

BENEFITS OF SMALL-SIZED CACHES FOR SCATTER-HOARDING RODENTS: INFLUENCE OF CACHE SIZE, DEPTH, AND SOIL MOISTURE

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Some granivorous rodents scatter hoard; they bury seeds in shallow pits throughout their territory. These buried caches can represent food stores for the hoarders, food for competitors, or a means of seed dispersal and propagation for plants. Large numbers of seeds may be buried in many caches throughout an area; thus, fate of caches has important consequences for granivores, other animals, and plants. This study examined the ability of Ord's kangaroo rat (*Dipodomys ordii*) to exploit artificial caches of different sizes, at 2 depths, and in substrates of differing moisture content. Kangaroo rats harvested significantly more caches in moist substrates and at shallower depths; however, small caches containing ≤ 5 seeds were removed infrequently by individuals regardless of substrate moisture and depth. As cache size was increased in moist sand, a threshold existed at each depth where caches were greatly exploited by kangaroo rats. Results suggest that pilferage of caches under natural conditions is not linear with respect to cache size in moist substrates. As cache size was increased in dry sand, no threshold of increased exploitation was observed for cache sizes used in this experiment. Results also suggest that pilferage of caches under natural conditions is not strongly influenced by size in dry substrates for relatively small caches. Overall, size and depth of caches greatly influence their fate. Perturbations, such as rainfall, also alter detection of caches. To reduce detection of caches by competitors, scatter hoarders should distribute relatively small caches, especially during wet conditions.

Key words: cache fate, cache size, *Dipodomys ordii*, plant–animal interactions, scatter hoarding

Granivorous rodents are important predators of plants in many ecosystems because of the large quantity of seeds they consume. However, some granivorous rodents benefit plants by dispersing seeds via food-hoarding behaviors (Longland et al. 2001; Price and Jenkins 1986; Vander Wall 1994). Scatter hoarders, which bury relatively small quantities of seeds in shallow, inconspicuous pits throughout their territory, may enhance reproductive success of plants. Scatter hoarders can increase dispersal distances of seeds (McAuliffe 1990; Vander Wall 1994), increase germination rates of seeds (McAdoo et al. 1983), and reduce loss of seeds to other foragers that consume seeds without caching them or that hoard seeds in places unfavorable for germination (e.g., larder hoards—Longland et al. 2001). Fates of seeds buried by scatter hoarders have 4 general outcomes (Longland et al. 2001; Price and Jenkins 1986; Vander Wall 1994): they may be consumed by scatter hoarders, they may be consumed by other granivorous foragers, they may survive and germinate, or they may die in the

soil. Because of these fates, caches of seeds have important ecological consequences for granivores, other animals, and plants.

Seeds of a number of plants are known to germinate and grow from caches of scatter hoarders (e.g., La Tourrette et al. 1971; McAdoo et al. 1983; McAuliffe 1990; Reynolds 1950, 1958; Reynolds and Glendening 1949; Vander Wall 1994; West 1968). In addition, establishment of new plants from caches is important for various communities (La Tourrette et al. 1971; Reynolds and Glendening 1949; Vander Wall 1994; West 1968). For example, examination of seedlings in a population of antelope bitterbrush (*Purshia tridentata*) showed that >99% originated from scatter hoards of yellow-pine chipmunks (*Tamias amoenus*), and regeneration of bitterbrush appears to be dependent on scatter hoards of chipmunks and other rodents (Vander Wall 1994).

Probably the most important benefit of caching is to store food for periods when food is scarce, which converts intermittent food sources into more reliable ones and enables individuals to have control over food supplies (Vander Wall 1990). The behavior of scatter hoarding presumably is related to an inability of individuals to protect, defend, and recover large concentrations of food (Clarkson et al. 1986; Stapanian

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and Smith 1978) compared to those that larder hoard (i.e., store large quantities of food at a single or few sites). Scatter hoarders protect resources by burying small quantities of food at many sites throughout their territory. Rodents that scatter hoard use memory, in part, to relocate buried caches (Collett et al. 1986; Devenport et al. 2000; Jacobs 1992; Jacobs and Liman 1991; Vander Wall 1991). Scatter hoarding protects against loss of concentrated, large stores of food (i.e., larder hoards) and reduces the need to defend stores. However, these caches are still vulnerable to other foragers, especially those using olfaction to locate buried food resources.

