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Rapid sequestration and recaching by a scatter-hoarding rodent (*Sciurotamias davidianus*)

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Many seed-hoarding species are faced with ephemeral pulses of seeds that result in competition at seed sources and the need to minimize hoarding time during the limited time seeds are available. Here we tested the hypothesis that a seed-hoarding species (Père David's rock squirrel [*Sciurotamias davidianus*]) rapidly scatter hoards seeds near seed sources to maximize harvest rate, and then subsequently recaches seeds to further reduce cache losses. We tracked the caches of wild walnut (*Juglans mandshurica*) scatter hoarded by *S. davidianus*, the exclusive dispersal agent of this highly preferred nut species. We followed dispersed nuts in both the field and in a large enclosure in a manner that allowed us to follow patterns of recaching through the scatter-hoarding process. In the field, *S. davidianus* initially cached close to nut sources and then subsequently recached nuts on multiple occasions progressively farther from sources, always in the same direction, at lower densities, and at sites with more vegetative cover (e.g., under shrubs). In enclosures, each of 6 squirrels first cached nuts closer to the nut source on the 1st day of observation, and then subsequently recached nuts closer to the nest, sometimes at decreasing densities. We suggest that, in addition to pilferage risk, cache spacing by *S. davidianus* may be influenced by the potential for competition at the seed source and proximity to the burrow or the core of the home range, and that caches might be managed to accommodate all of these factors. Future studies should consider how such recaching behavior influences patterns of cache recovery, the ultimate distribution of dispersed nuts, and seed fates.

Key words: cache management, pilferage, predation risks, rapid sequestering hypothesis, scatter hoarding

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Scatter-hoarding behavior, whereby food is stored in individual, widely dispersed caches, is considered a food-hoarding strategy that evolved in many rodents and birds to overcome periods of food shortage and at the same time reduce the potential risk of losses to pilferers (Vander Wall 1990; Vander Wall and Jenkins 2003). Numerous studies have shown that scatter hoarders adjust their caching strategies to minimize pilferage risk and maximize the probability of cache retrieval (reviewed by Vander Wall and Jenkins 2003; Dally et al. 2006). In the presence of a conspecific competitor, for example, hoarding subjects (primarily birds and rodents) have been shown to cache farther from food sources (Heinrich and Pepper 1998; Dally et al. 2005), space caches farther apart (Stapanian and Smith 1984; Daly et al. 1992; Leaver et al.

2007), recache more frequently (Dally et al. 2005; Clary and Kelly 2011), cache at more-secure sites (Bugnyar and Kotrschal 2002; Dally et al. 2004; Steele et al. 2008) or in open habitats where the probability of predation is high but cache pilferage is reduced (Steele et al. 2014), shift from scatter hoarding to larder hoarding (Zhang et al. 2011), or engage in deceptive caching behavior (Steele et al. 2008).

The high costs and frequency of pilferage led several authors to propose models for the evolution of hoarding, and in particular scatter hoarding, based on the social conditions faced



by hoarders (Andersson and Krebs 1978; Smulders 1998), the likelihood of reciprocal pilferage (Vander Wall and Jenkins 2003), and the optimal spacing of scatter hoards (Stapanian and Smith 1978, 1984; Clarkson et al. 1986). Stapanian and Smith (1978) and later Clarkson et al. (1986), for example, proposed that the spacing of scatter hoards represented a trade-off between benefits accrued from spacing caches (i.e., reduced pilferage) and the costs of cache retrieval, which results in optimal spacing of caches (hereafter the optimal density model).

Although the optimal density model is widely cited, especially in studies of rodents, direct experimental support for the model is limited (Stapanian and Smith 1978, 1984; Clarkson et al. 1986; Hurly and Robertson 1987; Gálvez et al. 2009). Other studies have failed to produce evidence for the optimal density model (Bossema 1979; Kraus 1983; Jensen 1985; Rice-Oxley 2008), and at least 2 studies suggest alternative strategies for cache spacing in some situations (Van Horik and Burns 2007; Steele et al. 2014). Other studies cite indirect evidence for the optimal density model (e.g., greater dispersal distances of larger seeds [Jansen et al. 2004; Xiao et al. 2004; but see Steele et al. 2014]), but strong support for this, otherwise compelling, hypothesis is not forthcoming.

One potential explanation for this is that scatter-hoarding animals are likely dealing with a range of factors other than pilferage risk (e.g., competition at food sources, predation risks, and the relative proximity of scatter hoards to the nest, burrow, or center of home range) that may concurrently interact to influence the spacing of caches through time. In addition, in many studies of scatter hoarding and seed dispersal by scatter hoarders, researchers have failed to follow the movement of seeds after initial caching, even though we now know that seeds may be recovered, recached, and redistributed numerous times during the scatter-hoarding process (Vander Wall et al. 2005; Carlo et al. 2011; Jansen et al. 2012).

One such factor that has received little attention but may be particularly applicable to granivorous scatter hoarders that are faced with periodic pulses of seed production at localized sources is the need to rapidly sequester seeds immediately during seed fall. Also known as the rapid sequestering hypothesis (after Jenkins and Peters [1992], but also see Stapanian and Smith [1978] and Clarkson et al. [1986]), the concept proposes that seeds should be rapidly stored in nearby scattered caches to quickly sequester food stores and reduce competition at seed sources, and then subsequently redistributed to further accommodate for the risk of cache pilferage. This hypothesis suggests that scatter-hoarding patterns may represent a compromise to deal with the intense competition at seed sources and the need to properly space caches to reduce pilferage risks (Jenkins and Peters 1992; Jenkins et al. 1995).

