T. striatus*' food stores.

This tactic was particularly successful because eastern chipmunks were found to

place their largest caches near objects. Like their smaller competitor, eastern

chipmunks also selectively searched around objects for potential caches. However,

the tactic failed for *T. striatus*, because *T. minimus* employed a countermeasure—

hiding most of their seeds well away from objects. This helped keep caches safe from

eastern chipmunks as they persisted in misplaced exploratory efforts. This

countertactic, together with small cache size, made heterospecific robbery by eastern

chipmunks a long and, ultimately, unprofitable activity. As seen in Experiment 1,

eastern chipmunks quite with more than twenty percent of available *T. minimus* caches still undiscovered. This was in spite of evident motivation to find the buried sunflower seeds, as revealed by the ingestion of every seed obtained and their persistence in trying to find more. Thus, the relatively small value of *T. minimus* caches apparently did not deter the pilfering efforts of eastern chipmunks, who engaged in more than ten times more exploratory digging of least chipmunks.

Although unsuccessful at robbing *T. minimus* caches, eastern chipmunks in Experiment 2 raided conspecific food stores relatively easily. Here, their area-restricted searching tactics targeted other eastern chipmunk caches, resulting in digging times and pilfering successs similar to that of least chipmunks in Experiment 1. Thus, it appears that *T. striatus* caches may lose their harvests to both heterospecific and conspecific competitors, and this vulnerability may explain their tendency to store so many seeds.

Least chipmunks were also successful conspecific robbers. In fact, they stole *T. minimus* caches at a greater rate (Experiment 2) than their heterospecific counterpart did (Experiment 1), which suggests that least chipmunks are particularly good at pilfering. Clearly, however, *T. striatus* caches are a more profitable target for least chipmunks, who not only find these caches more quickly and with less effort, but can harvest significantly more seeds once they find the caches.

Besides their greater value, the four-fold larger caches of eastern chipmunks almost certainly contributed to the smaller chipmunks' pilfering success reported for Experiment 1 in another way. Vander Wall (1991) reported that other species find more large than small artificial caches after digging in close proximity to cache sites,

and they find more shallow than deep artificial caches (Vander Wall et al., 2003), lending support to the assumption that odor cues increase with cache size and decrease with depth. Studies with other sciurids (e.g., McQuade et al., 1986) suggest that olfaction does not come into play for cache discovery until animals begin digging on or near a cache. This is especially true when the substrate is dry (Vander Wall, 1991; 2000), as in the present study. Consistent with this, as our chipmunks engaged in exploratory digging, they often buried their nose in the sand, and it was apparently an olfactory signal that shifted their behavior from searching to active excavation. This sequence of behavior is very similar to that of yellow pine chipmunks, as described by Vander Wall (1991). That least chipmunks were apparently relying on an olfactory signal to pinpoint cache sites was strongly suggested by a few instances in which they detected the exact location of a cache with no preliminary digging. It is possible that least chipmunks possess particularly keen olfactory sensitivity, but to date, there is no supporting evidence of such a hypothesis. Furthermore, Vander Wall (1991) reported similar indications of olfactory pinpointing of cache sites by yellow pine chipmunks pilfering conspecifics. This, coupled with the finding that *T. striatus* caches were pilfered with equal success by both least chipmunks (Experiment 1) and other eastern chipmunks (Experiment 2), leads us to conclude that the much larger eastern chipmunk caches released stronger signals. Therefore, the heterospecific pilfering success of least chipmunks in Experiment 1 is better explained by the vulnerability of *T. striatus* caches, rather than the olfactory ability of *T. minimus*. Thus, the difficulty of suppressing odor cues from large caches is one more

competitive disadvantage faced by larger animals. It is noteworthy that eastern chipmunks did not attempt to weaken the signal by deeper burial.

Interpretation of the lopsided pilfering advantage found for least chipmunks calls for some perspective. Pilfering has important consequences for hoarders, and is central to theoretical treatments of the evolution of hoarding behavior (Brodin & Ekman, 1994; Clarkson et al., 1986; Smith & Reichman, 1984; Smulders, 1998). Of particular interest is how animals can tolerate the high levels of robbery frequently reported (e.g., Clarke & Kramer, 1994; Daly et al. 1992). Vander Wall & Jenkins (2003) point out that much robbery may be "reciprocal" between and within species, perhaps with little net loss to individuals. However, unreciprocated interspecific robbery could be more problematic. If our findings extend to the naturally coexisting populations of chipmunks used in this study, then we have identified an instance of nonreciprocity, and one that could potentially exist among other communities of caching animals. However, it is likely that uneven reciprocity among animals of differing size could still promote community stability by maintaining competitive equilibrium. A simulation study indicates that the interspecific exchange of resources from cache robbery may enhance and stabilize the population growth of multiple species, and that the growth of a single species may be enhanced indirectly by increased interspecific pilfering ability (Price & Mittler, 2003).

In keeping with this perspective, we note that despite the seemingly extravagant gains obtained from robbery, the smaller chipmunks in our study inflicted relatively small losses on their larger competitor. While it is true that least chipmunks in Experiment 1 discovered all eastern chipmunk caches, they stopped eating and re-

caching after taking only about 33% of the larger animals' stores. Even if this laboratory pilferage rate held for natural settings, the loss sustained by eastern chipmunks would probably not be devastating. But, we suspect that actual losses would be smaller. For example, in our study, caches were the only source of food available and time was practically unlimited. In nature, other food sources are present and time is limited. Under a more realistic scenario, the two species could strike a balance between competition for primary resources and indirect competition for harvested resources, permitting stable species coexistence, consistent with Price and Mittler's (2003) analysis.

Unlike hoarding, the origins of pilfering behavior have received little attention. Clearly, robbers need victims, so it is likely that pilfering behavior emerged later. We cannot offer a formal evolutionary account of pilfering, but can point out some interesting associations that bear further analysis. For instance, the results of the present study are consistent with those of others in showing that ground-caching birds (e.g., Balda, 1980; Bossema, 1979; Bugnyar & Kotrschal, 2002) and rodents (Jenkins & Breck, 1998; Vander Wall, 1991) preferentially put caches near natural objects and borders. Paralleling this is the bias of pilferers to search around just such objects and borders (birds: Tomback, 1977; Vander Wall, 1982; rodents: Clarke & Kramer, 1994; Daly et al., 1992; Jenkins & Breck, 1998; Vander Wall, 1991; Vander Wall & Peterson, 1996). Historically, in searching for their own caches, animals are therefore likely to have stumbled on those of others. It would not be a large step for pilfering to evolve from phenotypes making just such adventitious discoveries. That animals actively search for others' caches in field or arena experiments where they have

hidden no food themselves is an indication that robbing has become independent of caching. But that robbers still search where they prefer to put their own caches suggests that the independence is not complete. It is in this regard that least chipmunks are exceptional—their pilfering searches are not the same as their preferred caching sites. Like most terrestrial cache robbers, they search around objects, but unlike them, they hide the majority of their caches away from objects, where others are not inclined to look. Least chipmunks display an unambiguous dissociation between the tactics used for caching and those used for pilfering. Perhaps similar dissociations will be found for other small competitors.

Small size has been linked to several behavioral adaptations. Smaller heteromyid species, in particular, are especially efficient foragers who can take advantage of lower quality food patches. Compared to larger animals, small species experience higher net gains for their locomotive foraging efforts (Morgan & Price, 1992), higher seed encounter rates (Ovadia et al., 2001), and are less sensitive to variance in patch profitability (Price, 1983). Although such foraging benefits have not been investigated in least chipmunks, it is not unreasonable to assume that they exist, given the wide distribution of *T. minimus* and their overlap with a variety of larger congeners. Likewise, it is likely that the pilfering gains enjoyed by least chipmunks in the current study extend to other small caching rodents (e.g., *Chaetodipus* spp, Leaver & Daly, 2001) and other species, helping to explain their competitive equilibrium.

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Figure 1. Relationship between cache-object proximity and object density for the first three caches made. Scatterplots and regression lines are given for scatter-caches made by *T. minimus* (filled circles) and *T. striatus* (open circles). Correlation coefficients and *P* values are shown for each species.

Figure 2. Exploratory digging near ($\leq$ 5 cm) (■) and away (▨) from objects by chipmunks when foraging for heterospecific caches. Values indicate median time spent digging, corrected for opportunity (area available near or away from objects). Both species dug more near objects (*n*=9; Wilcoxon signed-ranks test). In addition, *T. striatus* spent significantly more time searching near objects than *T. minimus* (*N* =18; Mann-Whitney U test).