Rodents and other mammals use olfactory cues to detect buried food items (Cahalane 1942; Howard and Cole 1967; Howard et al. 1968; Johnson and Jorgensen 1981; Reichman and Oberstein 1977; Vander Wall 1993b, 1995, 2000). Olfactory detection of seeds by rodents is influenced by a number of factors, including depth in soil, quantity of seeds or cache size, and moisture content of seeds and substrate (Lockard and Lockard 1971; Reichman 1981; Reichman and Oberstein 1977; Vander Wall 1993a, 1993b, 1995, 1998, 2000).

To date, little is known about placement and fate of buried caches by many species of scatter-hoarding rodents. However, scatter hoards are known to be detected and removed by intra- and interspecific competitors (Daly et al. 1992; Leaver and Daly 2001; Vander Wall 2000), and rates of pilfering by competitors can be extremely high, especially in moist substrates (for review, see Vander Wall and Jenkins 2003). For example, rodents of 3 species detected and removed 99.8% of buried caches in moist substrates compared to only 13.3% in dry ones in laboratory experiments (Vander Wall 1995). In a field experiment, simulated rainfall events resulted in rodents removing up to 100% of buried caches after 4 days (Vander Wall 1998). Vander Wall (1998) reported considerable variation in foraging abilities of rodents and suggested that size and depth of caches strongly affect olfactory signals. Because rates of pilfering can be exceedingly high and because there are costs associated with scatter hoarding (such as the time and energy spent in procuring, transporting, burying, and recovering seeds), scatter hoarders should distribute caches to maximize net returns to the owner. For hoarding to be adaptive, benefits for individuals that hoard must outweigh benefits of not hoarding (Andersson and Krebs 1978). Andersson and Krebs (1978) also stated that hoarding can be adaptive if individuals that store items have a greater probability of recovering their own caches than other individuals in the population. However, this generalization is not always true. In fact, scatter hoarding also could be adaptive even if hoarders recover less of their own caches than do other individuals, as long as individuals that hoard seeds benefit more than if they did not hoard at all (also see Vander Wall and Jenkins 2003). Thus, as a result of selection imposed by competitors, scatter hoarders should place caches at locations, at depths, and in quantities that lower the probability of caches being detected and exploited. Experiments examining how different factors affect the ability of rodents to detect and exploit caches will lead to a better understanding of how scatter hoarders select placement of caches.

The objective of the present study was to examine the ability of a granivorous rodent (Ord's kangaroo rat [*Dipodomys ordii*]) to exploit artificial caches of different sizes (1–40 seeds), at 2 depths (12 and 24 mm below surface), and in substrates of differing moisture content (moist and dry). Specifically, I examined fate of small-sized caches to determine the largest size that would remain unexploited by kangaroo rats under controlled conditions. To date, only limited data exist on removal of buried caches as a function of cache size and environmental condition. My study quantified exploitation of small artificial caches in a natural environment without altering foraging behaviors of individuals by confining them in cages, using unfamiliar substrates, or housing them in laboratories. I selected Ord's kangaroo rats as subjects and conducted experimental trials in the Sandhill Region of Nebraska because rodents in the family Heteromyidae have some of the best-reported abilities to locate and harvest buried caches (Vander Wall 1995; Vander Wall et al. 2003); data for *Dipodomys* are unclear concerning the ability to detect caches in moist substrates (Vander Wall et al. 2003); and *D. ordii* is abundant and the only species of *Dipodomys* in the Sandhill Region of Nebraska (Jones 1964), thus, I was able to accurately identify the species exploiting artificial caches.