Here we sought to study the scatter-hoarding behavior of Père David's rock squirrels (*Sciurotamias davidianus*), which we suspected may show this pattern of caching and recaching when dispersing and storing nuts of the wild walnut (*Juglans mandshurica*) in northern China. In previous studies in this region, we observed that plant seeds were scatter hoarded by

rodents rapidly (< 3 days) near seed sources (< 20 m), and then shortly thereafter (3–10 days) either recached or moved to unknown sites (Li and Zhang 2003, 2007; Lu and Zhang 2004; Zhang et al. 2008, 2013). In this study, we sought to determine if *S. davidianus* first hoards seeds near the seed source, perhaps to maximize harvest rate, and then transports seeds or nuts elsewhere within the home range or into the nests or burrows, to reduce food loss.

Here we first conducted experiments at 2 independent field sites in 2 consecutive years to determine if nuts are scatter hoarded and then recached as hypothesized from earlier observations. We then tested individual squirrels in a large seminatural enclosure to determine if these individuals indeed showed this pattern of scatter hoarding and recaching, especially in relation to the home burrow. We hypothesized that seeds were first scatter hoarded to rapidly sequester available nuts and then recached and ultimately moved to the burrow.

MATERIALS AND METHODS

Study area.—We conducted experiments at the Liyuanling field station in the Donglingshan Mountains of northern China (40°00'N, 115°30'E; 800–1,400 m above sea level). This area has a temperate continental monsoon climate with an annual average temperature of 6.5°C and an annual average precipitation of 600 mm. The site is dominated by shrublands, secondary forests, and abandoned farmlands. Liaodong oak (*Quercus liaotungensis*), wild apricot (*Prunus armeniaca*), *J. mandshurica*, elm (*Ulmus laciniata*), larch (*Larix principis-rupprechtii*), and wild peach (*Amygdalus davidiana*) are common plant species in secondary forests and shrublands, whereas annual herbs, shrubs, and sparsely planted trees dominate the abandoned farmlands (Lu and Zhang 2004; Zhang et al. 2013). The Chinese white-bellied rat (*Niviventer confucianus*), Korean field mouse (*Apodemus peninsulae*), and *S. davidianus* are common, and the striped field mouse (*A. agrarius*), the rat-like hamster (*Tscherskia triton*), and the Siberian chipmunk (*Tamias sibiricus*) also are present but are less abundant across the study area (Zhang and Zhang 2008). These rodent species all engage in scatter or larder hoarding of seeds, or both, and are responsible for most of the consumption and dispersal of the seeds and nuts of the trees listed above (Lu and Zhang 2008; Huang et al. 2011).

Study species.—*Sciurotamias davidianus* is a common diurnal species across northern China (Thorington et al. 2012) that frequently scatter hoards large seeds, nuts, and drupes, such as those of *J. mandshurica* and *A. davidiana* (Lu and Zhang 2007, 2008; Zhang 2007; Zhang and Zhang 2008; Huang et al. 2011). We chose to specifically study the dispersal of *J. mandshurica* by *S. davidianus* because this squirrel is a predominant scatter hoarder of tree seeds in the region and because the walnut's large size (6.1 ± 1.0 g mass [mean \pm SD]; 34.1 ± 2.4 mm long, 23.8 ± 2.0 mm wide, including endocarp, $n = 50$) and hard woody endocarp (2.7 ± 0.5 mm thickness, 5.1 ± 0.9 g mass per nut) prevent access by other

rodent species (Zhang and Zhang 2008). The squirrel's large size (210.2 ± 7.3 mm body length, 222.1 ± 23.2 g body mass, $n = 26$) and strong jaw (0.51 ± 0.05 g masseter mass, $n = 17$) allows it exclusive access to these nuts at our study sites (Zhang and Zhang 2008). This in turn provided us a unique opportunity for directly observing the scatter-hoarding behavior of *S. davidianus* in the field by tracking the caches of nuts of *J. mandshurica*. *J. mandshurica* is widely distributed in northern China, including our study area. The fruits of *J. mandshurica* mature and fall to the ground in September and seedlings emerge in April and May of the following year. The nut kernel of *J. mandshurica* is high in crude protein (28.1 g per 100-g kernel) and crude fat (62.3 g), and has low tannin content.

Field experiments.—Experimental nuts were collected randomly in a forest of *J. mandshurica*, $> 2,000$ m from the site of the experimental field plots. Nuts were tagged following the tin-tag method developed by Zhang and Wang (2001) and now widely used (e.g., Xiao et al. 2006; Gómez et al. 2008; Zhang et al. 2008, 2013). A coded tin-tag (30×10 mm, 0.1 g) was attached to each nut using a 3-cm piece of fine steel wire, allowing efficient recovery of 40–70% of cached seeds as well as efficient tracking across repeated caching events (Xiao et al. 2006).

We first conducted field experiments in a secondary forest near the field station in September 2006 and again in 2007, during early autumn, the period of seed fall for *J. mandshurica* and the peak period of hoarding by *S. davidianus* (Zhang 2007). Field experiments were conducted in forested sites (70% canopy cover) dominated by *Q. liaotungensis*, *U. laciniata*, *P. armeniaca*, *A. davidiana*, *L. principis-rupprechtii*, and *J. mandshurica*. Litter, bare ground, annual herbs, and some dwarf shrubs composed the habitat beneath the canopy. The forest was adjacent to shrublands and abandoned farmland at the foot of the forested slope.

In each year of the study, we selected 2 plots (100×100 m) separated by 300 m to ensure independence of observations: plot 1 was located on a north-facing slope of $30\text{--}45^\circ$, and plot 2 on a northeastern-facing slope of $30\text{--}50^\circ$. Each plot was divided into 4 quadrants (I, II, III, and IV) to generate a Cartesian coordinate system (± 50 m on both x and y axes) to allow unique identification of each location on the 100×100 -m plot (Fig. 1).

A total of 100 tagged nuts of *J. mandshurica* were carefully placed in a 1-m^2 area in the center of each plot in each year (400 in total over the 2 years). Nut fates were checked daily between 1130 and 1500 h over 15 consecutive days until few of the nuts remained at the origin and the frequency of recaching had waned. For each cache, we determined a set of cache characteristics including the quadrant (I, II, III, or IV) in which it was found, the coordinates within the quadrant (x and y) to within 10 cm, the general habitat (forest, forest edge, or open area), and the microhabitat at ground level (shrub, grass, or bare ground—see Li and Zhang 2003). The location of each cache was then marked at a fixed distance and compass bearing using a uniquely coded stake to facilitate relocation of the

cache and determination of cache fate. When it was determined that a cache was removed, it was then possible in many cases to verify if it had been moved, recached, or eaten.