Figure 3. Median rates of standardized caloric gains from pilfering (■) and losses to pilferers (▨). Values are represented as Kcal obtained or lost per minute of exploratory (off-cache) digging, standardized for body size (*N*=18; Mann-Whitney U test).
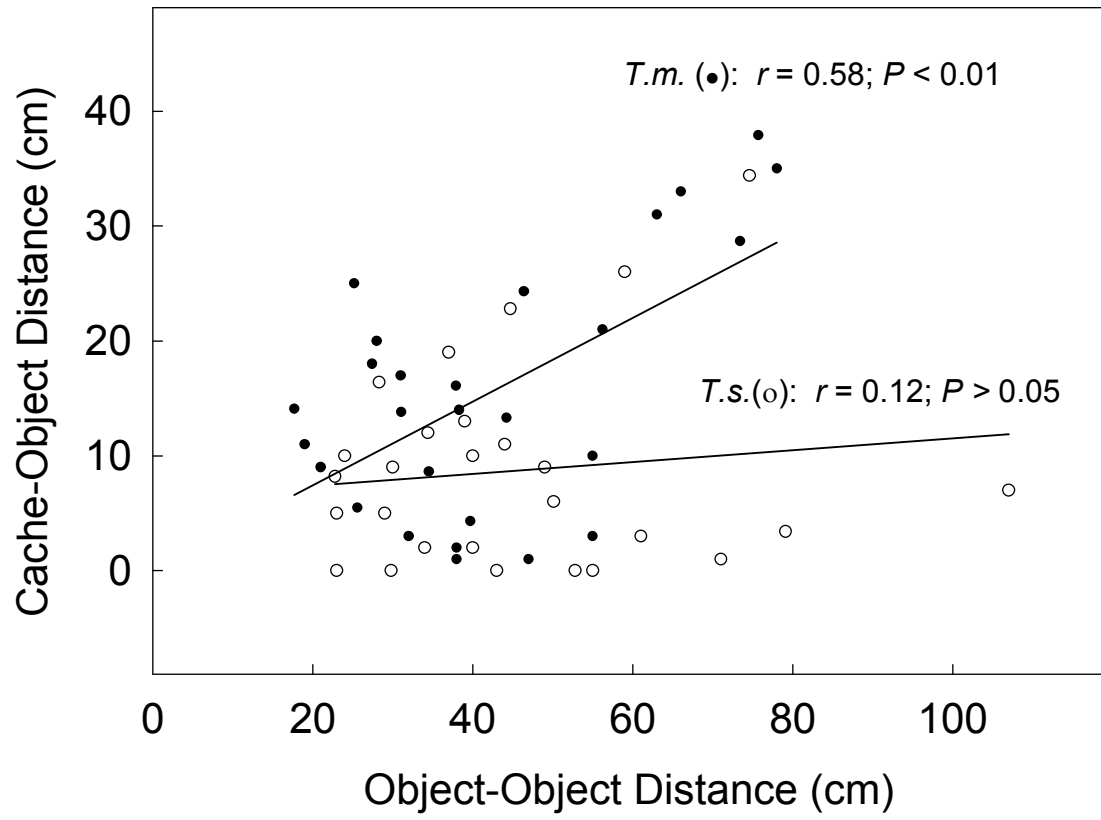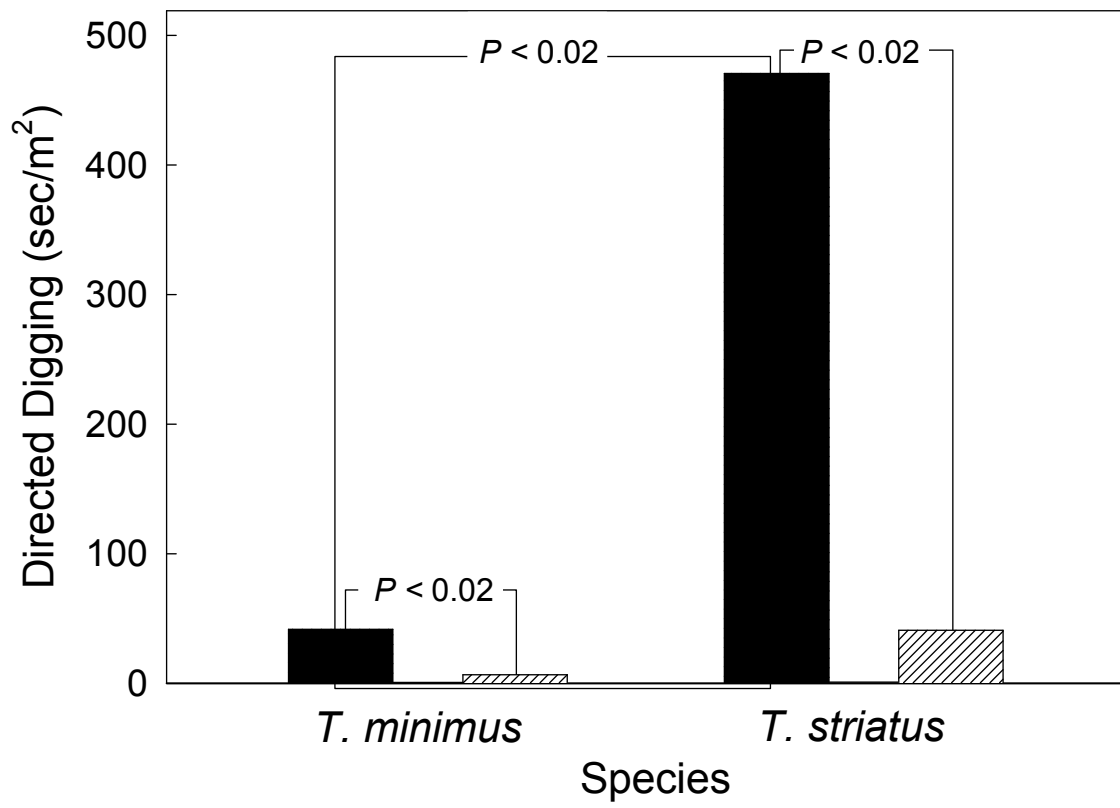
Figure 1

