

Scatter hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches

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We observed radio-implanted Merriam's kangaroo rats disposing of 10-g bonanzas of rolled oats in 48 trials in the field. The principal determinant of the initial disposition of discovered food was apparently its distance from the day burrow: food found within about 10 m was mainly larder hoarded, whereas food encountered farther afield was usually dispersed immediately in shallow caches. Cache sites were newly dug for the purpose and not reused; most caches were nearer the current day burrow than was the food source, but a few were placed far from both the cacher's day burrow and its habitual nocturnal range. An experiment with artificial caches indicated that security from discovery increases with spacing and with proximity to perennial shrubs. Nine kangaroo rats cached dyed food, and fecal dye traces revealed extensive pilferage from five of them, by both conspecifics and other rodent species. Limited evidence indicates that food encountered nearer home and initially larder hoarded was more secure from pilferage than food initially scattered, and yet kangaroo rats were observed to scatter caches soon after initial larder hoarding. A kangaroo rat whose dyed stores escaped pilferage fed from them at intervals for at least 12 days. Even cachers who incurred pilferage made as much, or more, use of their caches as any thief, suggesting that scattering caches may be a defense against catastrophic losses. [*Behav Ecol* 3:102-111 (1992)]

Morris (1962) coined the term "scatter hoarding" to describe the behavior of dispersing stored food in multiple, small packets. Because spatial dispersions of stored food can vary continuously, Vander Wall (1990) distinguishes scatter hoarding from larder hoarding on the basis of single versus multiple depositions to the storage site; we refer to the two sorts of stores as "caches" versus "larders." Larder hoarding is more prevalent in mammals, even with foods like seeds that are readily partible into small caches (Smith and Reichman, 1984), but a number of rodent species scatter nuts and seeds (Vander Wall, 1990).

If the function of hoarding is to sequester food from competitors for later use, a concentrated larder is practical only if it is defensible or well hidden. It follows that larder hoarding tends to be associated with territorial exclusion and that larders are often situated in occupied dens near the territory's center, in accordance with considerations of both larder security and central-place foraging economics (Orians and Pearson, 1979).

The adaptive logic of scatter-hoarding decisions is more complex and less well understood (Covich, 1987; Kramer and Nowell, 1980; Sherry, 1985; Vander Wall, 1990). Scatter

hoarding is apparently more time consuming than larder hoarding and certainly places more demands on memory (Balda et al., 1987; Jacobs, 1991); moreover, scatter hoarding makes one's food stores less handy when inclement weather or other circumstances impede excursion. One possible explanation for scatter hoarding is that it reduces the risk of major losses to cache robbers rather than simply minimizing the expected mean loss (Hurly and Robertson, 1990; Morris, 1962). Decisions about the number, size, specific locales, and spatial dispersion of caches influence the expected costs of scatter hoarding, and these costs must be elucidated before the behavior can be understood. Theory and research have dealt with the time and travel costs of caching and cache recovery and with the impact of the spacing of artificial caches on cache survival (reviewed by Vander Wall, 1990). However, almost nothing is known about pilferage from the actual caches of scatter hoarders.

Kangaroo rats (*Dipodomys*; Rodentia: Heteromyidae) are nocturnal, burrow-dwelling rodents of North American arid zones. They forage in open ground and transport the seeds they find in external fur-lined cheek pouches to be consumed or stored elsewhere. Hoarding practices and use of space vary within the

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genus. *D. spectabilis* builds and occupies defended mounds (Jones, 1984; Randall, 1984), around which activity is concentrated and centered (Schroder, 1979) and in which substantial stores are amassed (Vorhies and Taylor, 1922). In *D. merriami*, by contrast, home ranges overlap extensively (Behrends et al., 1986), and nesting burrows (day burrows) are less elaborate, are typically situated nearer the periphery than the center of the foraging range (present authors' unpublished data), are frequently switched or abandoned (Behrends et al., 1986), and seldom contain substantial stores (present authors' unpublished data; Kenagy, 1973; Monson and Kessler, 1940).

As the contrasts above suggest, *D. merriami* appears to be mainly a scatter hoarder. In captivity, this species buries seeds in caches containing about 1 g of seeds and, like other scatter-hoarding birds and mammals, has an excellent memory for cache locations (Jacobs, 1991). Reynolds (1958) set out small piles of non-native seeds and found caches, which he attributed to *D. merriami*, when seeds sprouted after a rain; he reported that the shallow caches were distributed in "random groups" around feeding stations at a mean distance of 14 m (range: 0.6–32 m). The travel necessary for establishing and recovering caches is demonstrably risky activity: in comparisons among contemporaneously radio tracked *D. merriami* of both sexes, individuals who traveled the farthest incurred the greatest risk of being preyed upon (Daly et al., 1990). Nevertheless, *D. merriami* pursues a wide-ranging, scatter-hoarding mode of existence that evidently demands greater travel than the territorial, central-place-foraging alternative practiced by *D. spectabilis*.

