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SCATTER-HOARDING BEHAVIOR OF DEER MICE (*PEROMYSCUS MANICULATUS*)

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ABSTRACT.—Deer mice (*Peromyscus maniculatus*) are known to larder hoard food, but their scatter-hoarding behavior is poorly documented. Eleven deer mice were each presented with 150 Jeffrey pine (*Pinus jeffreyi*) seeds in 10 × 10-m enclosures in Jeffrey pine forests on the east slope of the Sierra Nevada. Subjects made a mean ± 1 s of 31.2 ± 30.0 caches per trial. Caches were shallow (most 2–12 mm deep) and usually contained only 1 or 2 seeds. Most caches were made at the edge of antelope bitterbrush (*Purshia tridentata*) shrubs in mineral soil or in thin layers of plant litter. These results suggest that deer mice might make a significant contribution to the dispersal of Jeffrey pine.

Key words: caching behavior, granivory, Jeffrey pine, mutualism, *Pinus jeffreyi*, seed dispersal, Sierra Nevada, *Peromyscus maniculatus*, deer mice.

Deer mice (*Peromyscus maniculatus*) store a variety of food items in larders in and near their nests. These larders may contain more than a liter of food, which is often segregated by plant species (Howard and Evans 1961, Eisenberg 1968). Frequently reported items include acorns, *Prunus* stones, and seeds of grasses and forbs (Criddle 1950, Howard and Evans 1961). Deer mice usually gather and store seeds and nuts in autumn (Cogshall 1928, Criddle 1950, Howard and Evans 1961, Barry 1976, Tadlock and Klein 1979, Jaeger 1982), and the larder probably serves as an important food reserve for the mice during winter. However, deer mice have seldom been reported to scatter hoard seeds. Eisenberg (1962, 1968) briefly described the preparation of small surface caches by captive members of the genus. Abbott and Quink (1970) found that white-footed mice (*Peromyscus leucopus*), close relatives of deer mice, scatter hoarded white pine (*Pinus strobus*) seeds under pine needle litter. Sullivan (1978), however, reported that deer mice did not scatter hoard conifer seeds at a site in coastal British Columbia.

The purpose of this report is to describe scatter-hoarding behavior of deer mice, including cache sizes, depths, and placement of caches in different microhabitats and substrates. We conducted the study in large enclosures in the field. Understanding scatter-hoarding

behavior of deer mice will allow us to appreciate better the role of food storing in the lives of deer mice and potential influences of deer mice on animal and plant communities. Results reported here were gathered as part of a larger study on interactions of deer mice and yellow pine chipmunks (*Tamias amoenus*) over cached pine seeds (Vander Wall 2000).

STUDY AREA

We conducted this study at the Whittell Forest and Wildlife Area, Washoe County, Nevada, in the Carson Range of extreme western Nevada about 30 km south of Reno, Nevada (39°15'10"N, 119°52'35"W). Elevation is 1975 m. Experimental enclosures were located in antelope bitterbrush (*Purshia tridentata*) shrubland openings in Jeffrey pine (*Pinus jeffreyi*) forest. Soils consist of decomposed granite.

METHODS

We conducted caching trials inside five 10 × 10-m rodent-proof enclosures. Enclosure walls extended ≈75 cm aboveground and ≈45 cm belowground and consisted of 6-mm hardware cloth supported on a wooden frame. Tops of the walls had 20-cm-wide aluminum flashing on the inside and outside to prevent rodents from leaving and entering the enclosures.

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In each enclosure we buried a plastic 20-L nest bucket in the ground such that the lid was level with the ground surface. Horizontal plywood dividers partitioned the nest bucket into 3 levels. Mice could move freely between levels through holes 4 cm in diameter in the partitions. The bottom level contained soil \approx 2 cm deep and sufficient cotton for subjects to make nests. A nearly horizontal segment of PVC pipe (25 mm diameter, \approx 50 cm long) connected the side of the upper level of the nest with the ground surface, permitting mice to enter and exit the nest bucket. We positioned a 2.5-cm-thick piece of Styrofoam[®] insulation just below the bucket lid to keep the nest bucket cool. This nest design permitted us to isolate and remove mice as needed. Most subjects readily accepted the buckets as nest sites.

