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PILFERING OF STORED SEEDS AND THE RELATIVE COSTS OF SCATTER-HOARDING VERSUS LARDER-HOARDING IN YELLOW PINE CHIPMUNKS

Stephen B. Vander Wall¹, Elaine C. H. Hager¹, and Kellie M. Kuhn¹

ABSTRACT.—Yellow pine chipmunks (*Tamias amoenus*) scatter-hoard food during summer and autumn but must form a larder as a winter food source before winter begins. Yellow pine chipmunks do not larder-hoard large quantities of food during the summer, apparently because a summer larder could not be defended from pilferers. We tested the assumption that the rate of pilferage from an unguarded larder would be significantly greater than the rate of pilferage from surface caches (which are also unguarded by yellow pine chipmunks) during the summer and autumn. Buried plastic buckets were used as artificial nests containing larders of 1000 sunflower seeds or 200 Jeffrey pine (*Pinus jeffreyi*) seeds. The pilferage of larder contents was monitored daily and compared to pilferage of surface caches. Animals (yellow pine chipmunks and deer mice, *Peromyscus maniculatus*) removed sunflower seeds from caches much faster than from larders, but caches of Jeffrey pine seeds disappeared much more slowly than pine seeds in larders. Further, animals removed pine seeds from larders more quickly than they did sunflower seeds from larders. The difference between seed species was probably because sunflower seeds have much stronger odors, which rodents readily detect, and because chipmunks prefer pine seeds over sunflower seeds. Yellow pine chipmunks must spend a considerable portion of their time foraging for seeds and may not be able to defend a large larder during summer.

Key words: food storage, granivory, *Peromyscus maniculatus*, pilferage, *Tamias amoenus*.

Food storage takes 2 general forms. Larder-hoarding is the accumulating of a relatively large quantity of food at one or a few locations as the result of numerous foraging excursions. The larder is almost always in some sort of cavity (e.g., underground chamber, hollow tree). An important trait of a larder is that its contents change over time; larder size is the sum of repeated provisioning visits minus consumption. Scatter-hoarding, on the other hand, is characterized by spacing food items in or on the surface of some substrate such as soil, bark, or foliage. Natural cavities are seldom involved. Because each cache is usually the result of one visit to the site, contents of caches generally do not change; they are simply present or absent. Hereafter, we will use “cache” to refer to scatter-hoarded food and “larder” to refer to larder-hoarded food.

The caches of many scatter-hoarding rodents and birds have been well characterized (e.g., Haftorn 1956, Macdonald 1976, Cowie et al. 1981, James and Verbeek 1983, Daly et al. 1992, Waite and Reeve 1993, Vander Wall 2003) because it is often easy to observe these animals make caches and examine cache contents. This

has led to a wealth of studies that have examined cache spacing (Stapanian and Smith 1978, Clarkson et al. 1986), cache retrieval (Sherry et al. 1981, Brodin 1994), cache pilferage (Vander Wall and Jenkins 2003), and other aspects of cache dynamics. On the other hand, little is known about the contents and characteristics of larders (Horne et al. 1998). Because larders are often large and valuable to the hoarder, animals hide them better than caches. Animals can be seen delivering food to their burrow, but manipulation of food within larders is seldom observed (the larders of red squirrels, *Tamiasciurus hudsonicus*, and acorn woodpeckers, *Melanerpes formicivorus*, are notable exceptions). The burrow or nest of an animal often has to be excavated to examine the contents of a larder, although in some instances artificial dens or nests can be used to monitor larder contents (Horne et al. 1998). For most animals, destruction of larders during excavation makes it difficult to monitor how they change over time. Descriptions of larder contents (e.g., Broadbooks 1958, Smith 1968, Elliott 1978, Post et al. 1993, Dearing 1997) are often little more than snapshots of the larders at a

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point in time; numerous larders must be sampled to understand how animals use them over seasons or years.

It is important to have a better understanding of larders and how animals use them. Seasonal changes in larder size and composition have implications for survival (Novakowski 1967, Seeley and Visscher 1985, Dearing 1997). Some animals that prepare both caches and larders switch from scatter-hoarding to larder-hoarding food seasonally (Clarke and Kramer 1994, K.M. Kuhn unpublished data). In some taxa (e.g., sciurid and heteromyid rodents), different species store food in different ways. For example, fox squirrels (*Sciurus niger*) scatter-hoard (Stapanian and Smith 1978), whereas red squirrels usually larder-hoard food (Smith 1968, Hurly and Robertson 1990). If we are to understand better the selective pressures that influence how animals store food and how the mode of food storage evolves, we need to understand how larders are constructed, used, and sometimes exploited by other animals.