MATERIALS AND METHODS

This study was conducted on the Bessey Division of Nebraska National Forest, Thomas County, Nebraska. From 5 to 24 June 2002, I conducted experimental trials in grasslands along a 5-km section of Forest Road 259. The center of the study site was 6.5 km east and 3.1 km south of Thedford (41°56.946'N, 100°29.567'W; elevation, 820 m). The research area is located in the Sandhill Region of Nebraska, which is characterized by rolling sand dunes covered with native grasses and forbs. These vegetated dunes vary in height, and the study area lies in a region with steep hills separated by lower hills and narrow valleys (Sherfey et al. 1965). Dominant vegetation consists of little bluestem (*Andropogon scoparius*), sand bluestem (*A. hallii*), prairie sandreed (*Calamovilfa longifolia*), switchgrass (*Panicum virgatum*), sand lovegrass (*Eragrostis trichodes*), yucca (*Yucca glauca*), and sunflower (*Helianthus*). The Sandhill Region is typified by warm summers, cold winters, limited precipitation, and low humidity. Mean annual precipitation is 52.1 cm, with about 78% falling as rain from April to September (Sherfey et al. 1965).

I conducted this experiment to examine exploitation of clumps of buried seeds (i.e., simulated artificial caches) by Ord's kangaroo rats. For the 1st part of the experiment, I located 10 active foraging runs of kangaroo rats. Active runs were located by searching for fresh footprints and tail drags along trails leading to and from burrows (tail drags refer to curvilinear impressions left in sand by the tail of an individual). To ensure that foraging runs represented different individuals, runs were separated by >0.4 km. This distance exceeds home ranges reported for *D. ordii* (Garrison and Best 1990). Based on previous trapping of 24 foraging runs of kangaroo rats in the area, runs generally were used by a single kangaroo rat (67%), although some runs contained 2 individuals (8%). Only a single run (4%) contained another species (deer mouse [*Peromyscus maniculatus*]), and 5 runs (21%) had no sign of current rodent activity. I am confident that individual kangaroo rats were not visiting >1 experimental site, but multiple kangaroo rats might have visited a single site over successive nights of the experiment. In this scenario, the individual with the best

ability to detect buried seeds likely would detect and harvest the most caches, thus not necessarily confounding results of the experiment.

Along each foraging run, I selected a single, flat area >10 m from entrances of burrows. At these sites, I positioned 2 metal trays perpendicular across runs. In each tray (43.5 cm long, 28.5 cm wide, and 2.5 cm deep), I placed 2.4 liters of sand that was collected from a nearby blowout, sifted to remove debris, and dried in sunlight. The depth of sand in trays was about 24 mm. Trays were spaced ≤ 6 cm apart, and their top edges were set flush with the surrounding substrate. At each site, 1 tray contained dry sand and the other contained moist sand. To moisten sand, I added 40 ml of water to the 2.4 liters of sand in a plastic container and mixed contents until sand was evenly moistened. The relative position of moist and dry trays at foraging runs was varied on successive nights.

Next, I buried 4 clumps of seeds (millet [*Panicum miliaceum*]) in each tray to simulate caches of scatter hoarders. Seeds were placed about 24 mm below the surface. To ensure that seeds were in a tight cluster (i.e., all seeds in contact with others), I 1st placed a thin layer of sand on the bottom of each tray. Next, I made small indentations, placed seeds in them, and slowly poured remaining sand into trays. Finally, I gently pressed down on sand in the moist tray to ensure that sand in each pair of trays was at the same height.

Piles were randomly placed in trays, although each pile was ≥ 2.5 cm from an edge of a tray or from another cache. I determined random configurations by dropping 4 seeds outside of trays and replicating the pattern inside; these seeds were removed from each site. Before experiments, millet was dried in an oven at 60°C for 24 h and stored in sealed plastic bags to ensure that seeds were dry at the start of trials. I selected seeds of *P. miliaceum* because they resemble seeds of native *Panicum* at the study site, because I have observed they are sought after by Ord's kangaroo rats, and because they are easy to work with because of their uniform size and roundish shape.