Figure 2

Figure 3
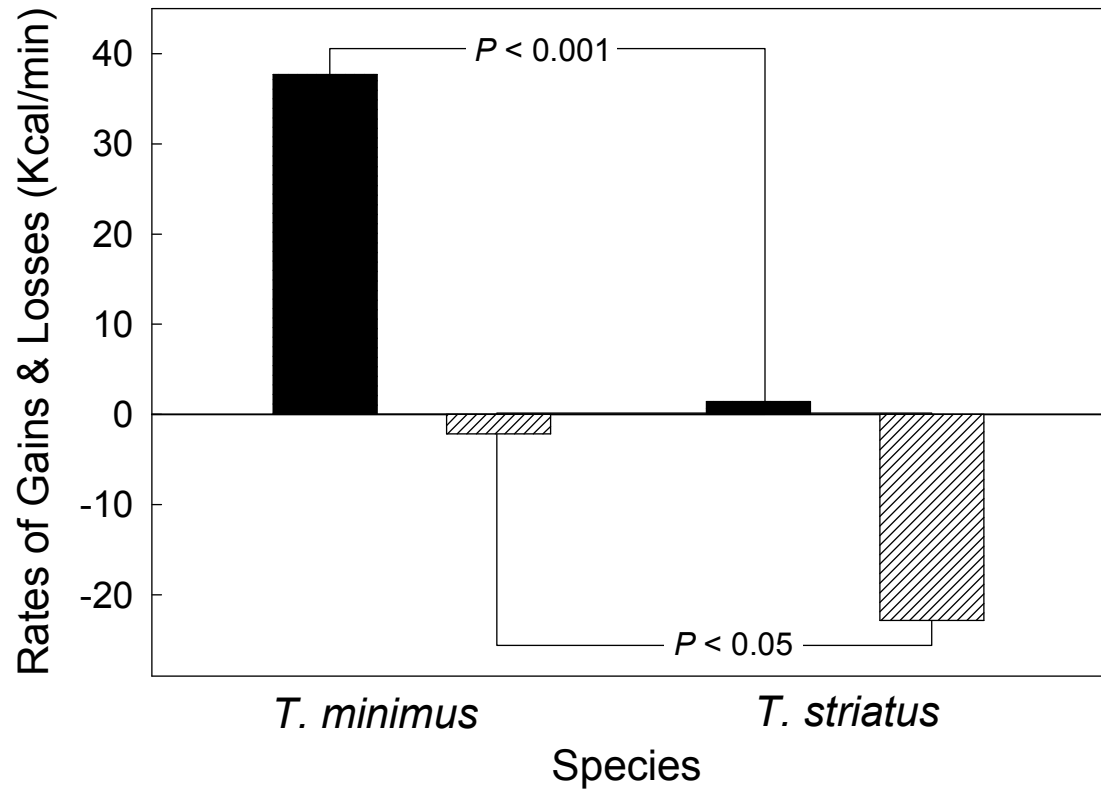
Chapter 2

Spatial Memory and Proximal Cues as Mechanisms of Cache Recovery

Scatter-cachers bury relatively small, widely dispersed quantities of seeds among multiple locations, and rely largely on memory to recover their caches for later consumption. In addition, proximal cues at cache sites, such as visual beacons, soil disturbances, and odor cues may also draw owners to their stored food. Importantly, the strength of these cues depends on the caching strategy of the owner. Thus, for scatter-caching animals, placement and construction strategies may be important predictors of recovery mechanisms. To investigate this relationship, I allowed two chipmunk species, known to differ in their caching behavior, to search for their caches when their food stores were intact (Treatment 1), and when caches, along with nearby substrate, were removed (Treatment 2). I found that both species exceeded chance in finding their cache sites under both conditions. Furthermore, it appears that eastern chipmunks, who preferentially cache near objects, can navigate to their hidden food by restricting their searching efforts around landmarks. Least chipmunks, on the other hand, probably rely on knowledge of individual cache sites, possibly in conjunction with olfaction, to recover their food stores which are typically buried in open areas.

Scatter-caching birds and mammals exploit temporary food bonanzas by hiding small quantities of food among multiple locations for later consumption. By storing food and eating it later, animals can quickly sequester food that would otherwise be available to competitors, while at the same time amassing food stores for periods of scarcity (Vander Wall 1990). Successful recovery of caches poses special challenges to owners. Since scatter-caches are dispersed and nearly indefensible, they should be buried in a way that deters pilferers but not owners in order for caching to be sustained as an evolutionarily stable strategy (Andersson & Krebs 1978; Stapanian & Smith 1978; Clarkson et al. 1986). Indeed, numerous behavioral studies, mostly with birds, have demonstrated that animals find relatively high proportions of their own caches compared to conspecific or artificial caches.

Successful relocation of cache sites has been attributed to several spatial orientation mechanisms. Cues emanating from the caches themselves may elicit excavation, representing probably the easiest form of relocation. Microtopograhical cues, such as soil disturbances or clumps of leaf litter can aid cache discovery (Clarke & Kramer 1994; Johnson & Jorgensen 1981; Murie, 1977). In particular, odor cues are especially salient for foraging rodents who are more likely to detect conspecific or artificial caches that are large (Vander Wall, 1991; Vander Wall et al., 2003; Chapter 1), shallow (Geluso 2005; Vander Wall et al., 2003; Johnson & Jorgensen 1981), buried in moist substrate (Geluso 2005; Vander Wall 1995; 1998; 2000; Johnson & Jorgensen 1981), or are themselves moist (Vander Wall 1993; 1998; Murie 1977). Not surprisingly, the relationship between size and depth is especially pronounced in damp environments (Geluso 2005). Few studies have pinpointed animals' reliance

on odor cues when recovering their own caches, but those that have suggest that the use of olfaction may vary across species. Devenport et al. (2000) found that ground squirrels returned to all of the cache sites even when contents were removed and substrate had been replaced. Thus, for ground squirrels, odor plays at most a minimal role. For other species, the use of olfaction may depend, at least to some extent, on the way in which caches are constructed. For instance, chipmunks (*spp. Tamias*) more quickly find large caches (Vander Wall 1991) or caches buried in sand compared to ash (Briggs & Vander Wall 2004).

On a larger scale, prominent landmarks can serve as visual beacons, guiding animals to their cache sites (Gallistel 1990). Visual cues are quickly associated with potential cache locations (Vander Wall 1996; Clarke & Kramer 1994; Payre & Longland 2000), which explains why robbers concentrate their foraging efforts near visual beacons (Vander Wall 1991; Daly et al. 1992), targeting the food stores of animals who preferentially cache there (e.g., Jenkins & Breck 1998; Vander Wall 1982; Tomback 1977; Chapter 1).

In addition to providing direct cues at cache sites, landmarks may also serve as more subtle cues. By learning and remembering the geometric relationships among multiple landmarks and hidden caches, animals can navigate more flexibly by employing new routes to otherwise unmarked locations (e.g., Kamil & Jones 1997; Goulde-Beierle & Kamil 1996; Gibson & Kamil 2001). This more complex form of spatial memory arms cache owners with an internal representation of their cache sites—one that, unlike other cache relocation mechanisms, cannot be easily exploited by competitors. Such navigational skills and their neurological substrates have been

demonstrated repeatedly, mostly among birds, as a primary mechanism of cache relocation (see Shettleworth 2000; Healy et al. 2005 for reviews). Fewer studies have investigated cache recovery in mammals, but those that have suggest similar reliance on memory for cache sites (Devenport & Devenport 1994; Devenport et al. 2000; Jacobs & Liman 1991; Macdonald 1976).

It is likely that all of these spatial orientation mechanisms—microtopographic and odor cues, visual beacons, and spatial memory—are used in combination, and probably in succession. While animals depend on spatial memory to guide them to the general vicinity of their caches, they subsequently rely on more proximal cues present at or near the cache site to pinpoint exact locations. Presumably, the strength of visual and olfactory signals depends on the caching strategy of the cache owner. However, to date, few studies have addressed the relationship between cache placement strategies and subsequent retrieval mechanisms. Devenport et al. 2000 reported that a relatively cryptic cacher (*Spermophilus tridecemlineatus*) pinpointed cache sites, even in the absence of visual beacons and odor cues, indicating a heavy reliance on memory (although the authors suggested soil compaction as a proximal cue). Other studies have demonstrated clear interspecific differences in caching behavior (e.g., Jenkins & Breck 1998; Thayer & Vander Wall 2005), however, the degree to which species-specific consistencies in caching behavior predict retrieval mechanisms remains largely unexplored.

Therefore, I set out to examine the relative reliance on proximal cues during cache retrieval by two species known to differ in their caching behavior. Least chipmunks (*Tamias minimus*) bury relatively small caches, and prefer to cache in

open areas away from objects. In contrast, eastern chipmunks (*T. striatus*), make

larger caches and prefer burying them near prominent objects (Chapter 1). I assessed

both species' success at recovering cache sites when their caches were intact

(Treatment 1) or after cache contents were removed and the substrate had been

replaced (Treatment 2). In both parts of the experiment, I eliminated

microtopographic cues by raking over the sand at cache sites. However, I did not

alter visual cues (prominent objects in the foraging arenas) in either treatment, since

the spatial layout of objects is an integral component of spatial memory (Gallistel

1990).

Thus, the primary aim of this study was to tease apart the reliance on two

mechanisms known to assist mammals in relocating their stored food—a more global

navigational system (spatial memory) and proximal cues at cache sites. A second aim

was to establish a correlation (if any) between relocation mechanisms and cache

placement tactics by comparing the recovery success of two chipmunk species who

use different caching strategies.

GENERAL METHODS

Subjects

Subjects were 26 eastern and 20 least chipmunks of both sexes that had either been

wild-caught at Seney National Wildlife Refuge in Seney, MI or were adult offspring

of wild-caught parents. Animals were captured during the summers of 2002 and 2003

from sympatric or parapatric populations using procedures described in Devenport et

al. (1998), and then transported to the Animal Cognition Laboratory at the University

of Oklahoma.   Here, they were implanted with identification microchips and given fur markings. Chipmunks were then housed in naturalistic enclosures with conspecifics and fed rodent pellets, seeds, nuts, and fresh produce. Animals had constant access to fresh water and minerals, and were kept on an artificial light:dark cycle that fluctuated seasonally.

Approximately one week prior to caching sessions, animals were removed from their group housing areas and transported to individual, polyurethane, litter-filled nest cages where they had access to rodent pellets and fresh water but no seeds (to induce caching). Animals remained housed in these nest cages until recovery sessions were complete, at which point I returned the chipmunks to their group housing areas.

Materials and Procedures

Caching and recovery sessions were conducted in one of two 1.8 X 1.8 m Plexiglas enclosures containing 6-8 cm of medium-grade sand. Four to five prominent objects were scattered throughout each arena, including logs, tree stumps with attached water bottle, running wheels, rocks, and concrete cinderblocks. I videotaped and observed caching and test sessions remotely.