Yellow pine chipmunks (*Tamias amoenus*) are common residents of semiarid pine forests in the western United States (Broadbooks 1958). They have relatively large home ranges (≈ 2 ha) that they share with dozens of conspecifics and other rodents (Broadbooks 1970, Kuhn unpublished data). They forage primarily for seeds. Observational studies (Kuhn unpublished data) and experiments using radioactive seeds (Vander Wall 1992, 1993) provide no evidence that yellow pine chipmunks larder-hoard food during summer and early autumn. Instead, they scatter-hoard seeds throughout their home range at depths of 5–40 mm. Burrow fidelity during summer and autumn is low. They construct winter nests in late autumn of plant fibers in a small chamber ≈ 20 –40 cm deep with 1 or 2 narrow tunnels ≈ 30 –50 cm long leading to the surface (Broadbooks 1958, Kuhn unpublished data). Burrow entrances are very inconspicuous, and the individuals that occupy the burrows are seldom seen near them. Instead, they spend most daylight hours foraging, grooming, and interacting with other chipmunks (Kuhn unpublished data). Several weeks before the onset of winter (late October to early November) yellow pine chipmunks construct a larder in their winter nest chamber. During this time yellow pine chipmunks transfer food from aboveground caches and

store it in the floor and walls of their winter nests. Because they do not deposit body fat and do not forage during winter, failure to accumulate a sufficiently large winter larder would likely result in death before spring.

The objective of this study was to investigate ecological reasons why yellow pine chipmunks refrain from larder-hoarding during summer. Because these chipmunks store food throughout summer and autumn, and because they need to have a large larder by winter, it is not clear why they do not form a larder during summer and maintain it until winter when they need it. A large accumulation of seeds in a nest chamber would be attractive to other animals, and so it would have to be defended to prevent pilferage. But larder defense takes time and restricts the movements of the larder owner, which would reduce the amount of time for searching for unstored seeds. Scatter-hoarding ensures that food resources are available to the forager during periods of food scarcity. This strategy may be particularly important in habitats where food availability is unpredictable. Defending a larder in summer and autumn likely would reduce the amount of food that could be gathered and scatter-hoarded. The larder defensibility hypothesis is based on the assumption that the rate of pilferage from an unguarded larder would be significantly greater than the rate of pilferage from caches (which are also unguarded in yellow pine chipmunks) during the summer and autumn.

We tested this assumption by constructing artificial but realistic yellow pine chipmunk nests and monitoring pilfering from larders placed in those nests while simultaneously monitoring pilferage of scatter-hoarded seeds. The relatively simple and shallow nests of yellow pine chipmunks make them ideal for studying larder pilferage using artificial nests constructed with man-made materials. A series of experiments (Vander Wall 2000, Vander Wall et al. 2003) has demonstrated that chipmunks and other rodents will readily adopt plastic buckets as temporary nests. In addition to their construction, these artificial nests are unrealistic in one important way: there is no nest "owner." However, this is not an issue in this experiment because we seek to test the consequences of having a summer larder that is not guarded because the owner spends most

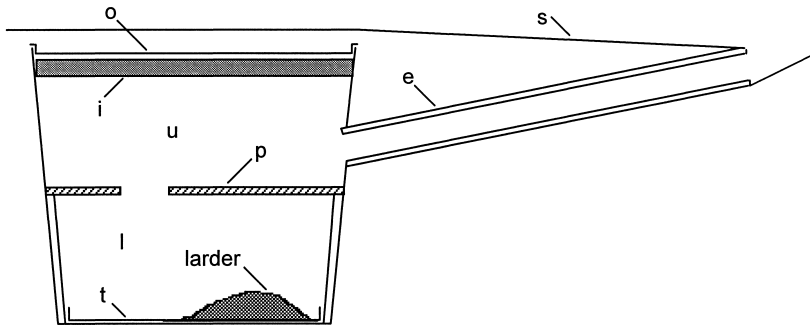


Fig. 1. Cross section of a nest bucket: **o** = outer lid buried about 2 cm under the ground surface (**s**); **i** = inner lid constructed of styrofoam insulation 17 mm thick to moderate nest temperature; **p** = plywood partition (6 mm thick with a 64-mm-diameter hole) dividing nest into upper (**u**) and lower (**l**) compartments; **t** = plastic tray containing the larder; **e** = entrance made of PVC pipe connecting upper nest chamber to ground surface. The nest entrance was placed under a shrub. Three diameters of entrance pipes were used to permit access by different sized rodents.

of its time away searching for more food (as do yellow pine chipmunks during summer and autumn).