For 5 nights, I conducted trials at each of the 10 sites. On the 1st evening, each cache consisted of a single seed; on the 2nd evening caches consisted of clumps of 5 seeds; on the 3rd evening, 10 seeds; on the 4th evening, 20 seeds; and on the 5th evening, 40 seeds. Size of artificial caches was increased systematically at each site to limit kangaroo rats from learning the whereabouts of this supplemental food source. Randomly assigning different-sized caches at experimental sites might have altered foraging intensity on nights succeeding larger-sized caches; thus, confounding the reliability of these data to determine the largest cache size that would remain unexploited by kangaroo rats.

Each evening, pairs of trays were deployed at experimental sites approximately at sunset and were examined 2–4 h later. Upon arrival at each pair, I examined tracks left in the sand. Because *D. ordii* leaves diagnostic footprints and tail drags, I could distinguish *D. ordii* from other foragers. After recording identification of foragers, I sieved contents of each tray separately and counted remaining seeds to determine the number of caches removed from each tray. When a cache was removed, generally all seeds in it were harvested; only occasionally were 1 or 2 seeds left by kangaroo rats. I considered caches removed even if 1 or 2 seeds were left by kangaroo rats. Other than these rarely missed seeds, I never observed kangaroo rats to harvest only a portion of seeds from larger-sized caches. Experimental trials for this part of the experiment were conducted from 5 to 21 June.

In the 2nd part of the experiment, procedures were identical to those described above except seeds were buried about 12 mm below the top surface of the sand. To ensure that seeds were in tight clusters at this depth, one-half of the sand was poured in trays and leveled. Again, I made small indentations in sand, placed seeds in depressions, and added remaining sand. Ten new sites were used for

these trials, and these sites were >0.4 km from all other sites, which represented new individuals. Trials for this part of the experiment were conducted from 12 to 24 June. Experimental trials from both parts of the experiment were conducted on the same evening during 5 evenings of the experiment.

A few of the original sites selected for experimental trials were abandoned because kangaroo rats did not visit them consistently ($n = 4$) or sign of another species of rodent was observed at a site ($n = 1$). For abandoned sites, all data previously gathered were disregarded and not reported herein. Additional sites were added until I obtained complete data at 10 sites for both parts of the experiment. This research followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) and was conducted under a protocol by the Animal Care and Use Committee at the University of New Mexico (protocol 20004).

To determine approximate moisture content of sand and seeds at the beginning of trials, I replicated trays containing moist and dry sand in the laboratory with sand from my study site. Samples of sand were taken immediately after mixing with water, and samples of seeds were taken after seeds were placed in moist sand for 1 and 2 h. Each sample was then weighed, placed in a drying oven for 24 h at 60°C, and reweighed to determine water content.

Data analysis.—I used repeated-measures analyses of variance (ANOVAs—SAS PROC MIXED; SAS Institute Inc., Cary, North Carolina) to assess the effects of substrate moisture (between-subjects factor) and cache size (within-subjects factor) on proportions of caches removed (response variable) at each depth because data collected on successive nights at each experimental site were not independent. In these analyses, experimental sites (i.e., foraging runs) were used as a block because pairs of trays (i.e., 1 moist and 1 dry) were placed at each site. I also ran repeated-measures ANOVAs (SAS PROC MIXED) to assess the effects of cache depth (between-subjects factor) and size (within-subjects factor) on proportions of caches removed (response variable) for both moist and dry substrates. In these analyses, experimental sites were independent of each other; thus, analyses lacked a blocking factor. Proportions of caches harvested from each tray were treated as 5 discrete values (0, 0.25, 0.5, 0.75, and 1) in analyses.