Caching Sessions

Approximately 30 min prior to caching sessions, I transferred individual chipmunks to single foraging arenas. When animals had adequately explored the room (as evidenced by their footprints throughout the sand), I initiated caching sessions by provisioning animals with a small bowl of unhulled sunflower seeds (black oil type). Typically, chipmunks readily consumed some seeds, and then began caching.

However, some animals were more reluctant, so session length varied, usually lasting about 45 min. To establish conditions of roughly equal opportunity during recovery sessions, I attempted to obtain a similar number of caches from each chipmunk. Therefore, I systematically ended each caching session after eight to ten caches had been buried.

Following caching sessions, I located caches and uncovered them to measure for size and depth. I wore unscented gloves to take measurements, since human scent can indicate the presence of seeds to foraging animals (Duncan et al. 2002). Depending on the treatment, caches were then either left intact or removed from the foraging arena (described below).

Relocation sessions

One to two days after caching sessions, I returned animals to their respective arenas where they were allowed to forage for their caches. During live viewing, I recorded order and percentage of caches found, and noted any re-caching for later removal. Videotaped sessions were later transcribed, during which specific behaviors were timed and analyzed. These measures included time engaged in excavation (on-cache) digging and exploratory (off-cache) digging. To determine if either species engaged in area-restricted searching, I further categorized exploratory digging into that done near (≤ 5 cm) and away from objects (> 5 cm).

Data analysis

Nonparametric analyses were used to analyze data within and between treatments, and descriptive statistics are reported as medians and interquartile ranges (as outlined

in Chapter 1). In addition, data was truncated and pooled for some comparisons to avoid pseudo-replication (after Leger & Didrichsons 1994; see Chapter 1).

RESULTS

Treatment 1: Recovery with caches present

<u>Methods</u>

My aim in this condition of the experiment was to assess and compare both species' success in finding their own caches when cache contents and consequently olfactory cues were present. Thus, I set out to determine chipmunks' recovery success when allowed to rely on spatial memory as well as odor and visual cues.

My subjects were seven least chipmunks and eleven eastern chipmunks. Following caching sessions and measurements (described in General Methods), I reburied the caches to match as closely as possible their original location, depth, and size. I then smoothed over the sand to eliminate microtopographic cues, further restoring the original condition of most cache sites. This process was completed at least 24 h before relocation sessions.

Since many animals cached more seeds than could be uncovered and/or eaten in a single foraging session, chipmunks were tested for up to two hours and often over two consecutive days. Recovery sessions ended after all caches had been found or after animals became inactive following prolonged foraging efforts. Most of the time, chipmunks consumed, pouched, or re-cached their recovered seeds. In some instances, however, they dug briefly at a cache site as if to confirm its location, and then re-covered it with sand. Thus, both of these behaviors were counted as

successful recoveries. All other measures, analyses, and comparisons of foraging success were conducted as described under General Methods. Analyses were conducted on a sample size of eighteen unless noted otherwise.

Results: Cache Placement & Construction

Least and eastern chipmunks constructed and distributed their food stores differently. *T. striatus* made larger caches (18.6 [14.5, 29.2] vs. 5.0 [2.2, 5.8] seeds per cache; $U=3$, $P<0.01$), yet buried them at a statistically equivalent depth (1.9 cm [1.2, 2.4] vs. 1.5 cm [1.1, 1.7]; $P>0.05$). Eastern chipmunks consistently buried seeds closer to objects in the foraging arena (5.2 [2.4, 7.8] cm), while least chipmunks preferred open areas (17.1 [13.8, 18.3] cm; $U=0$, $P<0.001$). Furthermore, least chipmunks appeared to target open areas. That is, as object-density increased, *T. minimus* cached farther from objects ($r=0.49$, $P<0.05$, $N=21$). However, eastern chipmunks cached near objects regardless of inter-object distance ($r=0.02$, $P>0.05$, $N=33$), differing significantly from least chipmunks ($t=5.58$, $P<0.001$, $N=54$). (To avoid pseudo-replication, only the first three data points from each subject were analyzed in the preceding regressions; after Leger & Didrichsons 1994).

Results: Cache Recovery

Both least and eastern chipmunks found all of their caches over the 2-day test period (100% [100.0, 100.0] for both species, $P>0.05$). Both chipmunks engaged in similar amounts of exploratory digging (*T. minimus*: 22.1 [5.8, 165.2] sec vs. *T. striatus*: 36.5 [9.2, 353.1] sec, $P>0.05$). Consequently, no statistical differences were found for rates of cache discovery (*T. minimus*: 29.5 [2.4, 101.9] caches/min vs. *T. striatus*: 3.0 [1.3, 35.3] caches/min, $P>0.05$).

Treatment 2: Relocation with caches removed

Method

My goal in this condition of the experiment was to assess chipmunks' accuracy in remembering their cache sites when odor cues were missing. Subjects were nine least and eight eastern chipmunks. Following caching sessions, caches were relocated, uncovered, and measured as described under General Methods. However, unlike Treatment 1, I removed all caches from the foraging arenas. To further eliminate odor cues at cache sites, left by either the animal (e.g., Devenport et al. 1999) or sunflower seeds, I displaced the sand by shoveling and raking, and then removed about one quarter of the sand, replacing it with a mixture of new and previously used sand. The sand was then raked smooth, and any objects moved during the replacement process were restored to their original position.

Since cache contents, along with any remaining olfactory cues, were absent in this condition, I defined a cache as "found" when its owner dug at or around the original cache site. Cachers have been shown to locate their sites within 5 cm (MacDonald 1997); however, the resolution of my video equipment allowed me to assess digging behavior occurring within 4 cm of cache sites. Thus, animals were recorded as having found caches if they dug within an 8 cm diameter of the original site. In almost all cases, animals eventually dug at their caches; however, least chipmunks sometimes ran directly to sites and then lingered briefly without digging. Therefore, I also counted a cache as "found" when an animal paused for at least 3 s within the 8 cm diameter of the cache site. An independent observer confirmed that

both of these criteria adequately distinguished animals' behavior at cache sites from that of random foraging.

All other measures, analyses, and comparisons of foraging success were conducted as described under General Methods. Analyses were conducted on a sample size of seventeen unless noted otherwise.

Results: Cache placement and construction

Eastern chipmunks cached in a manner consistent with the findings of Treatment 1 (for between-treatment comparisons of cache size, depth, and cache-object distance, $P>0.05$, $N=19$). Least chipmunks made similar-sized caches (for between-treatment comparison, $P>0.05$, $N=16$). However, compared to Treatment 1, *T. minimus* in Treatment 2 buried caches at slightly shallower depths (0.9 [0.8, 1.2] cm; $U=9.0$, $P<0.05$, $N=16$) and placed them in closer proximity to objects (12.0 [5.3, 14.2], $U=12.0$; $P<0.05$, $N=16$). It is unclear why least chipmunks' behavior in the current study differed somewhat from earlier observations (i.e., Treatment 1 of the current study; Chapter 1), but it is a point to which I will return later.

Results: Cache relocation

Despite the absence of olfactory cues, the success demonstrated in Treatment 1 persisted, with both species finding nearly all of their cache sites, although *T. striatus* relocated significantly more when caches were absent than did *T. minimus* (100% [87.5, 100.0] vs. 80% [41.6, 92.8]; $U=14.0$, $P<0.05$). Compared to their success when caches were present, least chipmunks in Treatment 2 found fewer of their caches ($U=10.0$, $P<0.05$), while eastern chipmunks performed similarly ($P>0.05$).

Random foraging alone might result in digging at some cache sites. Therefore, to determine if either species' relocation success was higher than expected from chance alone, I compared the percentage of actual caches found by each animal to the likelihood of such success, based on the area occupied by their caches. For each animal, I computed the percentage of available foraging area contained by the cumulative area of their "found" caches (including the 8 cm diameter surround the sites)—that is, the probability of encountering caches via random search. For both species, the high percentages of actual caches found (100% and 80%) exceeded chance, since on average, cache area accounted for only 0.09% of the available foraging area. Thus, in the absence of olfactory cues, both species were remarkably accurate in relocating their cache sites.

Both chipmunks engaged in very little exploratory digging or searching behavior (*T. striatus*: 39.1 [4.1, 620.1] s; *T. minimus*: 24.9 [9.7, 88.2] s; $P>0.05$) and were quick to locate cache sites, on average finding about seven caches per minute of exploratory digging (*T. striatus*: 8.7 [0.5, 34.9] caches/min vs. *T. minimus*: 5.3 [3.3, 29.9]; $P>0.05$).