METHODS

We conducted this study in the Whittell Forest and Wildlife Area in Little Valley, Washoe County, about 30 km south of Reno, Nevada, USA (39°15'0"N, 119°52'35"W). Little Valley is in the Carson Range in extreme western Nevada at an elevation of ≈1975 m. Open Jeffrey pine (*Pinus jeffreyi*) forests with an understory of antelope bitterbrush (*Purshia tridentata*), greenleaf manzanita (*Arctostaphylos patula*), tobacco bush (*Ceanothus velutinus*), and Sierra chinquapin (*Castanopsis sempervirens*) dominate the lower slopes of the valley. Soil consists of decomposed granite. The region experiences summer droughts from June to October.

We constructed artificial nests using 7.6-L plastic buckets 24 cm high × 22 cm wide (Fig. 1). A partition divided the nest bucket into 2 nearly equal-sized chambers. We placed seeds (the larder) in the bottom compartment. A slightly inclined segment of PVC pipe ≈60 cm long connected the upper chamber to the ground surface. The whole "nest" was buried under 2–5 cm of soil (bottom of nest was 25–30 cm deep) next to a shrub such that the PVC pipe met the ground near the base of the shrub among plant litter. We attempted to make the nest entrance inconspicuous by covering the entrance pipe with plant litter.

To determine what size (species) rodents might pilfer artificial chipmunk larders, we used entrance pipes of 3 inside diameters: small (25 mm), medium (34 mm), and large (50 mm). In previous studies we found that an entrance pipe 34 mm wide was appropriate for yellow pine chipmunks. Henceforth, we refer to these as small-(S), medium-(M), and large-(L) diameter nests, indicating the size of the largest rodents that could potentially enter them. Small nests accommodate deer mice (*Peromyscus maniculatus*, 15–20 g) and juvenile yellow pine chipmunks. Medium nests permit entry of these rodents and adult yellow pine chipmunks (40–50 g). Large nests accommodate all these rodents plus long-eared chipmunks (*Tamias quadrimaculatus*, 70–90 g) and golden-mantled ground squirrels (*Spermophilus lateralis*, 150–250 g).

We selected 2 sites about 500 m apart and established 30 nest buckets at each site during mid-June 2002. At each site there were 10 nests of each of the 3 entrance sizes spaced ≈20 m apart and arranged in regular order along a transect (i.e., S, M, L, S, M, L, etc.). We conducted 2 series of trials with nest buckets at the same sites, the 1st with larders consisting of ≈1000 black-oil sunflower seeds (≈55 g) and the 2nd with larders consisting of 200 Jeffrey pine seeds (≈20 g). These larders are smaller than real winter larders, which often contain >200 g of seeds. Jeffrey pine seeds are native, highly preferred seeds frequently eaten by rodents at this site, and sunflower seeds are

nonnative seeds, which we included to determine whether seed species influenced the rate of pilferage. At each site there were typically 20–50 yellow pine chipmunks, 2–13 long-eared chipmunks, 5–10 deer mice, and 2–10 golden-mantled ground squirrels (Vander Wall 2003, Roth and Vander Wall in press), all of which occupy large, overlapping home ranges and exhibit little or no territoriality.

We initiated the sunflower seed trials on 1 August and the Jeffrey pine seed trials on 20 August 2002 by placing a larder in the lower nest chamber. We visited each nest daily to inspect larders, and, if we suspected that rodents had entered the nest (e.g., presence of seed shells, feces, foreign material in the nest chamber), we estimated how many seeds had been eaten, removed, or, in 2 nests, added. We estimated eaten sunflower seeds by measuring the volume of seed shells (we determined in the laboratory that 1 mL of seed shells equals \approx 5 intact seeds). Eaten pine seeds were determined by counting shells. The number of intact seeds remaining was estimated by measuring seed volume and comparing it to the initial volume of the larder (180 mL for sunflower and 92 mL for Jeffrey pine). We identified rodent visitors by size of fecal pellets in nests, presence of nest material moved into nests (only by deer mice), and directly by seeing animals in or fleeing from nests. At the end of each visit, we returned all remaining intact seeds to the larder, reburied the nest bucket, and made sure the entrance was open (some rodents filled the PVC pipe with soil). At the end of the sunflower trials, we removed any remaining sunflower seeds and left the nests empty for 2 weeks until the pine seed trials began. Nest buckets remained fairly cool, registering 19°–23°C during midday, several degrees below ambient temperature.