We then measured the dispersal distance, defined as the straight-line distance from the caches to the nut sources (D_{C-S}), and a proxy of cache density, the nearest straight-line distances between caches (D_{C-C}), calculated as $\sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2}$. The survival time (S_T) of each cache was recorded as the number of days the nut remained in the cache. The expected frequencies of caches across habitat and microhabitats within the experimental plots were estimated from a random sample of 20 quadrats (5×5 m, 20 m apart) within the plot.

Analyses were performed with SPSS version 16.0 (SPSS Inc. 2008). Life tables were used to calculate the median survival times of the tagged nuts. Cox regression was used to further identify differences in nut survival between plots and years as well as the interaction between the 2. A Kruskal–Wallis *H*-test was used to determine differences across cache type (1st, 2nd, and 3rd caches) for each measurement of cache distribution D_{C-S} , D_{C-C} , and S_T . Paired comparisons of the 1st and 2nd caches (but not the 3rd cache because of limited sample sizes) were then determined with a Mann–Whitney *U*-test across all measures of cache distribution (D_{C-S} , D_{C-C} , and S_T) by plot and year separately.

Enclosure experiments.—Our field observations suggested that the pattern of caching and recaching by *S. davidianus* enabled the animals to first sequester nuts quickly and then gradually redistribute scatter hoards closer to their burrow or center of their home range, perhaps allowing the animals to eventually move nuts into their burrow (larders). To test this, in September 2008, we conducted experiments in a 50×40 -m enclosure by tracking the caches hoarded by 6 individual *S. davidianus*.

The squirrels used in the enclosure experiments were captured in the forest adjacent the field station (> 500 m from the experimental field plots) using live traps ($12 \times 12 \times 25$ -cm steel cages). In August 2008, 30 traps were placed 5 m apart along 5 transects (150 m long, > 200 m apart), baited with fresh peanuts, and covered with a board to protect animals from rain and direct sunlight. Small pieces of cucumber were provided as a water source and dry leaves were used as nest material. Captured animals remained healthy during all trapping sessions. The traps were set between 1130 and 1300 h, checked between 1900 and 2000 h on the day we set up the traps, and checked again at 0600–0700 h, 1200–1300 h, and 1900–2000 h every day in the following 3- to 5-day period.

Each captured squirrel (including trap) was covered with a cloth bag and carefully transferred to the laboratory. Pregnant females and other species were released immediately at the capture site. No lactating females were captured during the period of trapping. A total of 10 squirrels (4 females and 6 males; 220.5 ± 21.4 g body mass) were captured and held in captivity. Each individual was sexed, weighed, and subsequently housed separately in a wheel cage ($100 \times 100 \times 120$ cm) in a well-ventilated room at ambient temperature (18--