Interestingly, eastern chipmunks concentrated their searching efforts near objects, engaging in little to no digging in open areas (30.7 s [4.1, 452.8] near objects vs. 0 s [0, 167.4] away from objects; $Z=2.36$; $P<0.05$). This behavior is not only consistent with other species who search near objects for caches (e.g., Vander Wall 1982; 1991, Daley et al. 1992), including other eastern chipmunks (Chapter 1), but also practical, since their own caches are often placed near such objects (Chapter 1). Least chipmunks displayed the same pattern of near-object searching (as found

previously in Chapter 1), but the difference was not statistically significant (23.0 s [3.7, 65.5] near objects vs. 5.5 s [0.4, 16.2] in open areas, $P>0.05$).

Eastern chipmunks dug at their cache sites more quickly than least chipmunks, as evidenced by shorter latencies to find their first cache (1.2 [0.7, 1.9] min vs. 4.1 [1.2, 16.8] min; $U=15.0$, $P<0.05$) and to find the first half of their caches (3.8 [2.8, 5.8] min vs. 17.1 [8.0, 26.8] min; $U=5.0$, $P<0.01$). Too few least chipmunks (only two) found all of their caches to yield a meaningful interspecific comparison of latency to find 100% of subjects' caches, and so this analysis was not computed.

Upon discovery that their cache sites were empty, least and eastern chipmunks showed marked differences in their subsequent behavior. Eastern chipmunks dug vigorously and persistently, frequently returning to previously visited sites, and often burrowing in and out of the sand, sometimes reaching the floor of the foraging arena. Least chipmunks, on the other hand, engaged in very little excavation digging, often just swiping at cache sites, and sometimes never returning. Consistent with other reports of *T. minimus* foraging behavior (Devenport et al. 1998, 1999), least chipmunks appear to avoid depleted patches. The interspecific difference in on-cache digging time was statistically significant (*T. striatus*: 175.2 [60.0, 240.1] s; *T.minimus*: 8.6 [6.9, 39.5] s; $U=9.0$, $P<0.01$).

DISCUSSION

The aim of this study was to assess the relative reliance on spatial memory compared to more proximal cues at cache sites in cache reloation. The distinct caching strategies of the two species under investigation suggested that proximal cues

might be more salient for eastern chipmunks (who bury relatively large caches next to prominent objects) and less so for least chipmunks (who bury small caches well away from objects; see Chapter 1). Thus, a second aim was to determine if species' cache recovery mechanisms varied in any way with their cache placement and construction strategies. In Treatment 1, both species searched for their caches in dry sand when both olfactory stimuli and landmarks were present, thus mimicking to some extent natural foraging conditions. In Treatment 2, animals searched for cache sites after microtopographic and odor cues had been experimentally eliminated. Importantly, landmarks were left in place since animals can use individual objects as visual stimuli or multiple objects to encode the layout of the area.

In Treatment 1, both species readily found their cache sites when given ample foraging time and expended similar effort (as measured by exploratory digging times) to do so. However, such high success under these conditions (100% for both species) is not necessarily attributable to memory alone, since both microtopographic and odor cues were also present.

When olfaction was eliminated as a viable searching strategy in Treatment 2, chipmunks nevertheless located their cache sites. Even though these sites occupied only a small percentage (less than 1%) of the foraging arena, animals quickly pinpointed most of them. Importantly, in Treatment 2, visual stimuli were left in place. Thus, any animals that preferentially cached near objects could increase the likelihood of recovery simply by concentrating their searching efforts around local beacons. Indeed, eastern chipmunks, but not least chipmunks, engaged in significantly more near-object exploratory digging, although *T. minimus* showed a

similar trend. Given the species-specific caching patterns reported earlier (Chapter 1) and for Treatment 1, this interspecific difference in foraging behavior is not surprising—eastern chipmunks search where their caches are typically placed.

Why least chipmunks shifted their cache placement strategy—burying caches closer to objects in Treatment 2—is unclear. In both Treatment 1 and in other caching studies (Chapter 1), compared to eastern chipmunks, least chipmunks clearly and consistently avoided objects. One possible explanation is the time of year in which caching was observed. Treatment 1 and experiments reported for Chapter 1 were conducted in the spring, summer or fall while about half of the observations for Treatment 2 fell during late winter (January and February). Least chipmunks are unique in that some of their caches consist of single, large boluses of around thirty hulled seeds sealed together with a thick layer of saliva (Devenport et al. 2001), while most others consist of just a few unhulled seeds.   In Treatment 2, least chipmunks that cached during winter ($n=4$) cached boluses nearly 100% of the time, while chipmunks observed during the spring and fall ($n=5$) buried boluses only 43% of the time. This resulted in a tendency for *T. minimus* caches to be larger in Treatment 2 compared to Treatment 1, albeit a nonsignificant one (19.2 vs. 5.0 seeds per cache). Thus, least chipmunks may construct, and possibly distribute their caches differently depending on the season. This seasonable variability may explain the converging interspecific patterns reported for Treatment 2 and is a trend that deserves closer investigation.

Although both species exceeded chance in relocating their cache sites when odor cues were removed, least chipmunks appeared to be somewhat affected by the

absence of odor. *T. minimus* experienced lower recovery success than *T. striatus* under the same conditions (Treatment 2). Perhaps even more important is the finding that least chipmunks in this condition (compared to those in Treatment 1) found significantly fewer caches in the absence of olfactory cues. This disparity suggests that odor plays a role in cache retrieval for least chipmunks. The absence of odor cues in the second treatment may have deterred least chipmunks, a species known to avoid depleted patches (Devenport et al. 1998; 1999). But even when intact, *T. minimus* caches probably emit very little odor, especially since they were much smaller and buried in dry sand (Geluso 2005; Vander Wall et al., 2003; Johnson & Jorgenson 1981). In fact, Vander Wall suggests that odor cues are relatively nonexistent for seeds buried in dry sand at similar depths and quantities to those reported in the current study. Yellow pine chipmunks could not find experimenter-made caches containing up to 25 seeds buried at only 10 mm unless seeds were hydrated (Vander Wall 1991), nor did they find many 20-seed caches buried as shallow as 20 mm (Vander Wall et al. 2003). Other rodents can detect seeds at depths similar to those reported here, but only when there are many (40-100 seeds) (Geluso 2005; Johnson & Jorgensen 1981). Together, these reports suggest that *T. minimus* buries seeds in quantities and at depths that are relatively undetectable. Thus, any reliance on odor cues in the current experiment was probably minimal.

An alternative explanation for the decline in foraging success of *T. minimus* when odor cues were absent could be the criteria used during recovery sessions. I required animals to dig or pause within an 8 cm radius of cache sites. Perhaps a more liberal criteria (i.e, larger radius) would have yielded different findings. Additionally,

least chipmunks engaged less frequently in continuous digging bouts than did eastern chipmunks. Their digging behavior is instead best described by "scratch-digging" (Morgan & Price, 1992). These brief, sporadic digs are probably adequate for least chipmunks to recognize that a cache has been depleted. However, this type of digging is more difficult to detect and to recognize on videotape. Thus, it is possible that some digging at cache sites, and therefore cache recoveries, were not observed and recorded.

In all, the comparative success of *T. minimus* is consistent with the use of spatial memory. Apparently, least chipmunks rely on their knowledge of specific cache sites to lead them to vicinity of their caches, at which point odor guides them to exact locations. To my knowledge, only two other studies have assessed the ability of mammals to relocate their caches in the absence of odor cues. In a laboratory experiment similar to the current one, yellow pine chipmunks found less than 40% of their caches when the substrate had been replaced (Vander Wall 1991). The recovery success of *T. minimus* in the current study is closer to that reported for thirteen-lined ground squirrels. From a suite of field experiments, Devenport et al. 2000 reported that ground squirrels recovered all of their cache sites even after contents were removed and overlying sod was replaced.

If least chipmunks do indeed rely partially on olfaction, they are not alone. Yellow pine chipmunks and long-eared chipmunks (*T. quadrimaculatusi*) find roughly 80% of their caches under dry conditions, recovery rates similar to those exhibited by naïve foragers (Vander Wall 2000; Briggs & Vander Wall 2004). Additionally, when odor cues are further reduced (by allowing animals to recover

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caches buried in ash substrate), performance worsens for yellow pine but not long-eared chipmunks (Briggs & Vander Wall 2004), suggesting that olfaction may be a more important cue for *T. amoenus*. It would be interesting to see if this difference is correlated with any interspecific differences in caching strategies.