To evaluate the impact of pilfering from larders relative to scatter caches, we established transects of artificial caches in the same area. Each cache contained 10 sunflower (initiated 1 August) or 2 Jeffrey pine seeds (initiated 20 August) buried 10 mm deep. We established 60 caches at each site (total 120 caches) spaced \approx 5 m apart. The cache sites changed between the sunflower and pine seed trials. We did not touch seeds or the ground near the cache sites during preparation to prevent human odors from providing cues to for-

aging rodents (Duncan et al. 2002). We also did not use any man-made markers (e.g., pin flags or stakes) to relocate caches because rodents use them to find buried seeds (Vander Wall and Peterson 1996). Instead, we used natural objects (e.g., twigs, pine cones, pebbles) in unique patterns to mark stations (Vander Wall 1994). We monitored these caches daily immediately after examining the larders. We conducted larder and caching trials simultaneously during dry periods (no rain during preceding 14 days) to limit the olfactory signal emitted by seeds (Vander Wall et al. 2003). Digging by rodents at the cache site indicated that seeds had been removed.

Seeds pilfered from larders could be eaten, moved to a new larder, or scatter-hoarded on the ground surface. We hypothesized that during summer and early autumn most seeds removed from larders would be scatter-hoarded because that is what happens to experimental seeds placed at bait stations aboveground (e.g., Vander Wall 2003). To determine the fate of seeds pilfered from larders, we established 5 nest buckets at a location >300 m from the other sites and placed 200 radioactively labeled Jeffrey pine seeds in each nest. Each nest bucket was equipped with a large-diameter (50 mm) entrance to permit entry of all rodent species. We arranged these nests in a “+” pattern with 1 nest at the center and the other 4 nests 20 m apart in cardinal directions. The seeds in each bucket were dyed a different color so that the origin of any relocated seeds could be determined. We labeled seeds by soaking each lot in 3 mL distilled water and scandium-46 until the seeds were thoroughly wetted, and then they were allowed to dry for 2 days. A single seed could be detected from \approx 30 cm using a Geiger counter. We placed the seeds in nest buckets on 4 September 2002. Nine days later we examined all larders to record how many seeds had been removed or eaten and began surveying the vicinity within \approx 30 m of nests with Geiger counters looking for seed caches and seed shells. When we found a cache, we removed the seeds and recorded seed color, number of seeds in the cache, and cache depth. Finally, we mapped the location of caches relative to the central larder using cardinal direction as axes.

We assessed the effects of larder entrance diameter (small, medium, or large), storage type

TABLE 1. Fate of artificial sunflower seed larders (1000 seeds) after 6 days and Jeffrey pine seed larders (200 seeds) after 4 days. Data are means \pm 1s. Eaten refers to seeds eaten in the nest chamber. There were 10 artificial nests for each nest entrance diameter and seed species.

Species	Nest entrance diameter	Eaten	Remaining	Taken
Sunflower	large	103 \pm 82	0 \pm 0	897 \pm 82
	medium	129 \pm 69	48 \pm 214	823 \pm 197
	small	157 \pm 133	118 \pm 293	725 \pm 264
Jeffrey pine	large	12 \pm 8	0 \pm 0	188 \pm 8
	medium	15 \pm 8	0 \pm 0	185 \pm 8
	small	51 \pm 25	0 \pm 0	149 \pm 25

(larder or scattered caches), and seed species (sunflower or Jeffrey pine) on the rate of seed removal using survival analysis and a Weibull distribution (Allison 1995). The response variables were the lower and upper limits on the time a larder or cache was known to have been present, expressed as days since the beginning of a trial. As some larders were removed piecemeal over 2 or more days, we arbitrarily deemed larders removed if 50% or more of the seeds had been taken. We made post-hoc comparisons among larder entrance sizes, storage types, and seed species by calculating chi-square statistics as described in Allison (1995). Bon Ferroni alpha levels were used to assess the significance of chi-square tests: $\alpha = 0.003$ (0.05/15 tests).

RESULTS

In sunflower seed trials, rodents took 89.7% of seeds from large-diameter nests, 82.3% from medium-diameter nests, and 72.5% from small-diameter nests within 6 days (Table 1). In addition, rodents ate 10.3% of seeds in large-diameter nests, 12.9% in medium-diameter nests, and 15.7% in small-diameter nests. Removal rates decreased with decreasing nest entrance diameter (Fig. 2A). Removal rates from large nests averaged 93.4% per day, medium nests averaged 57.3%, and small nests 30.1%. Rodents removed seeds from nests with large entrances 2.4 times faster than from nests with medium entrances ($\chi^2 = 25.23$, $P < 0.0001$), and they removed seeds from nests with medium entrances 2.0 times faster than those from small entrances ($\chi^2 = 15.03$, $P < 0.001$). Larders in nests with large entrances usually were emptied within 1 day after being discovered (12 of 20 cases), whereas nests with medium-sized entrances were emptied or nearly emptied within 1 day of being discovered on only

6 occasions. Nests with small entrances, on the other hand, disappeared more slowly, taking an average of >5 days to be depleted once discovered.