Several authors have claimed that kangaroo rats' caching behavior makes seeds unavailable to ants and birds. Caching is unlikely, however, to be completely effective against other rodents. Reichman and Oberstein (1977) found that captive *D. merriami* could detect and excavate 0.8-g seed packets buried at a depth of 20 cm, whereas caches of rolled oats, which we have uncovered in the field after seeing kangaroo rats make them, are usually buried only about 2–3 cm deep, and the animals allocate up to 1 g to each cache. Boyd and Brum (1983) claim that Mojave Desert *D. merriami* cache naturally collected *Larrea tridentata* seeds at depths of 2.5–5 cm.

In this paper, we report observations and field experiments with Merriam's kangaroo rats aimed at characterizing scatter-hoarding behavior and detecting pilferage. Where are caches situated relative to the food source, the home burrow, and one another? Is food differentially disposed of according to where it is discovered within the home range? Is there

significant pilferage? By whom? And does spatial dispersion of caches protect them from discovery?

METHODS

Study site and habitat

This research was conducted at the University of California's Boyd Deep Canyon Desert Research Station, about 3 km south of Palm Desert, California, USA (33°42' N, 116°22' W). The study site is located on the alluvial plain of Deep Canyon at about 250 m elevation and is centered upon a 1-ha grid of 100 trap stations in a 10 × 10 array at 10-m intervals. Each station is the site of a single Sherman live trap (8 × 9 × 30 cm). Beyond the trapping grid, markers (labeled stone cairns or stakes) extend in all directions at 10 m intervals, permitting researchers to quickly identify any locus in the mapped area (about 11 ha) as a pair of X and Y coordinates to a precision of 1 m.

The substrate is a mixture of pebbly "desert pavement" and sandy washes up to 40 m wide, with rocky patches and a few boulders. Mean annual precipitation at the Boyd Center Laboratory (1.4 km from our study site, at 290 m elevation) from 1961 to 1989 was 14.6 cm (SD = 10.0; range = 3.4–47.8 cm). The mean daily maximum temperature ranges from about 20°C in January to about 40°C in July, and the mean daily minimum is from about 11°C to 27°C. Vegetation is denser and of more diverse species composition than in most *D. merriami* habitats. Essentially similar to our site is one nearby described in detail by Zabriskie (1979), at which 14% of the soil surface lay under the canopy of perennial shrubs, of which creosote bush (*Larrea tridentata*) was the commonest species.

Radio tracking and general fieldwork practices

We radio tracked kangaroo rats at the Deep Canyon field site annually from 1980 to 1990, during research periods of 1–7 months, beginning in November or December. At the beginning of each research period, we trapped on 4 to 6 consecutive nights to assess survival of marked animals, to mark those newly captured, and to select animals for implantation with radio transmitters emitting individually identifiable signals. We concentrated radio tracking efforts on centrally located, neighboring resident animals, tracking up to 25 simultaneously. For detailed accounts of radio implantation and tracking procedures, see Behrends et al. (1986) and Daly et al. (1990). We left the 100 grid traps in place throughout each research period, but opened them only

on certain trapping nights (usually once or twice per week after the initial 4 to 6 trapping nights; see Daly et al., 1990). A trapping night entailed baiting each of the 100 traps at dusk with about 1 g of rolled oats, checking for captures and closing the traps 2–5 h later. We recorded trap site, species, sex, individual identity, weight, and reproductive condition of each captured animal, then released it (unless scheduled for radio removal or implantation) at the capture site. Rodents were distinctively marked by toe clipping until 1988, and by passive integrated transponders (PIT tags, Destron) after 1988.

Primary radio tracking data consist of daily locations of each animal's day burrow and hourly locations for 6–14 h on most nights. In addition, we collected more than 1000 h of nocturnal focal-animal follows (durations 15 min–6 h), during which we radio located a target animal and followed on foot, avoiding sudden or rapid movements, while recording whereabouts as continuously as possible (typically by speaking softly into a tape recorder), observing the subject under dim headlamp illumination, and making behavioral observations opportunistically. Although it must be conceded that individuals vary in observability and that it is difficult to determine to what extent human presence influences the behavior of even a well-habituated animal, most kangaroo rats seem unconcerned about human observers after a few hours of focal following.