Least chipmunks may have particularly sensitive olfactory abilities, and thus are hindered the most by the absence of odor cues. However, there is no evidence to date to support the hypothesis that least and eastern chipmunks differ in olfactory sensitivity. Furthermore, it is important to note that least chipmunks still found nearly all (eighty per cent) of their empty cache sites. If *T. minimus* had been relying mostly on olfaction to relocate their caches, their success would have been much lower.

Eastern chipmunks in both conditions of the experiment were equally successful, indicating that olfaction may play only a small role in cache retrieval for this species. *T. striatus* apparently also relies on memory for caches sites. Eastern chipmunks preferentially placed and searched for their caches close to objects in both treatments. Thus, eastern chipmunks appear to use objects less to learn complex geometric relationships (i.e., to "map" their environment), and more to form simple visual associations. By using landmarks as beacons to guide them towards places where they usually cache, eastern chipmunks increase their foraging success. This strategy is not without cost, since it is one that can be exploited by pilferers (e.g., Chapter 1, Daly et al. 1992; Clarke & Kramer 1994; Vander Wall 1991; 1995).

Proximal visual cues are known to contribute to memory for cache sites. For many birds, disturbance of local cues has little effect on cache recovery rates as long as more distal cues are preserved (Herz et al. 1994; Gould-Beierle & Kamil 1996). For them, local cues become less necessary as long as the global layout of the naturalistic study areas (confirmed by distal cue constancy) remains the same, indicating that animals navigate according to their knowledge of the geometric layout of their environment (Kamil & Jones 1997; 2000).

However, foragers can also use landmarks to navigate without the cognitive costs of spatial mapping. Area-restricted searches near objects can guide animals to cache sites. For instance, gray jays (*Perisoreus canadensis*) retrieve more of their caches when additional landmarks are situated near cache sites (Bunch & Tomback 1986). Furthermore, when searching for artificial caches, yellow pine and eastern chipmunks are quick to find caches marked with experimenter-placed flags, stakes, or twigs (e.g., Clarke & Kramer 1994; Vander Wall 1996). In addition, scatter-caching heteromyid rodents concentrate their searching efforts near naturally occurring seedlings (Pyare & Longland 2000).

As beacons, visual cues may play a relatively prominent role in cache recovery. In a carefully controlled laboratory experiment, McQuade et al. (1986) systematically displaced local visual cues, odor cues, or distal arrays of landmarks after gray squirrels (*Sciurus carolinensis*) had learned the location of buried seeds. Squirrels had the most difficulty locating these learned sites when local visual cues were switched. The disturbance of distal landmarks impaired the squirrels' behavior less, but had more of an impact than did changes in odor cues. Thus, gray squirrels

rely most heavily on visual cues (beacons), less on distal arrays of landmarks, and least on olfaction to relocate learned sites. Visual cues are apparently important indicators for eastern chipmunks as well.

The way that eastern chipmunks situate their caches makes visual association a profitable foraging strategy for this species. Prominent objects are consistent indicators of likely cache sites, and this is exactly where eastern chipmunks search. It should be noted that the directed searching strategy employed by eastern chipmunks significantly reduces the amount of potential foraging effort. The area surrounding objects (≤ 5 cm) accounts for only about 20% of the total area of the foraging arena used in this study. So, eastern chipmunks (and other such foragers) are assured a higher probability of cache encounters by preferentially exploring near objects and avoiding open areas.

There are benefits to the use of beacons compared to a more integrated spatial representation, namely a reduction in neural tissue dedicated to spatial memory (reviewed by Healy et al. 2005, but see Brodin and Lundborg 2003). On the other hand, the costs are not insignificant. Unlike spatial memory, object-cache associations are not unique to owners. Objects serve as beacons to potential robbers as well as to cache-owners, making eastern chipmunks more vulnerable to pilferage. Indeed, as seen in Chapter 1, eastern chipmunks lose their caches to interspecific and conspecific robbers at more than three times the pilferage rate experienced by least chipmunks. For eastern chipmunks, loss could be especially devastating, since so many seeds are contained in each cache (sometimes up to seventy). Perhaps this explains why eastern chipmunks dug vigorously and persistently at their apparently

depleted caches sites—the potentially high payoff of such large caches might warrant the increased energy expenditure incurred by digging.

Least chipmunks, compared to eastern chipmunks, may rely more heavily on memory for exact cache sites and less on simpler object-goal associations, since this species usually caches well away from landmarks. However, as discussed above, odor cues are probably important for the pinpointing of exact locations. While odor cues also invite pilferage, the costs may be minimal. Robbers take longer to find *T. minimus* than *T. striatus* caches, and must engage in effortful exploratory digging to do so (see Chapter 1), probably because the small caches made by *T. minimus* emit a relatively weak odor cue.

To my knowledge, this study is the first to show that caching animals remember and locate their cache sites successfully when two important local cues are missing—odor and microtopographic disturbances. By re-distributing and replacing the caching substrate, I eliminated all local cues with the exception of nearby objects. That both species still identified a majority of their caches is quite remarkable and attests to the adaptive significance of spatial memory. Apparently, the *types* of memory employed are somewhat different—*T. striatus* relies more on cache-object associations, while *T. minimus* may encode the spatial layout of their environment. The types of retrieval mechanisms employed by owners can affect foraging success in two ways: by determining recovery success, and by predicting pilfering vulnerability. Thus, interspecific differences in recovery mechanisms might be an important indicator of the competitive abilities of scatter-caching species and is a topic that deserves future attention.

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Chapter 3

Least Chipmunks (*Tamias minimus*) as Pilfering Specialists

Robbery of scatter-caches may be an especially beneficial strategy for small foragers who are otherwise out-competed at the site of harvest. The potential benefits of pilfering for small species, including direct supplementation of their own food stores as well as costs inflicted on the original cache owners, suggest that small animals may actually prefer to steal. I tested this idea in a naturalistic laboratory arena by allowing least chipmunks (*Tamias minimus*) to forage simultaneously for their own and conspecific caches. I found that chipmunks preferentially exploited their competitors' caches over their own, and did so despite a significant reduction in foraging efficiency. I conclude that the strategic pilfering of at least one small mammal, *T. minimus*, may in part contribute to this species' widespread sympatry with several larger scatter-cachers.

Traditional theoretical treatments of the evolution of scatter-caching maintain that animals should cache in a way that deters robbers but allows for retrieval by owners (Andersson & Krebs 1978; Stapanian & Smith 1978; 1984; Clarkson et al. 1986). Thus, animals should reduce their risk of robbery as much as possible, mostly by cryptic placement (e.g., Vander Wall 1993; Devenport et al. 2000; Clarkson et al. 1986; Chapter 1), but also through vigilant defense (e.g., Clarke & Kramer 1994).

More recent and somewhat controversial reformulations view cache robbery as a form of reciprocity that may underlie the stability of some scatter-caching communities (Vander Wall & Jenkins 2003; Price & Mittler 2003). This re-evaluation of the evolution of caching is in part a response to consistent reports of relatively high pilferage rates—rates that are seemingly inconsistent with traditional scatter-caching models (i.e., Andersson & Krebs 1978; Stapanian & Smith 1978; 1984). Pilfering rates vary with species and type of investigation, but frequently animals lose as much as or more than thirty percent of their food stores per day (reviewed by Vander Wall & Jenkins 2003).

While theorists have shifted their perspective of robbery from a risk that must be minimized by owners to a beneficial foraging strategy for pilferers, little is known about how robbers might benefit from stealing. The few studies that have taken this perspective suggest that pilfering stands to be a relatively lucrative foraging strategy, especially for some smaller species. For instance, small pocket mice (*Chaetodipus* spp.), compared to their larger counterparts (*Dipodomys merriami*), are more proficient robbers of congeneric and heterospecific caches (Leaver & Daly 2001).

Consistent with this pattern is the pilfering success of least chipmunks (*Tamias minimus*), who are better pilferers of heterospecific caches than at least one larger congener (*T. striatus*) (Chapter 1). These species differences suggest that at least some cases of pilfering are not reciprocal.

The foraging benefits to strategic pilferers are two-fold. First, animals can directly supplement their own food stores. Small animals, in particular, stand to gain from robbing larger competitors (e.g., Chapter 1), since cheek pouch capacity, and therefore cache size, both increase with body size (Price et al., 2000; Vander Wall 1998; Jenkins & Breck 1998). Second, robbers may benefit from the costs inflicted on their competitors (e.g., Chapter 1), another advantage to small foragers who are often physically displaced by larger competitors at the site of harvest (e.g., Leaver & Daly 2001). These potential benefits suggest that small mammals might specialize, to some extent, in robbing the food stores of others.