We found chipmunk feces in large- and medium-diameter nests on 10 occasions and observed juvenile yellow pine chipmunks emerging from nests with small-diameter entrances. We found deer mouse feces in small-diameter nests on 2 occasions, and deer mice brought nest material into small nests on 10 occasions. One of the small-diameter nest buckets was adopted by a deer mouse as its nest. Over a period of 6 days, the mouse repeatedly brought nest material into the bucket and added seeds to the larder, increasing its volume by $\approx 50\%$. New seeds brought into the nest included sunflower (from other nest buckets) as well as those of bitterbrush and manzanita. We found no evidence that golden-mantled ground squirrels had entered large-diameter nests.

Scatter-hoarded sunflower seeds (10 seeds per cache) disappeared very rapidly (Fig. 2A). Removal rates along 2 transects were the same: 98.3% per day. Seeds in scattered caches did not disappear significantly faster than seeds in large-diameter nests ($\chi^2 = 3.48$, $P = 0.062$), but sunflower seeds in caches disappeared 1.9 times faster than seeds in medium-diameter nests ($\chi^2 = 23.32$, $P < 0.0001$).

In the Jeffrey pine seed trials, rodents took 94.0% of seeds ($n = 200$) from large-diameter nests, 92.5% from medium-diameter nests, and 74.5% from small-diameter nests (Table 1) within 4 days. In addition, rodents ate 6.0%, 7.5%, and 25.5% of seeds in large-, medium-, and small-diameter nests, respectively. Removal rates from medium- and large-diameter nests were the same, averaging 96.2% per day ($\chi^2 = 0.32$, $P > 0.50$). Removal of seeds from nests

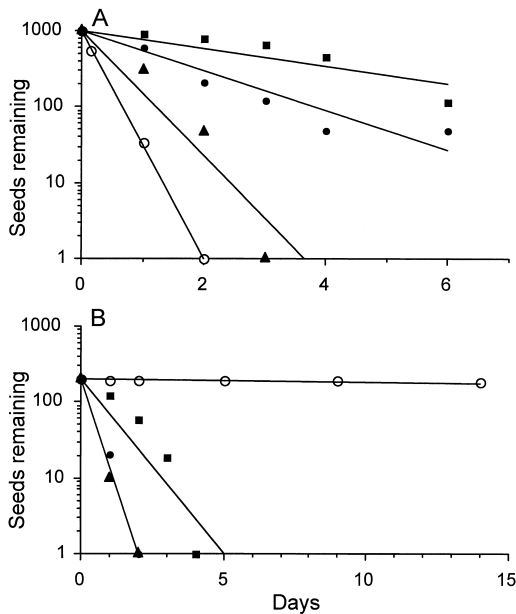


Fig. 2. Rates of removal of sunflower seeds (A) and Jeffrey pine seeds (B) from larders and from scatter caches. Closed triangles = larders in nests with large (50 mm diameter) entrances; closed circles = larders in nests with medium (34 mm) entrances; closed squares = larders in nests with small (25 mm) entrances; open circles = scattered caches (10 seeds for sunflower or 2 seeds for Jeffrey pine buried 10 mm deep) on the ground surface.

with small entrances (78.2% per day) was slower, only about 0.36 and 0.32 times as fast as seeds in medium- and large-diameter nests ($\chi^2 = 29.43$ and $\chi^2 = 32.90$, respectively, $P < 0.0001$ for both). Larders with large or medium entrances were always emptied within 1 day of being discovered, but only 8 small-diameter nests were emptied within 1 day of being discovered.

In the pine seed trials, deer mouse feces occurred in 1 large, 1 medium, and 6 small nests. One small-diameter nest bucket, the same one as in the sunflower trial, was adopted by a deer mouse, which moved in nest material and more seeds. By day 3 it had increased the volume of the larder by 91%. New seeds included sunflower (apparently from the previous trial), Jeffrey pine (from other nests or native seeds), and those of bitterbrush and manzanita. By day 4 the nest and larder had been destroyed by a black bear (*Ursus americana*). We found chipmunk feces in 14 large-diameter nests, 19 medium-diameter nests, and

4 small-diameter nests. Golden-mantled ground squirrel feces were found in 4 large-diameter nests.