General procedure of provisioning trials

To observe hoarding behavior, we conducted 48 trials in which radio-implanted kangaroo rats already habituated to observers were provided with small food bonanzas in the field. These trials were conducted over the course of 6 years with 26 subject animals provisioned 1–3 times each. In each trial, we radio located the target kangaroo rat, either in its day burrow before emergence at dusk or during its nocturnal travels, and placed a petri dish containing 10 g of rolled oats on the ground nearby. We then stood back and kept the dish under watch with headlamp illumination, verifying by radio signal that the target animal was indeed the discoverer and collector of the food, and shooing away any interlopers (other kangaroo rats and pocket mice) until the target animal had emptied the dish. Provisioned animals usually collected the full 10 g, but on five occasions we terminated trials when provisionees failed to return to the dish for a prolonged period after taking 5.7–8.3 g.

In most trials, one observer kept watch at the food dish and recorded the duration of cheek-pouch loading episodes and of absences between loadings, while a second observer fol-

lowed the provisioned kangaroo rat to see where the food was taken. For each round-trip excursion from the food dish, we recorded whether the animal returned to its day burrow, as well as the coordinates of successive locations visited by the animal, whether or not caching was observed. Caching behavior is distinctive; the animal inserts its snout in a shallow depression and rocks as it empties its cheek pouches. Kangaroo rats on our study site placed about 0.3–1.0 g of oats in each cache, then covered it with soil to a depth of 0.5–3.0 cm. (We have verified that this behavior represents caching by temporarily exposing the cache's contents after seeing kangaroo rats cache pouched oats upon release from traps, but only a few caches were verified in this way during the 48 provisioning trials because of concern that our interference might affect the cache's discovery by pilferers or its treatment by the cacher; see "Pilferage observed directly" in the Results section.) Observation of caching was limited, however, by our efforts to avoid startling the animals or approaching too closely and by the apparent secretiveness of cachers, who make rapid zig-zag runs, duck through shrubbery, and seem reluctant to cache while being watched. Thus, most cache sites could not be determined precisely.

Some further details of procedure changed over years, and these changes can be described with reference to three "series" of trials.

Variable procedures of successive series of provisioning trials

Series 1

We conducted 18 trials with 6 subjects in December 1983. Five kangaroo rats (3 females, 2 males) were randomly selected from among 13 then being radio tracked, and each was provisioned on 3 successive nights. We presented food on the first night at about 2000 h (after an initial four or five hourly radio locations) and on the second and third nights immediately after dusk. Provisioning sites were situated 2, 2, 3, 10, and 17 m from the five recipients' initial day burrows. (One animal switched day burrows daily over the three trials.) We recorded locations hourly from dusk to midnight for all radio-implanted animals on provisioning nights, as well as on several successive nights before and after.

A sixth animal with exceptional spatial habits was also provisioned for 3 successive nights, after the others. This female's day burrow site lay outside her nocturnal range, to which she ran directly upon emergence after sunset each night. During 91 scheduled hourly radio locations between dusk and midnight and during focal follows totaling 270 min, she never

returned to her day burrow or approached within 24 m of it, although she was found to have returned there each day. To see what an animal who so assiduously avoided her day burrow area during her nocturnal travels would do upon finding food in the farthest corner of her habitual range, we provisioned her at a site which she visited nightly 109 m from her day burrow on 3 successive nights.

Series 2

To compare hoarding behavior when food was discovered near home versus farther away, we ran 20 trials with 11 kangaroo rats (6 females, 5 males) in December 1985. Seven subjects encountered food near the day burrow entrance on one occasion (mean distance 1 m) and at another shrub 8–39 m away (mean 24 m) on another occasion; repeat trials for the same subject were separated by 3–9 nights (mean 5.9). For two other animals, efforts to provision near the day burrow entrance failed, and they received two trials each at different sites between 10 and 17 m from the day burrow. Two additional females were each provisioned only once, at distances of 1 and 2 m from their respective day burrows.

Series 3

We conducted the final 10 trials with dyed food to detect pilferage. Nine subjects were used. We provisioned the first (female 1000) with red-dyed oats for 2 successive nights in December 1986; food was presented 1 h after sunset at sites 13 and 12 m from her day burrow, and the caching trips and post-trial behavior of this well-habituated animal were closely observed. We then trapped the 1-ha grid according to our standard routine (see above), with undyed rolled oats as bait, on the first, third, and fifth nights after provisioning and assessed fecal dye presence.

We conducted eight further dyed-food trials in the next two Decembers, with each animal provisioned only once. Subjects (5 females, 3 males) were animals who had been reliably captured on prior trapping nights. Distances between food sources and day burrows were 0, 3, 4, 9, 15, 18, 19, and 31 m. We separated provisioning trials in time and space to facilitate correct attribution of trace amounts of dyes to their sources, conducting two red-dye trials and two green-dye trials each year. In each case, the grid was trapped on the two nights immediately after provisioning and on several subsequent nights, and fecal dye was assessed in all captured rodents.