RESULTS

Trays moistened with 40 ml of water resulted in sand having a mean moisture content of 1.3% at the beginning of trials, and seeds in moistened trays contained averages of about 5.9% water after 1 h and 8.3% after 2 h. Trays containing dry sand had a mean moisture content of 0.3% at the beginning of trials, and seeds in dry sand contained averages of about 1.4% water after 1 h and 1.4% after 2 h. Because of differences in temperature and humidity at the field site, moisture content of the top layer of sand at the end of trials probably was slightly lower on warm, dry evenings; however, sand always remained moist below the surface layer. In every tray where kangaroo rats did not remove even a single cache, fresh footprints and tail drags of kangaroo rats were observed, indicating that individuals had indeed visited all trays and had an opportunity to detect and remove caches.

Cache depth.—Foraging success of Ord's kangaroo rats was influenced by depth of caches in dry sand (Table 1). In moist sand, no difference in exploitation was observed (Table 1); however, kangaroo rats harvested significantly more 10-seed

TABLE 1.—Results of a repeated-measures analysis of variance examining the effects of cache depth (12 and 24 mm) and cache size (1–40 seeds) on proportions of artificial caches exploited by Ord’s kangaroo rats (*Dipodomys ordii*) in central Nebraska in a moist and dry substrate.

| Source | df. | F value | P |
|-------------------|-----|---------|--------|
| Moist sand | | | |
| Depth | 1 | 1.19 | 0.28 |
| Size | 4 | 31.33 | <0.001 |
| Depth × size | 4 | 12.98 | 0.25 |
| Dry sand | | | |
| Depth | 1 | 5.31 | 0.02 |
| Size | 4 | 4.11 | 0.004 |
| Depth × size | 4 | 2.00 | 0.10 |

TABLE 2.—Results of a repeated-measures analysis of variance examining the effects of substrate moisture (moist and dry) and cache size (1–40 seeds) on proportions of artificial caches exploited by Ord’s kangaroo rats (*Dipodomys ordii*) in central Nebraska at 2 depths.

| Source | df. | F value | P |
|-----------------------|-----|---------|--------|
| Depth of 12 mm | | | |
| Moisture | 1 | 50.31 | <0.001 |
| Size | 4 | 31.33 | <0.001 |
| Moisture × size | 4 | 12.98 | <0.001 |
| Depth of 24 mm | | | |
| Moisture | 1 | 52.50 | <0.001 |
| Size | 4 | 34.55 | <0.001 |
| Moisture × size | 4 | 18.29 | <0.001 |

caches at a depth of 12 mm (34 caches) than at a depth of 24 mm (8 caches; $\chi^2 = 16.10$, *df.* = 1, *P* < 0.001; Fig. 1). Combining total caches exploited in both moist and dry sand, *D. ordii* harvested 143 caches at a depth of 12 mm below the surface compared to 90 caches at a depth of 24 mm. Depth