Scatter-hoarded Jeffrey pine seeds (2 seeds per cache) were removed very slowly. Mean rate of removal was 0.55% per day. Jeffrey pine seeds in large-diameter nests disappeared 86 times faster than seeds in scattered caches ($\chi^2 = 297.28$, $P < 0.0001$), seeds in medium-diameter nests disappeared 76 times faster than seeds in scattered caches ($\chi^2 = 305.16$, $P < 0.0001$), and seeds in small-diameter nests disappeared 27 times faster than seeds in scattered caches ($\chi^2 = 202.52$, $P < 0.0001$).

The rate of sunflower and Jeffrey pine seed removal from nests with large entrances was not significantly different, but pines seeds were removed 3.3 times faster from medium-diameter ($\chi^2 = 14.46$, $P < 0.0001$) and 2.3 times faster from small-diameter ($\chi^2 = 23.20$, $P < 0.0001$) nests than were sunflower seeds. However, sunflower seeds were removed 43 times faster from surface caches than pine seeds ($\chi^2 = 352.03$, $P < 0.0001$).

In the radioactive Jeffrey pine seed experiment, 4 of the nests were emptied within 3 days, and the 5th nest was not emptied until 9 days after initiation of the experiment. We found a total of 380 caches in the vicinity of the 5 experimental nests (Fig. 3). Caches from the first 4 nests appeared to be the work of yellow pine chipmunks (based on size, depth, and distance from the source), whereas caches from the 5th nest appeared to be made by deer mice. The chipmunk caches ($n = 258$) contained 429 seeds with 1.7 ± 0.9 seeds per cache (mean \pm 1s). Mean distance between source nests and caches was 14.6 ± 9.4 m (range = 0.8–53.2 m). The deer mouse caches were smaller (1.2 ± 0.7 seeds per cache), shallower, and closer to the nest bucket (5.9 ± 3.4 m, range 0.5–17.1 m away). Overall, we accounted for 77% of the seeds originally placed in larders.

DISCUSSION

Several lines of evidence from the nest buckets indicated that chipmunks had pilfered seeds from most of the medium- and large-diameter larders. The yellow pine chipmunk is the most abundant species of rodent in the study area (Vander Wall 2002). Long-eared chipmunks are less common and cannot fit

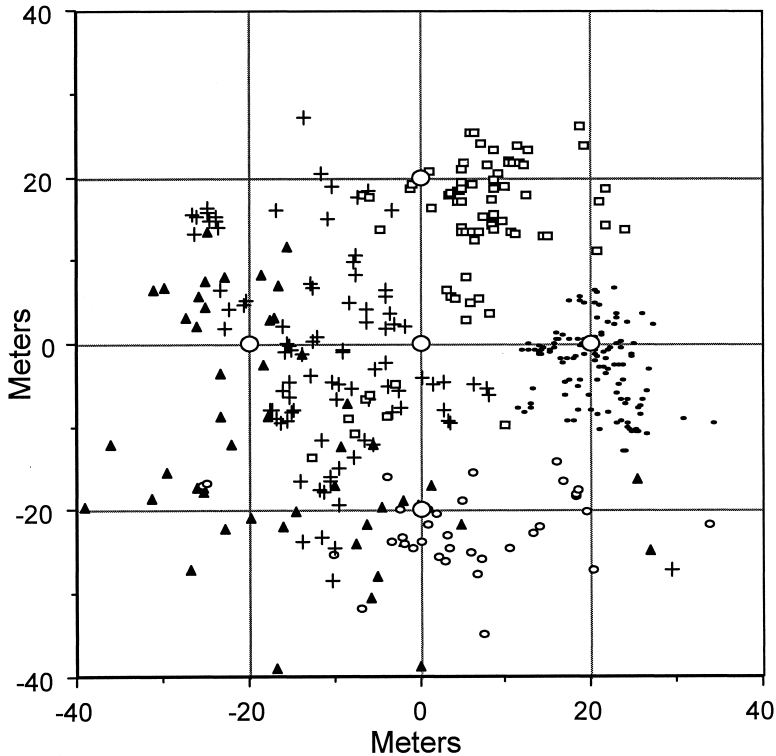


Fig. 3. Dispersion of Jeffrey pine seed caches from seeds taken from 5 nest buckets (large circles). Each symbol represents a cache of seeds taken from a different larder: Crosses = central nest; open squares = north nest; closed circles = east nest; open circles = south nest; closed triangles = west nest. Closed circles represent caches apparently made by a deer mouse. All other caches appeared to be made by yellow pine chipmunks.