Fecal dye assessment and detection of pilferage

To prepare dyed food, we dipped oat flakes briefly in a strong solution of red dye (Eosin

Y, Fisher) or green dye (Fast Green FCF, Fisher) and spread them on paper towels until dry. Feeding experiments with captive animals in the laboratory demonstrated that (1) feces collected 24 h after providing an animal with dyed oats strongly colored water into which the feces were dropped; (2) dye was conspicuous in the feces of an animal provided with just 1 g of the dyed food; (3) dye was scarcely detectable in feces passed 48 h after dyed oats were removed and replaced with ad libitum undyed oats; and (4) kangaroo rats accepted dyed oats as readily as undyed and when provided with both ate them in proportion to the available quantities. (Some other dyes were found to affect palatability in laboratory tests and were therefore not used in field trials.)

On each trapping night during provisioning series 3 (see below), we collected two to eight fecal boluses from each captured rodent, in addition to the usual data (species and individual identity, sex, weight, and condition measures). We placed collected feces in glass vials labeled with the trap number and took the vials to the laboratory, where we added a few drops of tap water to each vial.

After 20–30 min, we examined vials for evidence of dye, which was subjectively judged strong, medium, faint, or absent by judges blind to rodent identity. Fewer than 10% of vials exhibited any such evidence, and those that did were usually unequivocal; some faint samples were deemed ambiguous in regard to the presence of red dye (see Results), but never in regard to green dye. We determined that these judgments were reliable in two ways: (1) in several trials, two or three judges independently categorized the vials as “definite,” “faint and ambiguous,” or “none” with perfect agreement; and (2) split-sample trials, in which the feces of more than 100 captured animals were split between two vials and judged blind, produced unanimously concordant judgments (i.e., no split sample ever produced one dye-present and one dye-absent judgment). Evidence for the validity of these judgments is that the samples in which dye was detected consistently proved to be those of the provisioned animal and its neighbors (see Results).

Thus, although the method may have allowed “misses” (failures to detect existing dye traces), we conclude that it did not produce “false positives” and hence that the results provide minimum estimates of the numbers of animals who consumed some of the oats from a given provisioning trial.

Seed survival as a function of spacing of artificial caches

An experiment to determine whether spacing among caches affects risk of discovery was

conducted at a site vegetationally and topographically similar to our principal study area but several hundred meters away. We filled plastic cups 3 cm in diameter and 4 cm deep with aquarium gravel and buried known numbers of millet seeds in the cups at a depth of 1 cm. We then dug small depressions of the same dimensions at various sites and placed each cup snugly within such a depression, its lip flush with the ground. We returned 24 h later to count the remaining millet seeds.

A total of 360 seed cups were thus situated in the field, in 120 triplets arranged as equilateral triangles. In each triplet, the three cups contained 4, 8, and 16 millet seeds, respectively. We situated the triplets without regard to the proximity of vegetation and recorded the distance from each cup to the nearest perennial shrub. Twenty triplets were established in each of six spacings: The sides of the triangles were 0.25, 0.5, 1, 2, 4, and 8 m in length. Cups that were not part of the same triplet were situated at least 50 m apart.

RESULTS

Observations of caching behavior

Provisioned kangaroo rats typically emptied the food dish in less than 30 min from the time of its discovery and occasionally in less than 10 min. This required 5–10 “loading” episodes in which the animal stuffed oats into its cheek pouches at the dish, departed, deposited the food elsewhere, and returned.

After loading at the food dish, kangaroo rats did one of three things: (1) took the food directly to the day burrow (all loads on 19 of the 48 trials, some but not all on an additional 8); (2) took the food to another nearby burrow within 6 m of the food source (all loads on 5 trials, some but not all on an additional 6); or (3) immediately scattered the food in caches (all loads on 11 trials, some but not all on an additional 12).

At least one act of caching was seen in 22 trials involving 18 kangaroo rats and 59 cache sites were discovered. Twenty-six of the discovered caches (44%) were situated in open terrain away from shrubs (mainly in sandy washes but also under the edges of stones or dead wood); 24 (41%) were placed under or at the edges of shrubs (usually small ones without evident burrows); and 9 (15%) were placed under the drooping canopies of palo verde (*Cercidium floridum*) trees. Up to three caches, separated by as little as 60 cm or as much as 40 m, were created from a single load before returning to the food dish.

Discovered cache sites were located at a median distance of 8 m from the provisioning site (range 0.5–49 m), but 9 different kangaroo rats were observed making at least one

cache more than 20 m from the food source. These distances probably underestimate actual food transport and cache dispersion because we occasionally lost sight of those animals who made longer trips and reestablished visual contact only as they returned to the provisioning site; six different kangaroo rats made rapid round trips to points more than 40 m from the food dish, but only two of the six were seen caching on these distant trips.

The lone animal who was provisioned more than 100 m from her day burrow in series 2 produced the most spatially dispersed set of caches: although she made most of her caches within 10 m of the food source on all three trials, she carried some loads much farther, up to a maximum of 65 m, and in several directions. The resultant dispersion was such that her caches were up to 85 m from one another, and a few of her caching trips took her 20 m or more beyond areas in which she was ever otherwise radio-located. On no caching trip did she approach within 40 m of her day burrow.