We placed a wooden feeder box measuring 40 \times 30 \times 10 cm near the center of each enclosure. The design (bottom, top, and 2 sides) excluded birds but permitted mice to enter along 2 sides to remove seeds. We placed a tin can containing water several meters from the feeder.

Between 2 July and 13 August 1997 and 1998, we conducted 11 caching trials. To begin a caching trial, we captured a deer mouse near the enclosure, weighed it, determined its gender, marked it with a numbered ear tag, and released it into the entrance of the nest bucket. The next day we placed 150 color-marked, radioactively labeled Jeffrey pine seeds (see Vander Wall 1992b for labeling procedure) in the feeder. We checked the feeder daily for 3 days, and if all or nearly all seeds had been removed from the feeder, we terminated the trial. Two caching trials lasted 1 day, 1 lasted 2 days, and 8 lasted 3 days. At the end of each trial, we removed the deer mouse from the nest bucket and searched the bucket for larder-hoarded seeds and hulls of eaten seeds. We removed any unharvested seeds from the feeder box and counted them. Then we searched the enclosure with a Geiger counter to locate scatter-hoarded seeds and hulls of eaten seeds. We carefully excavated each cache to determine cache depth and number of seeds per cache. We also collected data on the microsite in which mice made caches. Cache locations were described as "open" (>10 cm from a shrub), "shrub edge" (within 10 cm of the shrub canopy edge), or "shrub interior" (under a shrub

>10 cm from the shrub canopy edge). We recorded data on the substrate (mineral soil, plant litter <1 cm deep, or plant litter >1 cm deep) at each cache site.

We tested whether deer mice preferred certain microhabitats or substrates for caching. For each cache made by a deer mouse, we selected a random site (x and y coordinates taken from a random numbers table) within the enclosure and determined its substrate and microhabitat as described in the preceding paragraph. All random sites were in portions of the enclosure that had actually been used by deer mice for caching. We compared use of substrates and microhabitats by 7 deer mice that made sufficiently large numbers of caches for analysis ($n > 18$) to the randomly selected sites using chi-square tests for goodness of fit (Zar 1996). We tested for heterogeneity and combined all data sets for an overall chi-square test where appropriate.

RESULTS

Deer mice took 66% of the seeds from the feeder during trials that lasted an average of 2.6 days. Mice ate 29% and cached 71% of the seeds taken. Deer mice made an average ($\pm 1 s$) of 31.2 ± 30.0 surface caches during 11 trials, with a range of 1 to 109 caches per trial. Caches were generally small. Most (71%) contained only 1 seed, and 1- and 2-seed caches accounted for nearly 96% of all caches (Fig. 1). Jeffrey pine seeds are relatively large (mean $\pm 1 s = 157 \pm 27$ mg), and in laboratory studies (Thayer and Vander Wall unpublished data) deer mice typically carried only 1 or 2 seeds, suggesting that most surface caches in this field study were from single loads. Of the 7 largest surface caches, 4 contained 4 seeds, 2 contained 5 seeds, and 1 contained 10 seeds. These large caches were presumably made in 2 or more loads. One subject made the 4 largest caches.

In 2 trials deer mice larder hoarded seeds in the nest bucket. One mouse cached 70 seeds in its nest (and made 14 surface caches), and the other mouse stored 40 intact seeds and also ate 25 seeds in its nest (in addition to making 1 surface cache).

Deer mice scatter hoarded most seeds at depths ranging from 2 mm to about 12 mm (Fig. 2). Many cached seeds (30%) were partially exposed or beneath <1 mm of plant litter. Most

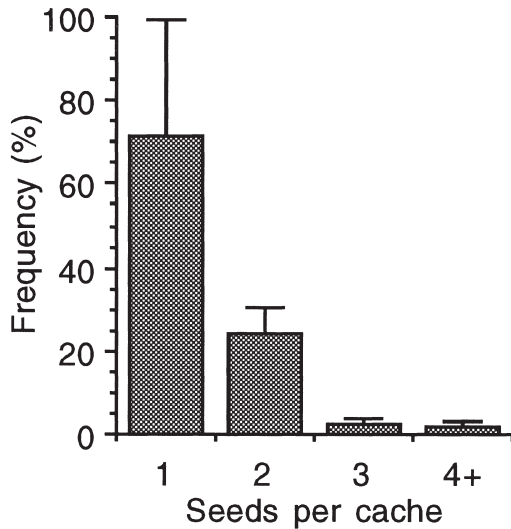


Fig. 1. Number of seeds in caches of 11 deer mice ($n = 378$ caches). Vertical lines represent $\pm 1 s_{\bar{x}}$.