into the medium-sized nest entrances. We found chipmunk feces in numerous buckets, and we observed yellow pine chipmunks near or emerging from several nests. The much slower rate of removal from the small-diameter nests suggests that the smaller and less common deer mice were active in those nests. In the Jeffrey pine trial, we found some evidence that yellow pine chipmunks also were entering small nests. These individuals were probably males, which are $\approx 10\%$ – 15% smaller than females, or juveniles. Golden-mantled ground squirrels had visited several of the large nests in the Jeffrey pine trial, but most activity in the large nests appeared to be that of yellow pine chipmunks. This general pattern was confirmed in the radioactive seed experiment; caches from 4 larders matched those made by yellow pine chipmunks, and 1 set of caches was similar to those made by deer mice.

We obtained strikingly different results when larders and caches were composed of sunflower seeds than Jeffrey pine seeds (Fig. 2). Rodents removed sunflower seeds from larders fairly rapidly, especially those with large- or medium-diameter entrances, but scatter-hoarded sunflower seeds disappeared significantly faster than larder-hoarded sunflower seeds. These data suggest that it would be safer for a chipmunk to larder-hoard sunflower seeds in a burrow with a small- or medium-sized entrance than scatter-hoard them on the ground surface because the larder-hoarded seeds would be pilfered at a slower rate. In contrast, pilferage rates of scatter-hoarded Jeffrey pine seeds were extremely slow, while larder-hoarded seeds disappeared very rapidly.

Seeds in nests with small- and medium-diameter entrances disappeared faster in the Jeffrey pine trials than in the sunflower trials, probably because Jeffrey pine seeds are highly

preferred by forest rodents. Yellow pine chipmunks readily accept sunflower seeds but sometimes ignore them when Jeffrey pine seeds are available. We suspect that the dramatic difference in rate of pilferage of surface caches of sunflower and Jeffrey pine seeds occurred because sunflower seeds emit relatively strong odors. Native seeds, represented here by Jeffrey pine, have probably experienced strong selection for minimizing emitted odors (we are exploring this possibility in a separate series of experiments, and preliminary results support this hypothesis). Detected seeds are more likely to be eaten whereas undetected seeds might eventually germinate. Thus, the strength of seed odors is likely to be inversely correlated with plant fitness. Sunflower seeds, on the other hand, have been subjected to strong artificial selection for size and oil content and any selection against odor has probably been relaxed. The difference in removal rates between sunflower and pine seeds indicates that the nonnative sunflower seeds are not good surrogates for native seeds in certain kinds of experiments, and that they could give misleading results in some studies of caching behavior because of the strong odors they emit. In this study we regard the test of relative pilferage rates in larders versus caches using sunflower seeds to be invalid because the pilferage rates of scattered caches differed so strikingly from those of caches of natural Jeffrey pine seed (Fig. 2). We recommend that sunflower seeds not be used in studies of cache pilferage; native seeds are more likely to yield meaningful results.

Scatter-hoarded Jeffrey pine seeds appear to be relatively safe from pilferers compared with unguarded larder-hoarded seeds. Scatter-hoarded Jeffrey pine seeds buried in dry soil appear to emit little or no detectable odors (Vander Wall 1995, 1998, 2000). If it should rain, however, seeds become more detectable by other rodents, but this does not appear to be too damaging to yellow pine chipmunks because the caches of all individuals are equally vulnerable (Vander Wall 2000, Vander Wall and Jenkins 2003). Larder-hoarded seeds, on the other hand, are vulnerable under all conditions. When eastern chipmunks (*Tamias striatus*), which maintain larders at all seasons whenever excess food is available, discover an unguarded nest of a conspecific, they make repeated pilfering trips with filled cheek pouches

until the owner of the burrow returns (Elliott 1978, Clarke and Kramer 1994). Kangaroo rats behave similarly (Daly et al. 1992). In our experimental larders, a yellow pine chipmunk could remove all 200 Jeffrey pine seeds in 8–10 visits, which could take as little as an hour. Deer mice, which can carry only 2–4 Jeffrey pine seeds per load (Vander Wall and Longland 1999), work much more slowly but could deplete a larder containing 200 seeds in a single night.