There was a tendency for the distance traveled with successive loads to increase (Figure 1). An index of this tendency within a trial is the rank order correlation between the maximum transport distance for each load and its ordinal number. By this index, the trend was in the direction of successively greater transport in 9 of the 11 trials in which subjects engaged in pure scatter hoarding and in the opposite direction on 2 ($p = .03$ by one-tailed sign test); however, in only one trial was the trend perfect in that every load ($N = 5$) was taken farther than the preceding one.

In four trials in which food was initially hoarded to a burrow other than the day burrow, the animal embarked on scatter hoarding immediately after sequestering the food. The four different kangaroo rats involved were all observed making caches, at distances ranging from 5 to 26 m away, within 6 min of having deposited their last loads in the burrow. Four additional animals who embarked on wide travels immediately after hoarding to a burrow appeared to be behaving similarly, although they were not seen caching food. Even those who initially scatter hoarded were sometimes observed making more distal caches a little later. One female traveled no farther than 16 m from the food dish until it was emptied, then embarked on a series of rapid round trips to several more distant points. Another female, who was tracked to points up to 24 m from the food source while initially scattering eight loads, was then seen making a new cache 33 m away, 47 min after having completed the trial.

In one case, a male was observed re-opening and emptying a cache he had made 52 min

earlier. We also checked the longevity of two caches (in different series) by temporarily uncovering them and then rechecking 90 min later. Both caches had disappeared, reinforcing the possibility that initial cache sites may often be only temporary. However, these caches may have been raided by animals other than the cacher; when a third cache was pilfered shortly after we uncovered and reburied it (see "Pilferage observed directly," below), we abandoned such checks.

The mean spatial position of discovered caches was closer to the cacher's day burrow than was the food source in 15 trials and farther away in just 7 ($p = .07$ by one-tailed sign test). Thus, caching generally entailed shifting the food a little closer to the cacher's day burrow, although not dramatically closer. Only 11 of 59 discovered caches (19%) were within 10 m of the cacher's day burrow, and 6 different animals were seen caching at least 30 m from home. At least a few cache sites were placed nearer to some other radio-implanted animal's day burrow than to the cacher's own; in the most extreme such example, a male in a series 2 trial made his final cache 31 m from his own day burrow and just 5 m from that of a female (who was in her burrow at the time).

Proximity to day burrow and the scatter-larder decision

The principal determinant of the initial disposition of discovered food was apparently its distance from the day burrow. All seven animals in series 2 took more loads to the day burrow in the trial when food was found near home than when it was found farther away ($p < .01$ by sign test). The disposition of cheek pouch loads as a function of this distance is summarized in Table 1.

Animals sometimes scattered a load or two when food was discovered near home, but they scattered all loads only if the food was encountered at some distance from home. The distance from food source to day burrow in the 11 trials in which animals scattered all

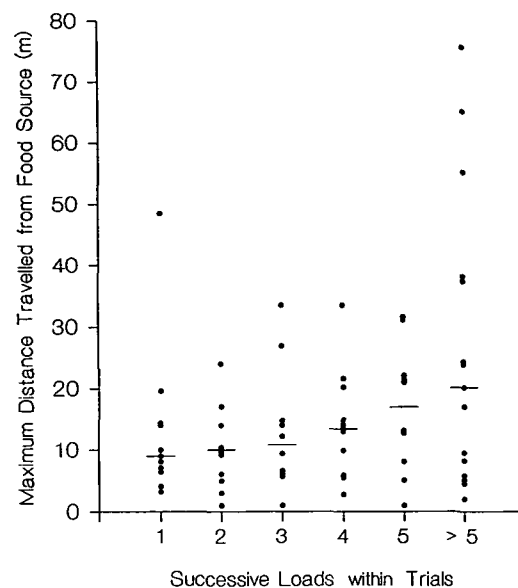


Figure 1 Maximum distances from the food source at which kangaroo rats were observed or radio-located while scatter hoarding successive cheek pouch loads for the 11 trials in which animals engaged in pure scatter hoarding. Each data point represents one round trip. The horizontal bars represent the median maximum distance for each ordinal load number.

loads ranged from 10 to 109 m (median 31 m). On the other hand, food found close to the day burrow was usually taken directly there: The distance from food source to day burrow in the 19 trials in which animals took all loads there ranged from 0 to 17 m (median 2 m). These distributions scarcely overlap (Mann-Whitney $U = 9$, $p < .0001$).

Corresponding distances for the five trials in which all loads were taken to a burrow other than the day burrow were 9–22 m (median 17 m), farther than when food was initially taken to the day burrow ($p < .01$ by Mann-Whitney test), but not different from trials in which food was initially scattered.