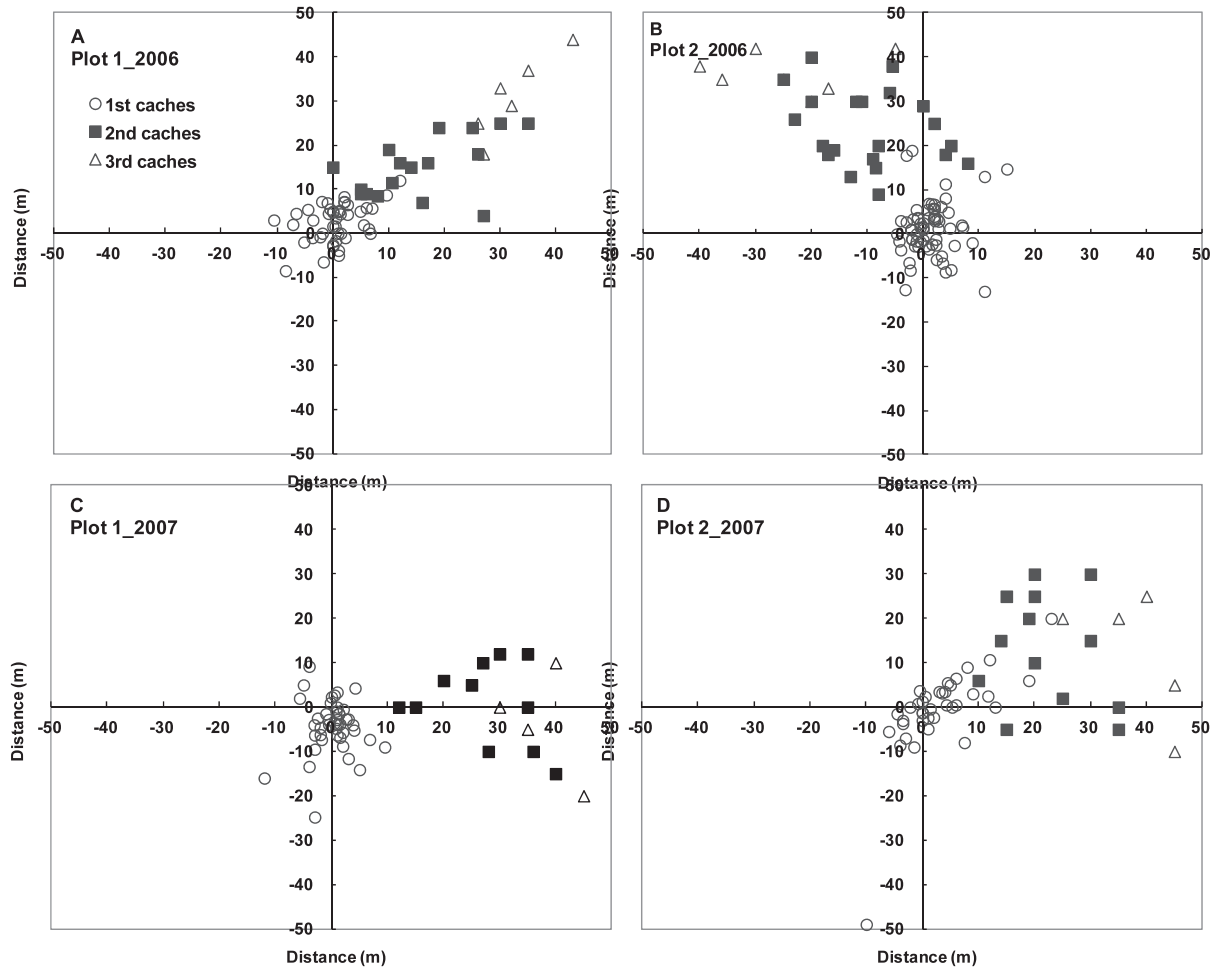


FIG. 1.—Spatial distribution of nuts of *Juglans mandshurica* scatter hoarded by *Sciurotamias davidianus* in a secondary forest, on 2 study plots in 2006 and 2007. Shown are the distributions of primary (1st caches), secondary (2nd caches), and tertiary (3rd caches) caches. The origin on each of the 4 plots indicates the seed source.

25°C) and a late-summer photoperiod (14L:10D). Water and nest materials (cotton) were provided ad libitum. Seeds and nuts of local plants (*Q. liaotungensis*, *P. armeniaca*, *J. mandshurica*, cultivated walnut [*Juglans regia*], etc.) were provided ad libitum to maintain a natural diet, and some peanuts (5–10 g per day per squirrel) were provided periodically as a daily nutritional supplement. Animals were acclimatized to the laboratory conditions at least a full week prior to behavioral experiments. All squirrels maintained their health and body mass during the period of housing and experimental trials. Immediately following experiments, all animals were released at the site of capture. All trapping, housing, and experimental procedures followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the local government and the Ethics Committee of the Institute of Zoology of the Chinese Academy of Sciences (SYXK(Jing—2007-0004)).

The enclosure was constructed in an open area at the field station. The walls of the enclosure (30 cm thickness) were constructed of bricks (150 cm above the ground and 30 cm below the ground surface). The enclosure was covered with

wire mesh (1.2 × 1.2-cm grid) to prevent animals from entering or escaping from the enclosure. The wire mesh was supported by a framework of 130 vertical steel tubes (2.5 m in height) distributed evenly across a 10 × 13-m grid inside the enclosure. The ground surface within the enclosure was covered with sandy soil (5–10 cm) as a hoarding substrate. Vegetation and branches were placed on the mesh to simulate ~50% canopy cover. Grass, branches, rocks, and bricks were dispersed on the surface to simulate ~20% ground cover around the enclosure. One wooden nest box (40 × 20 × 20 cm) and a water dish were placed in 1 corner of the enclosure, and a feeding station, where tagged nuts were presented, was established in the corner diagonally opposite the nest box. To maximize the likelihood of sensitivity to competition during each experiment, a caged squirrel (120 × 30 × 30-cm cage size, 4 male squirrels were used as competitors) was placed near the feeding station (5–30 m) on 1 or 2 occasions per day for 5–20 min per occasion. The distance, frequency, and time the competitor was presented were determined randomly, with one restriction: that the same distance, frequency, and time were not repeated on consecutive days during the same experimental trial.

A total of 6 squirrels (4 females and 2 males; 214.5 ± 25.7 g body mass) were observed in the enclosure experiments. Each subject was kept in the enclosure for 6 days during each experimental trial. Day 1 was designated for acclimation and the remaining 5 days for observation. A squirrel was introduced into the enclosure at 1200 h on day 1. Thirty tinned nuts of *J. mandshurica* were provided on day 2 and checked daily thereafter between 1200 and 1400 h to map caches and record incidents of nut consumption. The nuts remaining at the feeding station were removed from the enclosure at the end of day 2. Squirrels were provided 20 peanuts (8–10 g) and fresh water daily. Following each 6-day trial, the enclosure was cleared of all nuts and nut fragments, and the water dish and nest were replaced. A 2-day waiting period was then observed until the next trial was initiated.

As in field studies, we used a Cartesian coordinate system to map caches in the enclosure (x-axis = 0–50 m, y-axis = 0–40 m [Fig. 2]). On each day after presentation of nuts, we recorded the location (x and y) and microhabitats (e.g., under cover, in bare ground, or near enclosure wall [~ 0.5 m]) of caches. Cache maps were generated to track the movement of caches (Fig. 2). For each type of cache (1st–4th caches) for which nuts were recovered, we calculated ($\sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2}$) the distances from the cache to the nut source (D_{C-S}), the nearest distances between caches (D_{C-C}), and the distance from cache to the nest (D_{C-N}). As for field studies, a Kruskal–Wallis *H*-test was used to test for differences between cache type for each measurement of cache distribution (D_{C-S} , D_{C-C} , and D_{C-N}), which was followed by pairwise comparisons of cache type (for caches 1–3) with Mann–Whitney *U*-tests.

RESULTS

Field experiments.—In the field studies, > 80% of the tagged nuts were harvested by squirrels by day 2 in 2006 (median survival time for plot 1 = 1.6 day, plot 2 = 1.6 day) and by day 10 in 2007 (plot 1 = 6.3 day, plot 2 = 7.0 day). The removal rates varied significantly between years (Wald = 68.976, *d.f.* = 1, $P < 0.001$). In all plots and years, *S. davidianus* exhibited a significant tendency to begin caching near the nut source and then subsequently recached nuts progressively farther away at lower densities, in a specific direction (Fig. 1).