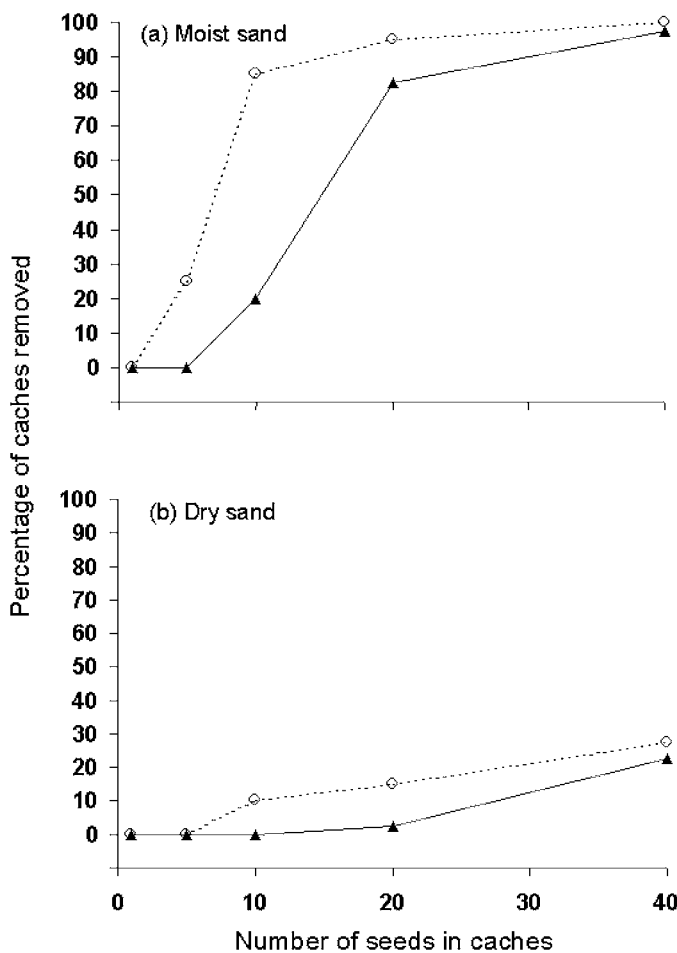


FIG. 1.—Exploitation of caches by Ord’s kangaroo rat (*Dipodomys ordii*) in a) moist and b) dry sand. Caches of different sizes were buried at 2 depths (open symbols = 12 mm deep; closed symbols = 24 mm deep).

influences removal of caches by kangaroo rats in moist sand (Fig. 1a). At each depth there was a threshold above which most caches were exploited by kangaroo rats. At a depth of 12 mm, the threshold was between 5 and 10 seeds/cache (25% of caches were removed when caches consisted of 5 seeds, but removal increased to 85% when caches consisted of 10 seeds); however, at a depth of 24 mm, the threshold was between 10 and 20 seeds/cache (20% were removed when caches consisted of 10 seeds, but removal increased to 83% when they consisted of 20 seeds). No threshold existed in dry sand for the cache sizes used in my experiment (Fig. 1b), although exploitation by kangaroo rats was consistently, but only moderately, higher at the shallower depth.

Moisture content of substrates.—Foraging success of Ord’s kangaroo rats was significantly influenced by moisture content of sand at both depths (Table 2). Overall, kangaroo rats removed significantly more caches in moist substrates (202 caches) than in dry ones (31 caches). In moist substrates, *D. ordii* removed almost all larger caches (≥ 20 seeds) regardless of depth (Fig. 1a). In contrast, kangaroo rats removed few caches and sometimes none when caches consisted of small quantities of seeds, even in moist substrates (Fig. 1). Interactions between moisture content of sand and cache size also were significant (Table 2).

Cache size.—The ability of Ord’s kangaroo rats to detect caches was significantly influenced by size of caches (Tables 1 and 2). As size of caches increased, kangaroo rats removed greater percentages of caches (Fig. 1).

DISCUSSION

Cache depth.—Kangaroo rats removed more caches at shallower depths. These differences likely were due to strengths of olfactory signals at the surface (Reichman 1981). Reichman (1981) proposed that odors emanating from 1 or more seeds behave like other molecules diffusing from a point source (i.e., as the inverse of the square of the distance). Thus, signals perceived by rodents at the surface should be stronger for shallower caches than for deeper ones of the same size. Considering the ability of competitors to use olfaction to pilfer caches, deeper caches should be less frequently pilfered. Devenport et al. (2000) reported that 13-lined ground squirrels

(*Spermophilus tridecemlineatus*) buried scatter hoards of sunflower seeds about 25 mm below the surface. These authors reported low rates of pilferage and attributed this to deeply buried caches.

Moisture content of substrate.—The ability of kangaroo rats to detect and harvest caches was enhanced in moistened sand, especially as cache size increased (Fig. 1). Increased exploitation of caches in moist substrates apparently is linked to increased detectability because of leakage of organic molecules when dry seeds absorb water (Duke et al. 1983; Simon and Mills 1983; Simon and Raja Harun 1972) and to increased vapor density of organic particles in moist substrates (Spencer et al. 1969; Taylor and Spencer 1990). These results are consistent with previous findings that foraging success of rodents increases with moistening of substrates or seeds (Cahalane 1942; Johnson and Jorgensen 1981; Vander Wall 1993b, 1995, 1998, 2000; Vander Wall et al. 2003).