Pilferage observed directly

During a series 2 trial, in which female 3100 was provisioned just 2 m from her day burrow but scattered most loads directly, we observed prompt pilferage of two caches by a single cache robber, male 0500, who lived 39 m away.

At 1755 h, on her seventh load, female 3100 made a cache 5 m from the food dish and 10 cm from the edge of a small cheese bush (*Hy-*

Table 1 Initial disposition of found food in relation to the distance between the food source and the day burrow

Distance from food source to day burrow (m)	Number of trials	Mean number of loads	Mean proportion of loads initially disposed of by		
			Taking to day burrow	Taking to other burrow	Scattering immediately
0–5	22	6.9	0.79	0.06	0.15
6–10	5	7.6	0.22	0.40	0.38
11–20	13	6.9	0.25	0.28	0.47
>20	8	7.4	0.00	0.18	0.82

menoclea salsola); when she left, we opened the cache, removed its contents to weigh them (0.70 g), replaced them with about the same quantity of oats, and covered them again. At 1759 h, on her eighth load, female 3100 made another cache under a log in a sandy wash 7 m from the food source and 11 m from the previous cache; we did not disturb this cache. At 1820 h (while female 3100 was more than 25 m away), male 0500 opened and emptied these two caches, which were 41 and 35 m from his own day burrow, in rapid succession, and recached their contents among some small cheese bushes 27 and 16 m from the sites where female 3100 had cached them, 26 m from his own day burrow and 22 m from female 3100's burrow.

Pilferage inferred from fecal dye traces

Sixteen to 47 rodents were trapped and assessed for fecal dye on trapping nights after series 3 trials. At least five of the nine animals provisioned with dyed oats were victimized by cache robbers.

For three subjects, the food dish was placed within 4 m of the day burrow, and none of these three incurred any detected pilferage. Females 2005 and 3020 took all food to their day burrows within 19 min of discovery, whereas male 0220 quickly deposited five loads in his day burrow before scattering two loads (caches were located 14 and 13 m away). Male 0220's feces exhibited dye 1 and 2 days after provisioning, but not at 5, 8, or 9 days. Female 2005's feces exhibited dye 1 day and 8 days after provisioning, but not on days 2 and 5. Female 3020's feces exhibited dye strongly on days 1, 4, 7, and 13, less intensely on days 2 and 10, and not at all on days 8 and 11, implying that she fed on dyed stores 12 days after provisioning.

For the other six animals, the food dish was placed at distances of 9–31 m from the day burrow, and five of these six animals incurred detected pilferage. None of these six animals took any food directly to their day burrows. Four animals (females 1000 and 4030; males 2400 and 2003) scattered all loads, taking 20–55 min to complete the task. The other two animals (females 1300 and 3040) initially took all loads down nearby holes other than the day burrow, but then set about scattering caches within 5 min of emptying the dish. Only male 2400, who exhibited dye on days 1 and 2 but not on days 5 and 8, apparently escaped pilferage.

This difference (pilferage from 0 of 3 who initially larder hoarded to the day burrow versus 5 of 6 who did not) is marginally significant ($p = .05$ by one-tailed Fisher's Exact test). It is unclear, however, whether the relevant fac-

tor was the food dish's placement (near versus far) or the hoarding behavior (day burrow versus scatter) because the two were perfectly correlated.

Ten individual rodents were unambiguously identified as pilferers, representing every nocturnal rodent species captured on the study site: three kangaroo rats (*D. merriami*; one female, two males), three cactus mice (*Peromyscus eremicus*; two females, one male), three spiny pocket mice (*Chaetodipus fallax*; all males), and one silky pocket mouse (*Chaetodipus formosus*; male). Six additional possible pilferers (fecal dye traces judged "faint and ambiguous") were a female *D. merriami*, a male *P. eremicus*, and four male *C. fallax*. Thus, a single animal's caches might be raided by several pilferers. On the first trapping night after female 1000's two nights of provisioning, dye was evident in the feces of 5 of the 39 rodents captured: female 1000 herself, two male kangaroo rats, a pocket mouse, and a cactus mouse. Female 4030 may have been robbed by as many as six pilferers after scattering eight loads on her single provisioning, for on the following night dye was evident in the feces of one pocket mouse and was ambiguous in three more, and on the second trapping night dye was also evident in one cactus mouse and ambiguous in one kangaroo rat, neither of whom had been trapped the previous night. Female 3040 was raided by two pocket mice; male 2003 was raided by two pocket mice and perhaps one cactus mouse; and female 1300 was raided by a conspecific female.