subjects spaced caches widely throughout the enclosures with distances between caches typically ranging from 25 to 100 cm. However, we did not analyze spacing patterns because caching behavior of subjects was probably constrained by enclosure walls.

Deer mice (11 subjects combined) placed most caches in mineral soil and in light plant litter (175 caches in each substrate) and only a few caches in heavy litter (Fig. 3A). The heterogeneity chi-square test for the 7 mice with $n > 18$ caches was significant ($\chi^2 = 29.603$, $df = 12$, $P < 0.01$), indicating that individuals differed in their substrate use. Two subjects used mineral soil extensively for caching (73% of 19 cache sites and 56% of 34 cache sites; $P < 0.005$ for both). When we dropped these 2 subjects from analysis, the 5 remaining subjects did not differ significantly in substrate use (heterogeneity chi square: $\chi^2 = 13.518$, $df = 8$, $P > 0.05$), and they demonstrated no significant preferences for caching in certain substrates (pooled chi square: $\chi^2 = 2.071$, $df = 2$, $P > 0.25$).

Deer mice cached seeds near edges of bitterbrush shrubs more than expected and appeared to avoid open areas (Fig. 3B). The heterogeneity chi-square test for 7 mice was not significant ($\chi^2 = 8.214$, $df = 12$, $P > 0.50$), indicating that subjects did not differ signifi-

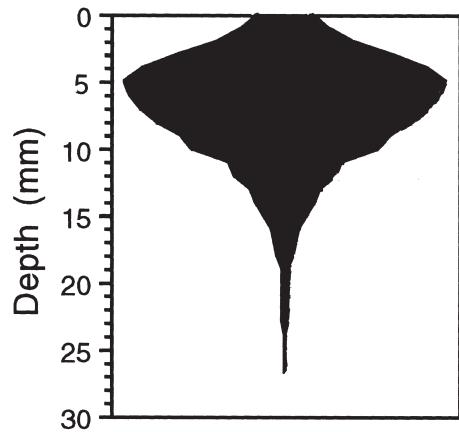


Fig. 2. Cache depth profile for deer mice storing Jeffrey pine seeds ($n = 296$ caches). Relative number of seeds buried at a given depth is proportional to the width of the profile.

cantly in microhabitat selection. The combined chi square showed a significantly non-random use of microhabitats ($\chi^2 = 27.400$, $df = 2$, $P < 0.001$).

DISCUSSION

These caching trials demonstrate that deer mice actively scatter hoard pine seeds. However, their tendency to scatter hoard is considerably less pronounced than that of yellow pine chipmunks. Under identical experimental conditions, chipmunks invariably took and cached nearly all seeds from the feeder in 1 day. At the end of this experiment (2.6 days), deer mice still had not harvested 34% of the seeds. Also, deer mice larder hoarded less than we anticipated based on published accounts. This may have been because the subjects were not sufficiently familiar with the artificial nests that we provided. In natural settings where mice are accustomed to their surroundings and have a home nest and burrow system, they may prefer to larder hoard in their burrows. However, nearly all subjects appeared to accept and use the nests, and other studies (Barry 1976, Tadlock and Klein 1979, Sanchez and Reichman 1987, Tannenbaum and Pivorum 1987) have shown that *Peromyscus* larder hoarded in artificial nests in laboratory settings. Another possible explanation is that we tested subjects at a season (midsummer) when