Within the first 2 days that a nut source was discovered, squirrels first scatter hoarded nuts near the source. By days 3–5, the primary caches were recached farther from the source in a specific orientation (Fig. 1; Table 1). Although we had no way of definitively determining if the same animal recached the nuts, the short time period over which this occurred makes it unlikely that caches were pilfered by naive animals. Both the distance to the source (D_{C-S}) and the distance between caches (D_{C-C}) increased significantly between the 1st, 2nd, and 3rd caches (all $P < 0.05$) with 2 exceptions: the D_{C-S} between the 2nd versus 3rd caching events in plot 1, 2007; and the D_{C-C} between the 2nd and 3rd caching events in plot 2, 2007. In contrast, cache survival time (S_T) increased significantly

between the 1st and 2nd caches (all $P < 0.05$), but not significantly so between the 2nd and 3rd caches ($P > 0.05$, with 1 exception in plot 2, 2007, in which the 2nd caches did not survive as long as the 1st and 3rd caches [Table 1]).

All caches (1st–3rd caches) were located on the forest (Table 2). Overall, *S. davidianus* tended to select bare ground for initial placement of caches (1st caches), but nuts were then transferred to other microhabitats (e.g., grass and shrubs) when recached (2nd and 3rd caches [Table 2]). Across the 2 experimental plots in both years of the study, the proportion of caches on bare ground ranged from 70.3% to 97.0% for the 1st caches ($85.5\% \pm 11.5\%$, mean \pm SD, $n = 4$), from 9.1% to 76.9% for the 2nd caches ($35.1\% \pm 29.9\%$), and from 25.0% to 100% for the 3rd caches ($68.8\% \pm 37.5\%$). In contrast, the proportion of caches in both grass and adjacent to shrubs generally increased after the 1st caches (Table 2).

Enclosure experiments.—In enclosure experiments, the 6 squirrels cached between 23% and 60% (7 and 18) of the tagged nuts per individual (Table 3). A few caches (1–5) were consumed by 3 individuals during the later days of the experimental trials. Squirrels 2, 3, 5, and 6 recached nuts 3 times, and squirrels 1 and 4 recached nuts 4 times. All individuals cached nuts close to the nut station (1st caches) on the 1st day of observations and then transferred the caches closer to the nest on the remaining 4 days of the experimental trial (Fig. 2; Table 3). Across the 1st–4th caches, the distance between caches and the source (D_{C-S}) increased significantly (all $P < 0.05$). In contrast, the distances to the nest (D_{C-N}) decreased significantly (all $P < 0.05$) and leveled off by the 2nd cache, with the exception of that of squirrel 5, which increased between the 1st and 3rd caches. The distances between caches (D_{C-C}) did not change significantly (all $P > 0.05$) across the different cache levels (1st–4th caches) except for those observed for squirrels 4 and 5 (Table 3). All individuals tended to hoard and rehoard nuts along the walls of the enclosure or under cover (71.4–100% of 1st caches, 82.7–100% of 2nd caches, and 100% of 3rd and 4th caches) rather than in open ground.

DISCUSSION

Our experiments on *S. davidianus* dispersing nuts of *J. mandshurica* indicate that squirrels first scatter hoarded these nuts close to nut source at high densities, and then in a relatively short time recached these nuts at greater distances from the source usually at lower densities. These observations are likely based on the caching of a single individual at each site and year, rather than multiple animals. Individual squirrels discovered our artificial patches immediately and appeared to move the nuts before other squirrels could converge on the site. Taken together, our field and enclosure experiments also suggest that the successive recaching of nuts results in movement of seeds in a highly directional pattern, possibly toward the nest or burrow. However, additional field observations will be necessary to verify this in the wild and discount any possible behavioral anomalies that may have