Even the most heavily raided animals, however, apparently were able to make as much or more use of their caches as any pilferer. In three cases, dye faded or disappeared from the feces of retrapped pilferers while remaining evident in the provisioned animal's feces. (However, not every known or suspected pilferer was recaptured every night.) In a fourth case, dye disappeared from pilferers' feces after night 2, but the provisioned animal (female 4030) and one pilferer were not retrapped for purposes of comparison. In the fifth case, dye disappeared from the provisionee and the sole pilferer together. Most importantly, there was not a single trapping night on which dye was detected in a pilferer's feces while absent from the provisionee's, nor even a case in which the provisionee's fecal dye trace was of a lesser intensity than that of any other animal.

Seed survival as a function of spacing of artificial caches

After 24 h, 37% of the 3360 millet seeds in 360 artificial caches had disappeared. Most cups were undisturbed ($N = 198$; 55.0%); a single seed was missing from another 22

(6.1%). If more than one seed was gone ($N = 140$), usually all were gone ($N = 121$) for all but one ($N = 13$). Cups from which more than one seed had disappeared were thus considered “discovered.”

A cup’s risk of discovery was unrelated to the number of seeds it contained: 47 4-seed cups (39%), 46 8-seed cups (38%), and 47 16-seed cups (39%) were discovered. Cups farther from perennial shrubs were more likely to be discovered: 67/196 (34%) of those within 1 m of the nearest shrub; 54/134 (40%) if 1–2 m away; and 19/30 (63%) if more than 2 m away ($p < .01$ by Moses’s ordered categories test; Moses, 1986: 416).

Seed removal appeared to be mainly the work of rodents. Gravel had been dug out of almost every cup from which seeds were missing; 10 cups were pulled from the ground (but moved no more than a few centimeters). We saw ants in a few emptied cups, but in each such case the gravel had evidently been dug out by a rodent; only one cup appeared undisturbed and yet was missing a seed.

Increased spacing within triplets reduced losses. At 25–50 cm spacing, 51% of cups were discovered; 40% were discovered at 1–2 m, and 26% at 4–8 m ($p < .01$ by Moses’s ordered categories test). The probability that a triplet would completely escape discovery was not significantly related to spacing (38% of triplets at 25–50 cm; 45% at 1–2 m; 55% at 4–8 m; $p > .10$), but the probability that at least one of the three cups would escape discovery was significantly related to spacing (63% of triplets at 25–50 cm; 73% at 1–2 m; 90% at 4–8 m; $p < .01$). Given that a particular triplet was discovered at all, increased spacing lowered the risk that all would be lost (Figure 2).

DISCUSSION

The initial choice between scatter- and larder-hoarding tactics depended primarily on the distance between the food source and home (Table 1). It is perhaps surprising that the switch from taking food home to taking it elsewhere occurred as little as 8–10 m from the day burrow, a distance these animals can traverse in less than 2 s (Kenagy, 1973). If larder hoarding is only a stop-gap en route to scatter, however, it may be worthwhile only when it can be achieved inconspicuously as well as quickly. Vander Wall (1990) notes the “secretiveness” of animals engaged in food caching, and kangaroo rats habituated to our presence seemed to become more evasive when scatter hoarding. In the only acts of cache pilferage that we observed directly, the robber raided in less than 1 min two caches that had been established successively in distinct microhabitats 11 m apart; a possible explanation is that

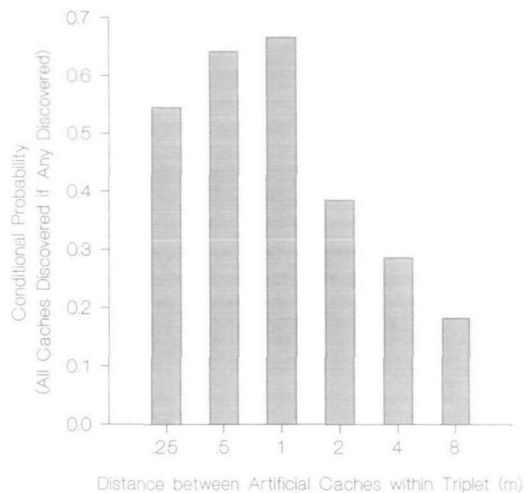


Figure 2
Effect of the spacing of artificial caches upon the conditional probability that all three caches in an equilateral triangular array would be discovered within 24 h if any one of them was discovered.

the pilferer had witnessed the caches being made.

Stapanian and Smith (1984) proposed that in order to space caches adequately to thwart pilferers while minimizing expected losses at the food source, a scatter hoarder should carry successive loads farther. Clarkson et al. (1986) used a model with more continuous costs of increasing cache density to predict that successive caches would be established farther from the food source only on average, as animals would continue to situate some near the source while maintaining a gradient of decreasing density. Marsh tits (*Parus palustris*) behave in contradiction to both models by carrying early items significantly farther than later ones (Sherry et al., 1982). Kangaroo rat behavior is more consistent with these models, matching Clarkson et al.’s (1986) analysis somewhat better than Stapanian and Smith’s (1984) (Figure 1). However, a few animals defied both models by making long trips and establishing distant caches early in the caching sequence.