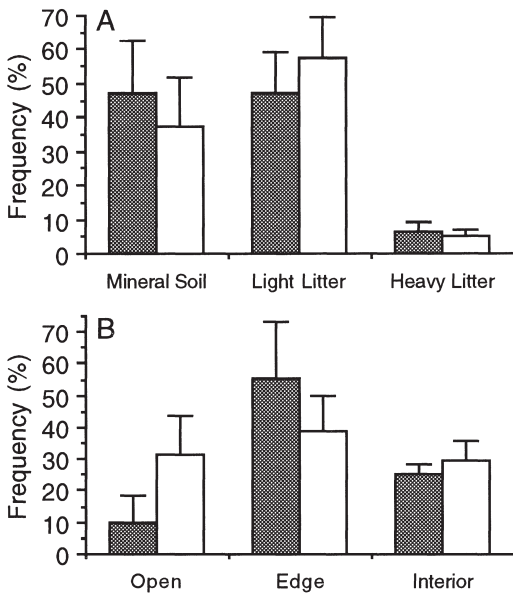


Fig. 3. A, Frequency of caches made by 11 deer mice in 3 substrates (shaded bars) compared to relative abundance of those substrates (open bars) in enclosures ($n = 373$ caches); B, frequency of caches made by 11 deer mice in 3 microhabitats (shaded bars) compared to relative abundance of those microhabitats in enclosures ($n = 374$ caches). Vertical lines represent ± 1 s.e. See Methods for definitions of substrate and microhabitat categories.

they larder hoard little food (e.g., Criddle 1950, Howard and Evans 1961, Barry 1976).

Deer mice in this study usually made small caches (1 or 2 seeds). In contrast, caches made by white-footed mice contained 20–30 eastern white pine seeds (Abbott and Quink 1970). This discrepancy is partially because eastern white pine seeds are much smaller than Jeffrey pine seeds. Most subjects in this study distributed caches widely within the enclosure and covered seeds with relatively little soil or plant litter. Except for the tendency of subjects to cache at the periphery of shrubs (and avoid open areas), deer mice in this study exhibited no strong, consistent patterns in cache site selection.

The fate of seeds scatter hoarded by deer mice under natural conditions has not been studied. Several alternatives seem plausible. First, some scatter-hoarded seeds are probably recovered later in summer by foraging deer mice and are either eaten or recached elsewhere. This seemed to be the most common fate of eastern white pine seeds cached by

white-footed mice (Abbott and Quink 1970). Second, other caches might be recovered by the hoarder and moved to the winter burrow later in autumn. Third, some caches are often pilfered by chipmunks and other rodents (Vander Wall 2000). Finally, some seeds may escape detection and germinate the following spring. Abbott and Quink (1970) observed that some eastern white pine seeds cached by white-footed mice germinated in spring, but because the mice ate many of the seedlings, they concluded that the rodent's net contribution to forest regeneration was probably minor. Unlike eastern white pine, which establishes almost exclusively as a direct result of wind dispersal, a large proportion of Jeffrey pine seedlings establish from caches made by rodents following initial wind dispersal. Most dispersal and establishment of Jeffrey pine in this region of the Sierra Nevada has been attributed to actions of yellow pine chipmunks (Vander Wall 1992a, 1992b, 1993b). However, ways in which deer mice cache Jeffrey pine seeds suggest that they also may be effective dispersers of Jeffrey pine.

It is difficult at this time to assess the importance of cache-site selection (substrate and microhabitat) in the effectiveness of deer mice as dispersers of pine seeds. Emerging pine seedlings generally have higher chances of establishing when seeds germinate in mineral soil, a substrate that some mice seem to prefer and which is found in open areas between shrubs. However, pine seedlings survive better when under shrub nurse plants (Vander Wall 1992a, Callaway and Walker 1997). Deer mice cached seeds under shrubs <30% of the time.

Under natural conditions, deer mice in these semiarid, eastern Sierra Nevada forests probably scatter hoard hundreds of seeds within their home ranges each year. Although they bury some seeds at depths too shallow to permit effective establishment of the seedling, many other seeds are buried more deeply, closer to optimum depth for germination and establishment (Vander Wall 1993a). Deer mice are usually considered to have a detrimental effect on regeneration of conifers (e.g., Abbott 1961, Black 1969, Gashwiler 1970), but the manner in which they scatter hoarded pine seeds in this study suggests that they may, in fact, play a positive role in the regeneration of some forests.

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