Pilfering "specialists" could significantly offset the reciprocity suggested by recent theory. For instance, Vander Wall & Jenkin's (2003) model posits that relatively high levels of pilfering are tolerated because pilfering victims "reciprocate" by robbing others. However, this system does not allow for cheaters. Animals that are particularly successful at hiding their own caches or at pilfering their competitors' caches could significantly tilt the playing field, possibly destabilizing any cooperative structure within the caching community. The high variability reported from field and laboratory studies of cache robbery indicate that species may differ on one or both of these characteristics. Among mammals, caching squirrels may experience minimal cache loss (less than ten percent: Stapanian & Smith 1978; Thompson & Thompson

1980). However kangaroo rats (*Dipodomys merriami*) and eastern chipmunks (*T. striatus*) may lose around half of their caches to conspecific competitors (Daly et al. 1992; Clarke & Kramer 1994, respectively), although these high rates may have been driven by unusually high field population densities due to experimental methods. Furthermore, interspecific comparisons indicate disparate pilferage rates. For instance, depending on odor intensity, yellow pine chipmunks may lose more of their food stores to conspecific and heterospecific pilferers than do deer mice (Vander Wall 2000) or gray jays (Thayer & Vander Wall 2005). And, as seen in Chapter 1, eastern chipmunks, compared to least chipmunks, are especially vulnerable to robbery. This variability, both across species and within caching communities, indicates that cache exploitation may not be completely reciprocal.

Animals that excel at robbery, cache concealment, or both, could potentially boost their competitive status. This is an especially likely scenario for small animals who are otherwise at a disadvantage because of their size. Besides direct benefits, the value of robbery may be heightened by losses imposed on the original cache owner. If true, it is reasonable to expect that some animals may prefer stealing over harvesting their own food. However, to my knowledge, neither theory nor data exist to address this hypothesis.

The focus of the current study, then, is to determine if *T. minimus*, a small species and successful robber (Chapter 1), will exploit its competitors' caches over its own. I allowed individual chipmunks to search in foraging enclosures containing their own and a competitor's caches. Conspecific competitors were used so that cache size and placement would be similar. Thus, any observed differences could be

attributed to a preference for robbery, and not simply to differential cues at cache sites (e.g., odor and visual cues; Chapter 2). I expected animals to find more of their own caches since owners remember the locations of their hidden food and will forage for them in the presence of conspecific or artificial caches (e.g., Jacobs & Liman 1991; Thompson & Thompson 1980; Vander Wall 1991). The central question in this study, however, is whether or not chipmunks will preferentially exploit their competitors' caches in the presence of their own certain food stores.

METHODS

Subjects

Subjects were twenty least chipmunks captured from sympatric populations at Seney National Wildlife Refuge in Seney, MI. Animals were transported to the Animal Cognition Lab at the University of Oklahoma and housed in naturalistic colonies where they were fed a mixture of rodent pellets, seeds, nuts, and fresh produce. Identification microchips and fur markings allowed for animal identification.

Prior to caching sessions animals were moved to individual polyurethane nest cages where they were fed as described above but had no access to seeds. Following test sessions, animals were returned to their group living quarters.

Materials and Procedures

Caching Sessions

Animals foraged and cached in 1.8 x 1.8 m sand-filled Plexiglas enclosures. However, during caching sessions, a clear Plexiglas sheet divided the arena into two equal-sized foraging compartments that measured 1.8 x 0.9 m. Two animals were

allowed to cache sunflower seeds, one in each half of the room. Early attempts at running animals simultaneously failed due to persistent aggression through the Plexiglas divider, and thus avoidance of caching behavior. Therefore, animals within a pair were typically run in succession. Before being provisioned with seeds, each animal was habituated to its half of the room for approximately 30 m, or until footprints indicated adequate exploration.

Sessions were viewed remotely and cache locations recorded on video monitors using dry-erase markers. To equate conditions on both sides of the room during subsequent test sessions, I attempted to obtain the same number of caches from both individuals of each pair (typically six to eight caches). Usually I accomplished this by counting and numbering caches remotely, and removing animals after they had buried the desired amount of caches (but see below). Any leftover sunflower seeds were removed after caching sessions. Neither the caches nor the arena was manipulated in any way prior to test sessions. Thus, during recovery sessions, the room remained in the condition in which it was left by the previous cacher. Only one exception occurred when I removed four of a single animal's caches prior to test. This adjustment occurred after a review of the videotaped caching session revealed that more caches had been made than previously recorded. Thus, the removal equated the number of caches on each side of the room.

Test Sessions

One to two days after caching sessions, I removed the Plexiglas divider and returned one of the animals from each pair to the arena where it could now forage for its own and its competitor's caches simultaneously. A total of ten animals were tested,

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counter-balanced for order. Test sessions typically lasted 1.5 h, and were only extended if animals exhibited long periods (more than 10 min) of inactivity.

Following test sessions and animal removal, I located and removed all caches, along with any new caches, and recorded the number of seeds remaining in each.

Data Analysis

During test sessions, I recorded the number and order of caches found on both sides of the room, along with the location(s) of any new caches. To further assess foraging behavior (and to confirm observations during live viewing), I reviewed videotaped sessions and recorded the cumulative time each animal spent in its own half and its competitor's half of the room for each of six consecutive 15 min time segments. Measurements were further divided into: 1) time spent at cache sites; 2) time spent re-caching; 3) time spent engaged in non-foraging behavior (e.g., periods of sleeping, vigilance, and wheel-running, and; 4) time engaged in general foraging behavior (all other activity).

Also transcribed from videotapes was cumulative time spent engaged in digging behavior, either at cache sites (i.e., excavation) or as a means of exploring (i.e., searching for new caches). Exploratory digging was further broken down into time spent near and away from objects so that any area-restricted searching strategies could be assessed.

From videotape reviews, I also estimated the number of seeds taken from each cache. Typically, during excavation at a cache site, least chipmunks consume seeds one at a time, digging briefly at the site, and then returning to an upright position to hull and eat or pouch each seed. This behavior is easily recognizable from the

overhead view of the video camera, and it allowed me to estimate the number of seeds removed from caches.

Wilcoxon Z tests were performed for within-subject comparisons, and all comparisons were conducted on a sample size of ten. Descriptive statistics are given as medians and interquartiles ranges.

RESULTS

Chipmunks foraged actively and spent the first few minutes investigating both sides of the sandbox. Some chipmunks visited their own cache sites quickly, as if to confirm their presence, and then continued foraging throughout the arena. Upon recovery of their own sites and discovery of their competitor's caches, least chipmunks responded by: 1) removing seeds to consume or pouch them; or 2) uncovering the seeds and then reburying them without removing any. After finding their own or conspecific caches, chipmunks revisited individual sites frequently, often up to twenty times over the course of the test session.

Roughly equal numbers and sizes of caches were buried on both sides of the foraging area (6.5 [6.0, 8.0] own caches vs. 7.0 [6.0, 8.0] conspecific caches, $P>0.05$; 8.9 [2.7, 19.0] seeds in own vs. 6.9 [2.2, 13.6] seeds in conspecific caches, $P>0.05$). As shown in Figure 1, chipmunks found similar percentages of their own and conspecific caches (100% [85.1, 100.0] and 92.8% [82.5, 100.0] respectively, $P>0.05$).

Subjects showed a clear preference for removing seeds from their competitors' food stores over their own. Of the caches found, chipmunks took seeds from 74.5% [47.5, 100.0] of conspecific caches, but from only 41.6% [12.5, 87.4] of

their own (*Z*=2.10; *P*<0.05) (Figure 1). Animals apparently distinguished between

the two types of caches immediately, because although they made repeated visits to

both cache types, they removed seeds during the first visit at 66.6% [36.6, 81.6] of

their competitors' caches, but only from 16.6% [6.2, 35.0] of their own caches

(*Z*=2.54, *P*<0.05). Instead, when visiting caches for the first time, they tended to

"check" their own, and, finding them intact, quickly reburied them. This preference

for exploiting conspecific caches resulted in a tendency for animals to more

frequently fully deplete their competitors' caches compared to their own (53.5%

[34.1, 75.0] vs. 33.0% [0, 87.4], but this trend was not significant (*P*>0.05).

Chipmunks varied in their re-caching behavior, making a median of 3.0 [1.0, 5.5] new

caches. Of the new caches made, 60% [71%, 85%] were from their own food stores

and 40% [15%, 93%] were made from conspecific seeds (*P*>0.05). They distributed

the new caches equally on both sides of the arena (own side: 33% [0%, 70%]; other

side 66% [29%, 100%]; *P*>0.05).