The radioactive seed study demonstrated a simple point: most seeds pilfered from larders are scatter-hoarded. This seems to be true for both yellow pine chipmunks and deer mice. Because a foraging yellow pine chipmunk cannot guard its larder, and because larder-hoarded seeds are likely to be pilfered and scatter-hoarded anyway, it would be more efficient for the foraging chipmunk simply to scatter-hoard the seeds itself. This behavior would benefit a forager in 3 ways. First, it would save time traveling to and from the nest, time that could be invested in other activities such as additional foraging, grooming, or predator surveillance. If food is found at some distance from the nest, which is generally the case for yellow pine chipmunks, a scatter-hoarding forager is likely to be much more efficient than one that larder-hoards because of reduced travel time. Second, by caching seeds itself (rather than having them cached by a pilferer), the forager retains a recovery advantage relative to other animals with which it shares its home range. The individual that makes caches retains spatial memories of its cache sites (Jacobs and Liman 1991, Vander Wall 1991, Jacobs 1992). Pilferers lack these memories and must depend on olfaction, which works poorly when the soil is dry (Vander Wall 1995, 1998), and random digging to find buried seeds. As long as seeds do not emit strong odors (which is probably true of most native seeds in dry soil), the animal that caches a seed has a recovery advantage (Vander Wall and Jenkins 2003, Vander Wall et al. 2003). Third, by scatter-hoarding, the cacher shields itself from catastrophic losses. An inherent advantage of scatter-hoarding over larder-hoarding is that when losses occur from a larder, they can be catastrophic (Henry 1986), whereas losses from scattered caches, although damaging, are usually far less serious.

In this experiment we did not move nest buckets to new locations between trials. This

procedure allowed for the possibility that rodents could learn the locations of artificial nests and return to pilfer larders repeatedly in successive trials. We believe that this condition accurately reflected the natural situation. Rodents can be expected to learn the location and explore the characteristics of all burrows and refuges in their home range (Elliott 1978). Knowledge of these sites may become important when an animal is at risk of predation or requires a resting site. Yellow pine chipmunks appear to change sleeping sites frequently during summer (Kuhn unpublished data), and summer sleeping burrows are probably visited frequently by other chipmunks during the day while the owner is away foraging. If we had moved our artificial nests to new sites between trials we might have underestimated the probability of larder pilferage in real summer nests.

On 2 occasions during this study, black bears destroyed nest buckets and consumed the larder. We suspect that bears first detected the odor of plastic and learned to associate the buckets with a food reward. Actual chipmunk nests are probably far more difficult for bears to detect, but this result does demonstrate an important principle: larders are vulnerable to a wider variety of pilferers than are caches and when pilferage of a larder does occur, it is usually catastrophic. From the chipmunk's perspective, this sort of pilferage is far more destructive than pilferage from caches because the larder is consumed. When caches are pilfered by other rodents, most of the seeds are recached elsewhere, and, consequently, the seeds are still potentially available to the animal that originally stored them (Vander Wall and Jenkins 2003).

Food-storage behavior of yellow pine chipmunks and eastern chipmunks is very different. Eastern chipmunks larder-hoard extensively during all seasons and also scatter-hoard some food during the spring and summer (Elliott 1978, Clarke and Kramer 1994). Eastern chipmunks have a relatively small home range; when they scatter-hoard, they cache most food near the nest entrance and defend these caches from potential pilferers. Cache residence time (i.e., amount of time an average seed remains at a cache site) is relatively short (≈ 1 hour; Clarke and Kramer 1994). Yellow pine chipmunks, on the other hand, forage over much

larger areas (≈ 2 ha), appear to scatter-hoard seeds throughout their home range, and do not attempt to defend their caches. Mean cache residence time is unknown but is on the order of weeks (Vander Wall 2002, Vander Wall and Joyner 1998). Yellow pine chipmunks must eventually accumulate a large mass of food to ensure survival over winter, but they delay formation of the winter larder until a few weeks before the onset of winter conditions, apparently because of the high rates of pilferage an undefended larder is likely to experience.

It is unclear whether the nest buckets might have influenced the rate of pilferage of artificial larders. The odor of the plastic buckets seems weak to humans but might be easily detected by rodents. We assume that most rodents initially detected artificial nests by searching visually for a burrow opening, which animals are likely to explore as potential refuges, future nest sites, or food sources. The odor of seeds and plastic may have been secondary cues, but this has not been established. Our daily digging and soil disturbance when we checked nest buckets might also have served as cues to foraging rodents. Studies of the dynamics of rodent larders (i.e., changes because of foraging or pilferage) are complicated by the destructive nature of sampling larders over time, and so some form of artificial burrow and larder may need to be part of any experimental design. Future studies should try to develop more realistic nest chambers that can be checked easily with minimal disturbance.

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