Several genera of rodents (*Peromyscus*, *Tamias*, and *Perognathus*) are known to increase foraging success in moist substrates. The present study demonstrates that this is true for at least 1 species of *Dipodomys*. In contrast, Vander Wall et al. (2003) reported that Panamint kangaroo rats (*Dipodomys panamintinus*) recovered more caches from dry substrates compared to moist ones, which was the opposite of what these authors had predicted. I suspect that their results were confounded by their experimental design, which probably altered natural foraging behaviors of individuals. In their study, individuals were housed in enclosures, and experiments were conducted on an artificial substrate. Additional research on *D. panamintinus* in natural habitats using nonobtrusive methods likely will demonstrate that these granivorous rodents can detect caches more readily in moist substrates than dry ones.

Cache size.—Overall, Ord's kangaroo rats removed more large caches than smaller ones (Fig. 1). When caches contained ≤ 5 seeds, most caches were not exploited by kangaroo rats regardless of substrate moisture and depth (Fig. 1). As size of caches was increased over successive nights, exploitation was not constant. In moist substrates, exploitation rates were low for small caches and high for large ones, as shown in Fig. 1a. The sigmoidal curves demonstrate that for each depth, there is a threshold size at which frequency of exploitation increases rapidly. This pattern was not evident in dry sand (Fig. 1b), although similar types of curves might be obtained if experiments were continued with larger caches. Low exploitation rates in dry sand suggest that even relatively large caches remain undetected in dry conditions. In dry sand, exploitation rates reached a maximum of 27.5% in this study (Fig. 1b). Percentages of exploitation might be slightly higher than expected in dry sand because of the paired design of moist and dry trays in my experiment. After discovering large quantities of seeds in moistened trays, individuals might have searched adjacent dry trays more intensely. Thus, under natural conditions, exploitation rates of these large caches in dry sand probably would be lower than my results demonstrate.

Differences in exploitation for cache size are linked to strengths of olfactory signals at the surface (Reichman 1981; Vander Wall 1993a). Olfactory signals perceived by rodents

presumably are stronger for large caches compared to small ones at similar depths (Vander Wall 1993a). Only a few studies have reported changes in foraging success with changes in cache size. Reichman and Oberstein (1977) noted a positive correlation between size of a packet of seeds and digging effort in kangaroo rats, and Vander Wall et al. (2003) reported that as caches get smaller and deeper, the ability of rodents to detect caches decreases, especially in a moist substrate. The present study is the 1st to demonstrate that exploitation of different-sized caches is nonlinear, and above a certain size at each depth, nearly all caches may be quickly exploited by competitors. My results suggest that at each depth, there is a maximal number of seeds that caches can contain and still remain undetected by naive foragers.

Cache size was confounded with time because of the design of the experiment. Did kangaroo rats harvest more large caches because caches were larger or because individuals gained experience at each site over time? Because of my design, kangaroo rats had limited abilities to learn about this supplemental food source at experimental sites because smaller-sized caches purposely were used 1st. Unless individuals detected and selected not to harvest small caches during the 1st few nights, only exploitation rates during the last nights might be confounded (i.e., after individuals discovered caches for the 1st time). Assuming that individuals failed to harvest small caches because of lack of olfactory signals, the 1st dramatic increase in exploitation rate (i.e., the threshold) at each depth is not confounded with time. Thus, I would predict that exploitation rates should be similar, if not higher, for all larger caches even if experimental procedures were not confounded by time and were run independently. In addition, because the relative positions of moist and dry trays varied and because relatively few caches were exploited in dry trays (Fig. 1b), this also suggests that high rates of exploitation on large caches were result of detection and not result of increased foraging intensity.

Recent papers have demonstrated that human scent on seeds can influence detection by granivorous rodents (Duncan et al. 2002; Wenny 2002). In my experiment, no specific attempts were made to reduce exposure of seeds to human scent, and moist and dry replicates were treated similarly throughout trials. According to these recent studies, rates of exploitation by kangaroo rats might be overestimated in the present experiment. If correct, threshold size of caches would shift to the right in Fig. 1a, and, thus, caches would likely consist of more seeds before reaching threshold levels. Although seeds in dry sand also contained human scent, still relatively few caches were exploited (Fig. 1b).