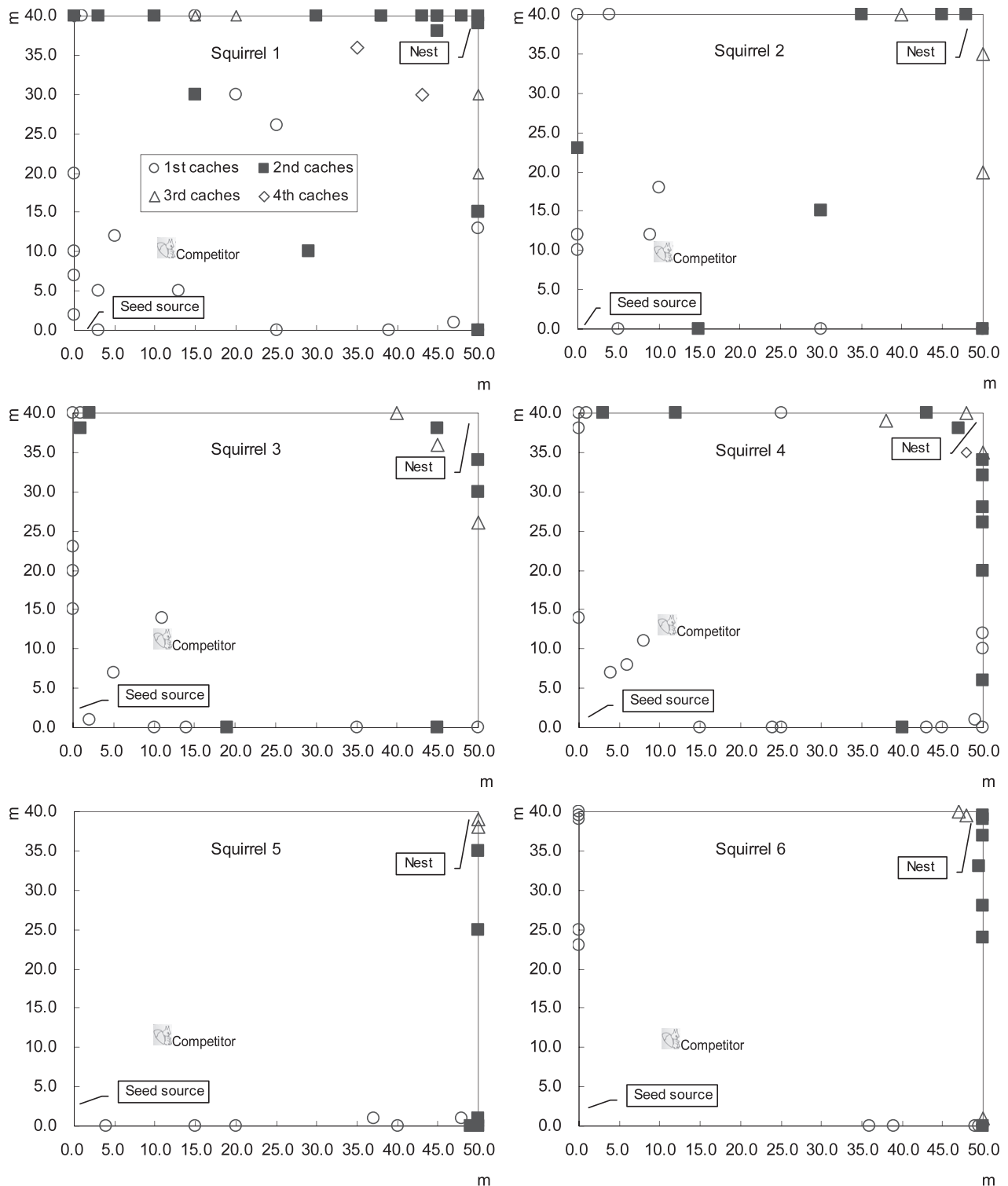


FIG. 2.—Movement of scatter-hoarded nuts of *Juglans mandshurica* by 6 individuals of *Sciurotamias davidianus* in the experimental enclosure. Shown are the distribution of caches and dynamics of cache movement from 1st, 2nd, 3rd, and (for 2 squirrels) 4th caches over 5 consecutive days. Note the initial placement of caches near the nut source, their progressive movement toward the nest, and the consistent use of the enclosure wall for cache sites.

resulted from captivity. Contrary to our expectation, however, nuts were never moved into the burrow.

These results suggest that scatter hoarding is a dynamic process that is potentially influenced by a multiplicity of

drivers in addition to the 2 primary factors (risk of pilferage and efficiency of cache recovery) considered in traditional scatter-hoarding models (e.g., optimal density model—Stapanian and Smith 1978; Clarkson et al. 1986). Our results suggest

TABLE 1.—Spatial distribution of caches of nuts of *Juglans mandshurica* nuts scatter hoarded by *Sciurotamias davidianus* in a secondary forest at 2 sites over 2 years (2006–2007). Shown are the distances between caches and the nut source (D_{C-S}), the nearest distances between caches (D_{C-C}), and the survival time (S_T). Different superscript lowercase letters (a, b, and c) indicate significant differences ($P < 0.05$, Mann–Whitney U -test).

Plot by year	Cache	<i>n</i>	$D_{C-S} \bar{X} (\pm SD)$ (m)	$D_{C-C} \bar{X} (\pm SD)$ (m)	$S_T \bar{X} (\pm SD)$ (days)
2006					
Plot 1	1st	44	5.8 (3.3) ^a	2.6 (1.1) ^a	3.2 (3.0) ^a
	2nd	17	22.6 (10.3) ^b	4.4 (1.8) ^b	6.1 (2.9) ^b
	3rd	6	44.8 (10.5) ^c	6.7 (2.2) ^c	6.3 (3.5) ^b
Kruskal–Wallis H -test			$\chi^2_2 = 43.382, P < 0.001$	$\chi^2_2 = 24.997, P < 0.001$	$\chi^2_2 = 13.671, P = 0.001$
Plot 2	1st	66	5.9 (4.4) ^a	2.2 (0.8) ^a	2.7 (2.7) ^a
	2nd	21	27.1 (9.0) ^b	4.1 (2.0) ^b	5.2 (3.0) ^b
	3rd	7	45.1 (7.4) ^c	7.0 (3.9) ^c	7.7 (3.2) ^b
Kruskal–Wallis H -test			$\chi^2_2 = 57.255, P < 0.001$	$\chi^2_2 = 32.075, P < 0.001$	$\chi^2_2 = 26.493, P < 0.001$
2007					
Plot 1	1st	43	6.4 (5.0) ^a	2.2 (1.1) ^a	2.3 (2.5) ^a
	2nd	11	28.8 (9.7) ^b	5.4 (2.2) ^b	3.9 (2.7) ^b
	3rd	4	39.0 (8.2) ^b	10.3 (3.9) ^c	6.0 (4.6) ^b
Kruskal–Wallis H -test			$\chi^2_2 = 31.298, P < 0.001$	$\chi^2_2 = 28.365, P < 0.001$	$\chi^2_2 = 8.957, P = 0.011$
Plot 2	1st	37	8.2 (9.2) ^a	2.8 (2.1) ^a	3.1 (2.7) ^a
	2nd	13	28.2 (8.8) ^b	8.0 (2.6) ^b	1.4 (0.7) ^b
	3rd	5	42.2 (6.3) ^c	10.8 (4.0) ^b	5.0 (4.6) ^a
Kruskal–Wallis H -test			$\chi^2_2 = 30.125, P < 0.001$	$\chi^2_2 = 29.840, P < 0.001$	$\chi^2_2 = 6.378, P = 0.041$

some additional factors that may contribute to cache spacing by rock squirrels: the need for rapid sequestration of seeds at seed sources, and the proximity to burrows or core areas of the home range.

The scatter hoarding of nuts close to the source in our study is best explained by the rapid sequestering hypothesis, first

suggested by Stapanian and Smith (1978) and Clarkson et al. (1986) and later more formally articulated by Jenkins and Peters (1992; see also Jenkins et al. 1995). This hypothesis suggests that seeds are first rapidly scatter hoarded close to a source to reduce competition but then subsequently redistributed as necessary to minimize pilferage and allow for long-

TABLE 2.—Spatial distribution of caches of nuts of *Juglans mandshurica* scatter hoarded by *Sciurotamias davidianus* in a secondary forest across 2 sites over 2 years (2006–2007). Shown are the distribution of caches by quadrant (I–IV), habitats, and microhabitat characteristics, and the expected values based on relative availability.