In addition to treating the two types of caches differently once found, foragers

also distinguished between the two sides of the arenas. As shown in Figure 2, over

the course of the test session, chipmunks spent over 40% more time searching

(engaged in exploratory digging) on their competitor's side compared to their own

(3.68 [2.49, 4.64] vs. 2.86 [1.73, 3.68] min digging ; *Z*=2.2, *P*<0.05). It is possible

that animals may have been drawn to that half simply due to novelty. However, this

appears not to be the case. Over the 1.5 h session, animals were active for similar

amounts of time on both sides of the room (17.7 [14.5, 22.7] min on own side vs. 18.8

[16.6, 26.9] min on conspecific side; *P*>0.05), biasing only their searching behavior

toward the competitor's side. Moreover, this bias did not change across any of the six, fifteen-minute time segment (for all six, $P>0.05$) (Figure 2).

Although animals found similar numbers of caches, they recovered their own caches at a higher rate (2.1 per min [1.8, 4.3]) compared to their competitor's caches (1.8 per min [1.2, 2.4]; $Z=2.09, P<0.05$). Once at the cache sites, chipmunks spent equal amounts of time excavating both types (2.1 [0.7, 4.0] min at their own caches vs. 2.7 [1.2, 3.7] min at conspecific caches; $P>0.05$) (Figure 2).

DISCUSSION

When given the opportunity to exploit conspecific food stores, least chipmunks readily did so, often foregoing excavation of their own caches. These findings indicate that chipmunks not only discriminate their competitors' caches from their own, but that they actually prefer them. Pilfering is costly and requires effortful searching and digging from a forager who could simply harvest its own caches using memory. Yet despite a drop in foraging rate, chipmunks preferred to exploit caches made by their competitors.

Chipmunks sought out and removed seeds from conspecific caches. This strategic foraging is inconsistent with a common assumption that robbery occurs via serendipitous discoveries by animals searching for their own caches (e.g., Thayer & Vander Wall 2005). While these chance encounters may often underlie pilfering behavior, they do not explain the current findings. When chipmunks returned to their own caches, they typically pinpointed sites rather quickly, presumably using mostly memory to do so, and did little off-cache digging near their caches. Furthermore, the

distributions of owners' and competitors' caches were topographically distinct, located on opposite sides of the foraging arena. Thus, chipmunks did not happen on conspecific caches by accident; rather, they strategically sought out caches that were not their own.

Chipmunks likely used several cues to locate conspecific caches. I minimized human interference by maintaining foraging areas as the cachers had left them. Since I did not clean or rake the sand, various microtopographic cues probably aided discovery. Sand disturbances at cache sites, local objects, and odor all draw robbers to potential cache sites (e.g., Chapters 1 & 2; Vander Wall 1982; 1991; Thayer & Vander Wall 2005; Johnson & Jorgensen 1981; Daly et al. 1992; Clarke & Kramer 1994).   Furthermore, by knowledge of their own cache sites, chipmunks could exclude their own half of the arena in favor of the competitor's side.

Other caching animals remember the sites of their own caches and typically find more of their own than their competitors' caches (e.g., Jacobs & Liman 1991; Thompson & Thompson 1980; Hardling et al 1995; Vander Wall 1982; MacDonald 1976; Thayer & Vander Wall 2005; Cowie et al. 1981). In the current study, chipmunks readily pinpointed their own sites, sometimes removing seeds, but frequently "checking" their site without seed removal, apparently using memory to locate their own caches. However, chipmunks found equal amounts of conspecific food stores, and in fact, worked harder to find and exploit them, despite the presence of their own caches.

Chipmunks in the current study searched for seeds in two separate halves of the foraging arena, a setup that probably invited pilferage. Animals could restrict

their searching to the microhabitat where a single cache was found to forage for nearby caches (e.g., Stapanian & Smith 1978). When owners' and competitors' caches are more interspersed, the ease of pilfering may be lessened somewhat. For instance, gray squirrels find about 80 percent of their own caches and close to half of artificial caches when both types of caches are evenly dispersed throughout foraging areas (Jacobs & Liman 1991). On the other hand, a preference for stealing may mitigate the recovery rate of animals' own caches. For instance, gray squirrels can find as many as 90 percent of artificial caches dispersed among their own, a finding interpreted by the author0s to indicate a heavy reliance on odor cues for cache recovery (Thompson & Thompson 1980). However, a preference for pilfering over retrieval would have yielded similar results, as seen in the current study.

The ease of robbery surely influences pilferage rates. When odor cues are enhanced, pilferage rates increase and often match recovery rates. For instance, yellow pine chipmunks find as many artificial caches as they do their own food stores under moist conditions (Thayer & Vander Wall 2005; Vander Wall 2000) or in a substrate less likely to conceal odors (Briggs & Vander Wall 2003). Apparently, when pilfering is relatively easy, at least some animals might be willing to exploit stolen food as much or more than their own.

In the current study, least chipmunks clearly preferred to steal food that was harvested and stored by other animals. For this species and other small foragers who are often out-competed at the site of harvest (e.g., Leaver & Daly 2001), robbery is an especially lucrative strategy. Thus, a willingness and preference to pilfer should be expected among species for whom potential payoffs are high. Increased exploitation

by some species could potentially offset the reciprocal pilfering otherwise suggested for caching communities (Vander Wall & Jenkins 2003; Price & Mittler 2003). While the damage inflicted by small species on larger competitors may be minimal, it may be enough to allow smaller animals to maintain sympatry with larger congeners. It will be interesting to see if the preference for robbery observed in the current study holds for natural populations and other small species.

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Figure 1. Median percentages of own and competitors' caches that least chipmunks found, exploited over the entire pilfering session, and exploited at initial cache discovery. Different letter above bars with corresponding fills indicate significant differences (Wilcoxon Z tests, $P<0.05$).

Figure 2. Median times spent excavating (on-cache digging) and time spent searching (off-cache digging) on least chipmunks' own side and on their conspecific competitor's side of the foraging arena. Only off-cache digging was significantly different (Wilcoxon Z test, $P<0.05$).
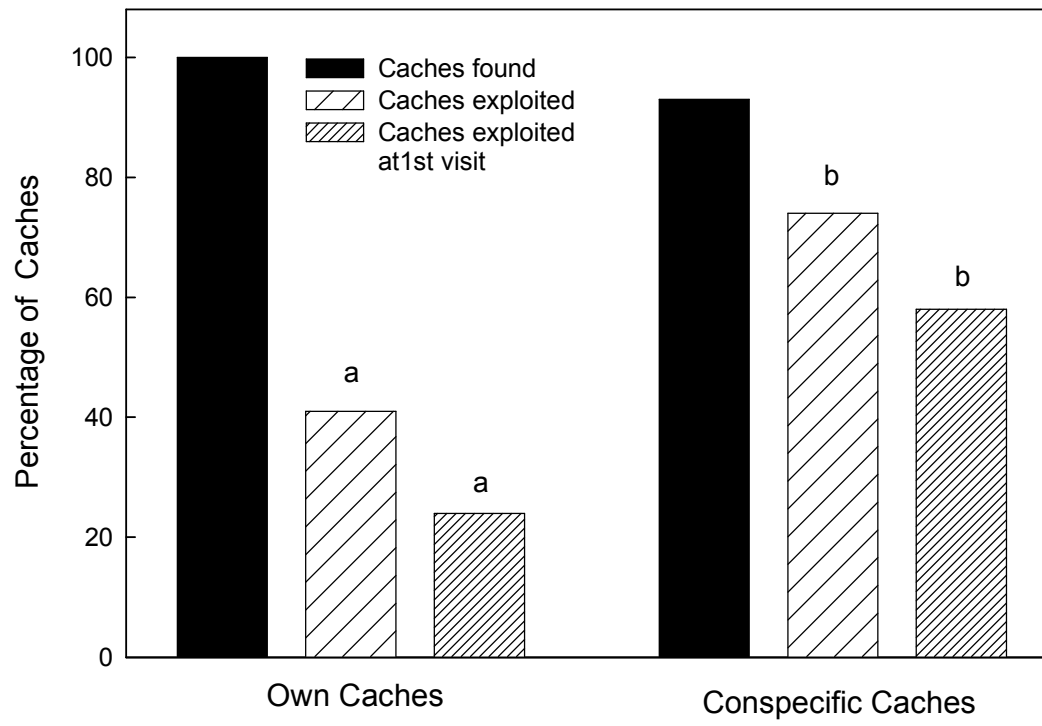
Figure 1.

Figure 2.