Cache placement.—In general, studies report that smaller and deeper caches are more difficult for rodents to detect (Reichman and Oberstein 1977; Vander Wall et al. 2003). Although this might suggest that scatter hoarders bury a few seeds in deep caches, any analysis of optimal caching behavior must consider both the benefits and costs associated in making and retrieving caches (Andersson and Krebs 1978). Vander Wall (1993a) proposed that optimal caching depths are those where benefits minus costs are greatest. This study demon-

strated that optimal caching depths should fluctuate with environmental conditions (e.g., soil moisture), and there is an optimal size for caches at each depth with respect to exploitation by competitors.

For scatter hoarders, trade-offs exist between distributing many small or a few large caches, as well as distributing shallow or deep caches. Distributing larger caches may result in fewer total caches (thus, less digging, less traveling, and fewer locations to remember), but higher pilfering rates. In contrast, small caches may result in greater numbers of total caches (thus, more digging, more traveling, and more locations to remember), but lower pilfering rates. Shallow caches likely require less energy but result in higher rates of pilferage, whereas deep ones likely require more energy but result in lower pilfering rates. Reported attributes of scatter hoards by granivorous rodents demonstrate that caches tend to be small in overall size. For example, scatter hoards made by 8 species of heteromyids (including 2 species *Perognathus*, 2 of *Chaetodipus*, and 4 of *Dipodomys*) were shown to sometimes contain only a few seeds and usually contained many fewer seeds than could be carried in cheek pouches (Price et al. 2000). Vander Wall (1993a) also showed that yellow-pine chipmunks cache between 6 and 30 seeds from a few millimeters beneath the surface of soil to about 30 mm deep. Although chipmunks exhibited considerable variation in caching depths, deeper caches contained more seeds. These observations lend support to the idea that scatter hoarders may distribute caches in accordance to trade-offs associated with depth and size to reduce exploitation and detection by competitors.

When expressing the concept of exploitation and detection of caches by naive foragers, caution must be used because these terms may not be equivalent. Individuals might detect caches by olfaction but choose not to harvest them, possibly because of limited energetic returns or costs associated with recovery. Density of seeds and particle size of substrates have been shown to affect profitability of harvesting seeds from soils (Price and Heinz 1984). I suspect in the present study that detection and exploitation were similar. In other experiments not reported herein, I have observed kangaroo rats foraging for single seeds that were scattered in trays to depths of 24 mm. In that study, I commonly observed individuals systematically processing and discarding much of the sand in trays. It seems unlikely to me that kangaroo rats would detect caches consisting of 10 seeds at 24 mm below the surface and select not to harvest them because of the energetic costs of digging. Thus, I suspect my smaller artificial caches were not harvested because of lack of detection and not because they were deemed unprofitable.

My results demonstrated that substrate moisture can dramatically increase exploitation of caches, and therefore, should alter optimal caching strategies. In dry environments with long periods lacking rainfall, scatter hoarders should distribute larger-sized caches. In dry environments with regular bouts of precipitation, scatter hoarders should distribute only small caches (i.e., those below exploitation thresholds). In ecosystems with distinct wet and dry seasons, I predict that scatter hoarders will alter hoarding behaviors to prevent losses of caches either by altering size, depth, or both. In addition to

distributing caches at particular depths and of certain sizes, other concomitant strategies to reduce pilfering may include selecting areas where soils remain dry (e.g., under natural shelters) or where soils dry quickly (e.g., in open areas without shade or on south-facing slopes). Scatter hoarders should select cache sizes that are likely to remain undetected by competitors, even when environmental conditions fluctuate (i.e., natural perturbations such as rain). Further research on seasonal aspects of caching behaviors in environments with distinct wet and dry seasons would be informative.

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