Plot by year	Cache	<i>n</i>	Quadrant <i>n</i> (%)				Habitat <i>n</i> (%)			Microhabitat <i>n</i> (%)		
			I	II	III	IV	Forest	Forest edge	Open area	Shrub	Grass	Bare ground
2006												
Plot 1	1st	44	19 (43.2)	13 (29.5)	7 (15.9)	5 (11.4)	44 (100.0)	0	0	3 (6.8)	1 (2.3)	40 (90.9)
	2nd	17	17 (100.0)	0	0	0	17 (100.0)	0	0	11 (64.7)	0	6 (35.3)
	3rd	6	6 (100.0)	0	0	0	6 (100.0)	0	0	2 (33.3)	1 (16.7)	3 (50.0)
Expected value (%)			25.0	25.0	25.0	25.0	70.0	10.0	20.0	20.0	35.0	45.0
Plot 2	1st	66	27 (40.9)	15 (22.7)	10 (15.2)	14 (21.2)	66 (100.0)	0	0	2 (3.0)	0	64 (97.0)
	2nd	21	5 (23.8)	16 (76.2)	0	0	21 (100.0)	0	0	17 (81.0)	0	4 (19.0)
	3rd	7	0	7 (100.0)	0	0	7 (100.0)	0	0	0	0	7 (100.0)
Expected value (%)			25.0	25.0	25.0	25.0	65.0	10.0	25.0	25.0	30.0	45.0
2007												
Plot 1	1st	43	5 (11.6)	9 (20.9)	13 (30.2)	16 (37.2)	43 (100.0)	0	0	4 (9.3)	3 (7.0)	36 (83.7)
	2nd	11	8 (72.7)	0	0	3 (27.3)	11 (100.0)	0	0	7 (63.6)	3 (27.3)	1 (9.1)
	3rd	4	2 (50.0)	0	0	2 (50.0)	4 (100.0)	0	0	2 (50.0)	1 (25.0)	1 (25.0)
Expected value (%)			25.0	25.0	25.0	25.0	70.0	10.0	20.0	20.0	35.0	45.0
Plot 2	1st	37	18 (48.6)	3 (8.1)	8 (21.6)	8 (21.6)	37 (100.0)	0	0	4 (10.8)	9 (24.3)	26 (70.3)
	2nd	13	11 (84.6)	0	0	2 (15.4)	13 (100.0)	0	0	0	3 (23.1)	10 (76.9)
	3rd	5	4 (80.0)	0	0	1 (20.0)	5 (100.0)	0	0	0	2 (40.0)	3 (60.0)
Expected value (%)			25.0	25.0	25.0	25.0	65.0	10.0	25.0	25.0	30.0	45.0

TABLE 3.—Spatial distribution of caches of nuts of *Juglans mandshurica* scatter hoarded by 6 individuals of *Sciurotamias davidianus* in the experimental enclosure. Shown are the distances between caches and nut source (D_{C-S}), the nearest distances between caches (D_{C-C}), and the distances between caches and the squirrel's nest (D_{C-N}). Different superscript lowercase letters (a, b, and c) indicate significant differences ($P < 0.05$, Mann–Whitney U -test).

Squirrel identification	Cache type	n	$D_{C-S} \bar{X} (\pm SD)$ (m)	$D_{C-C} \bar{X} (\pm SD)$ (m)	$D_{C-N} \bar{X} (\pm SD)$ (m)
Squirrel 1	1st	18	26.8 (17.5) ^a	6.2 (4.3) ^a	47.1 (11.5) ^a
	2nd	17	51.4 (10.7) ^b	4.6 (4.6) ^a	21.0 (17.7) ^b
	3rd	7	52.1 (6.6) ^b	5.9 (3.9) ^a	21.7 (13.5) ^b
	4th	3	47.5 (6.6) ^b	6.3 (5.5) ^a	25.9 (20.9) ^b
Kruskal–Wallis H -test			$\chi^2_3 = 20.784, P < 0.001$	$\chi^2_3 = 1.930, P = 0.587$	$\chi^2_3 = 19.155, P < 0.001$
Squirrel 2	1st	9	24.8 (15.9) ^a	8.4 (7.1) ^a	50.2 (7.0) ^a
	2nd	7	42.5 (18.7) ^b	7.7 (6.0) ^a	28.6 (21.5) ^b
	3rd	3	57.2 (3.6) ^b	10.1 (8.5) ^a	11.7 (7.6) ^b
Kruskal–Wallis H -test			$\chi^2_2 = 8.170, P = 0.017$	$\chi^2_2 = 0.501, P = 0.779$	$\chi^2_2 = 7.959, P = 0.019$
Squirrel 3	1st	12	23.0 (15.0) ^a	6.1 (4.8) ^a	51.6 (6.2) ^a
	2nd	7	45.7 (15.0) ^b	4.2 (2.1) ^a	29.9 (21.6) ^b
	3rd	3	56.9 (0.6) ^b	3.8 (1.7) ^a	10.1 (3.8) ^b
Kruskal–Wallis H -test			$\chi^2_2 = 10.334, P = 0.006$	$\chi^2_2 = 0.588, P = 0.745$	$\chi^2_2 = 10.336, P = 0.006$
Squirrel 4	1st	17	33.2 (16.1) ^a	3.8 (5.5) ^a	44.6 (9.8) ^a
	2nd	11	52.6 (8.3) ^b	6.7 (7.9) ^b	21.0 (16.0) ^b
	3rd	3	59.3 (4.3) ^b	2.8 (2.1) ^a	6.3 (5.1) ^b
	4th	1	59.4	1	5.4
Kruskal–Wallis H -test			$\chi^2_2 = 15.488, P < 0.001$	$\chi^2_2 = 4.960, P = 0.084$	$\chi^2_2 = 16.649, P < 0.001$
Squirrel 5	1st	7	30.6 (17.7) ^a	4.5 (3.1) ^a	46.5 (8.4) ^a
	2nd	6	52.7 (4.8) ^b	2.5 (3.8) ^{a,b}	29.8 (15.7) ^b
	3rd	2	63.1 (0.4) ^c	1.0 (0.0) ^b	1.5 (0.7) ^c
Kruskal–Wallis H -test			$\chi^2_2 = 10.357, P = 0.006$	$\chi^2_2 = 5.631, P = 0.060$	$\chi^2_2 = 9.254, P = 0.010$
Squirrel 6	1st	10	39.0 (9.4) ^a	1.25 (1.1) ^a	45.9 (5.5) ^a
	2nd	7	58.8 (5.0) ^b	2.2 (1.8) ^a	11.4 (13.9) ^b
	3rd	3	58.0 (6.9) ^b	1.0 (0.0) ^a	14.7 (21.5) ^b
Kruskal–Wallis H -test			$\chi^2_2 = 13.822, P = 0.001$	$\chi^2_2 = 1.626, P = 0.443$	$\chi^2_2 = 13.598, P = 0.001$