The utility of scatter hoarding is compromised to the degree that a pilferer who discovers a cache becomes likelier to discover others. In particular, pilferers might improve their detection rates by adopting area-localized search tactics after a discovery (Tinbergen et al., 1967), so caches should be spaced sufficiently to eliminate this tactic’s utility. Our finding that increased spacing of artificial caches protected the caches from discovery is similar to that of other studies, although not all experiments have found such effects (review by Vander Wall, 1990). Reduced risk of losing all caches within a triplet was conspicuous at nearest-neighbor distances of 2 m or more (Figure 2), and provisioned kangaroo rats indeed typically distributed caches at least 2 or 3 m from one another, although pairs of caches were twice created as close as 60 cm.

The finding that artificial caches were more

vulnerable when situated farther from perennial shrubs is surprising in view of considerable evidence that kangaroo rats escape competition from pocket mice in such open areas (Price and Brown, 1983). It remains to be seen whether the same is true of natural caches and also whether kangaroo rats show adaptive preferences for relatively safe cache sites. Observed cache sites in the present study are unlikely to be representative: Differential visibility probably biased us toward a better detection rate for caching in open terrain, whereas our presence may have biased behavior in the opposite direction, as animals sought cover to cache in secrecy. Also surprising was the fact that cache discovery was unaffected by cache size over the range of 4–16 millet seeds.

An incidental implication of the present results is that the conclusions drawn from certain studies using dyed foods to characterize species differences in foraging microhabitats may need revision. Price (1977) and Lemen and Rosenzweig (1978) scattered differentially marked seeds in different microhabitats and inferred foraging preferences from fecal residues; kangaroo rats had eaten mainly seeds found in open spaces, while pocket mice had apparently fed more widely. The possibility of pilferage was not considered, however, and it is possible that pocket mice used a narrower range of foraging microhabitats than these authors inferred, never foraging far from shrubs but raiding kangaroo rat stores often enough to create the impression of having done so.

The fecal dye results and the intensity of pilferage imply that Merriam's kangaroo rats are short-term hoarders (Vander Wall, 1990) who cache food for recovery within hours to a few days, rather than for use months later. When stores escaped pilferage, however, dyes disappeared and reappeared in cachers' feces up to 13 days after provisioning, and we never checked for even longer storage.

This study provides the first evidence of which we are aware that scatter hoarders suffer significant pilferage. The short survival of artificial caches could have turned out to be artificial: caches created by the animals themselves might have proven to be secure. But such was not the case. Five of nine kangaroo rats provisioned with dyed food lost cache contents to other rodents within 24 h.

The results suggest that scattering is more likely to incur pilferage than larder hoarding, raising the question why the animals ever scatter hoard. A hypothesis for future study is that scattering entails acceptance of lower expected yield in exchange for reduced risk of major loss. This would be analogous to the variance-reducing function of "risk-sensitive" foraging

tactics (Real and Caraco, 1986): If the expected fitness value of increments in stored food exhibits diminishing returns, then strategies that reduce the variance in expected losses to rivals can be favored over those that simply minimize the mean loss. The fact that scatter hoarders who suffered pilferage nevertheless retained a large share of their stores is consistent with this possibility, as is the finding that increased spatial dispersion of artificial cache triplets did not affect the risk of partial loss but lowered the risk of total loss.

Three animals who larder hoarded dyed food to the day burrow incurred no detected pilferage, and the day burrow is indeed an area of relatively exclusive use as compared to most of the home range (Behrends et al., 1986). However, other observations suggest that day burrows are not completely secure. Kangaroo rats on our site typically plug their burrows by day but leave them open by night, and outside the context of provisioning trials, we have seen both kangaroo rats and pocket mice enter the current day burrows of temporarily absent residents; we once saw a pocket mouse emerge from such an intrusion with bulging cheekpouches. At present, we cannot conclude that larder hoarding by Merriam's kangaroo rats is anything other than a short-term, rapid-sequestering tactic employed before scattering, since at least a few animals embarked on scattering expeditions shortly after larder hoarding. Only further study can determine whether larders ever persist, whether they really incur less pilferage on average than scattered caches, and, if so, whether scatter hoarding reduces the risk of major loss.

Other questions about the adaptive logic of kangaroo rat scatter hoarding raised by our results and demanding further research include whether the interspecific flow of pilfered resources is balanced or parasitic; whether pilferage is a distinct mode of behavior from foraging for uncached seeds and, if so, whether some animals specialize as "scroungers" (Barnard, 1984); and why kangaroo rats disperse their caches so widely, including even placing them beyond areas that the cacher routinely visits or passes near.

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