term storage (Jenkins and Peters 1992). Jenkins and Peters (1992) reviewed a number of earlier studies whose results they claim are best explained by the potentially intense competition at seed sources. Indeed, seed production in many systems, including the temperate forests in which we worked, results in ephemeral pulses of seeds at which granivores will rapidly remove seeds until depleted. The rapid rate at which seeds were initially cached suggests that these animals were responding to the potential for competition at seed sources. Although the patterns of caching suggest that a single individual was responsible for the caches at each plot, it is likely that squirrels were responding rapidly to prevent discovery of nuts by potential competitors. In other systems, we have observed removal of seeds in as little as 48 h under some conditions by 1 or a few individual rodents, despite the potential for intense competition from other rodents, which were abundant in the area (Moore et al. 2007; M. A. Steele, pers. obs.).

Although the scatter-hoarding models presented by Stapanian and Smith (1978) and Clarkson et al. (1986), in fact, accounted for competition at food sources, the 2 models offered opposite predictions. Whereas both models predicted that at a pulsed food source, food items should be cached first near the source, Stapanian and Smith (1978) predicted that subsequent caches (e.g., secondary caches) will be placed

farther from the source, at equal densities, and that caches made for short-term gains will be placed at the same densities as longer-term caches. Clarkson et al. (1986), however, predicted that after placing caches close to the source, successive caches will be placed both close and far from the source and that resulting cache densities will be higher at the source and lower farther from the source. Our results, however, appear to support elements of both predictions: *S. davidianus* first cached close to nut sources at high densities and then moved all nuts farther from the source, and possibly closer to the nest, but not always at lower densities. This suggests that squirrels may risk short term pilferage of caches to maximize the number of nuts that they store.

Numerous other studies on a diversity of rodent species including white-footed mice (*Peromyscus leucopus*—Abbott and Quink 1970), eastern gray squirrels (*Sciurus carolinensis*—Leaver et al. 2007; Hopewell et al. 2008), eastern chipmunks (*Tamias striatus*—Clarke and Kramer 1994), yellow pine chipmunks (*Tamias amoenus*—Vander Wall 1995), Central American agoutis (*Dasyprocta punctata*—Gálvez et al. 2009), and Ord's kangaroo rats (*Dipodomys ordii*—White and Geluso 2012) report partial evidence of rapid sequestering. However, in most of these studies it is often difficult to know this for sure because it is often impossible to

know the status of all caches of each individual, whether multiple individuals contributed to the observed caching patterns, patterns of recaching, and final fates of cached seeds. Indeed, these are all critical limitations of most seed-dispersal and scatter-hoarding studies. As an example, several studies have inferred optimal spacing of caches based on dispersal distances. It is widely shown, for example, that rodents tend to disperse larger, more profitable seeds farther from their source (Jansen et al. 2004; Xiao et al. 2004, 2005; Moore et al. 2007)—an outcome often assumed, perhaps erroneously, to result in optimal spacing of scatter hoards. Recent research (Steele et al. 2014), however, suggests that this pattern may instead result from heterogeneity in the habitat and variation in predation risks.

Our results also indicate that recaching and movement of scatter-hoarded seeds is directed toward the animal's burrow. Contrary to our expectations, however, this ground-dwelling species, which typically nests in rocky outcrops, and is known to predominantly scatter hoard seeds but also larder some seeds, especially in captivity (Lu and Zhang 2007, 2008; Huang et al. 2011; Thorington et al. 2012), showed no tendency to deposit seeds inside the nest in our enclosure studies. In fact, the evidence for larder hoarding by this species when in captivity may have resulted from the restrictive size of enclosures (< 10 × 10 m) of previous studies (Lu and Zhang 2007, 2008; Huang et al. 2011). It is not known if limited larder hoarding occurred in our field experiments, but based on the relocation of scatter-hoarded nuts, it appeared that these nuts were not moved to burrows (H. Zhang, pers. obs.). Our results contrast those from studies on *T. amoenus*, where it is shown that although the species regularly scatter hoards in summer and early fall (Vander Wall 1992, 2002), individuals recover a significant portion (56–74%) of their own caches (Vander Wall et al. 2006) to provision their larders, on which they are entirely dependent for winter survival (Kuhn and Vander Wall 2008, 2009). Similar seasonal shifts in storing strategy are reported for *D. ordii* (White and Geluso 2012). It would seem that in our study, movement of scatter hoards closer to the burrow would allow both efficient access and perhaps opportunity to defend caching areas, although this latter suggestion is only speculative. In our study, it is possible that seeds may ultimately be moved to burrows toward winter because abandoned endocarp fragments of *J. mandshurica* and *J. regia* were often observed at the entrances of the squirrels (H. Zhang, pers. obs.).

We suggest that this pattern of rapid sequestration of seeds by individual rodents during periods of seed fall, followed by various patterns of recaching may be quite common in many systems. As evidenced by recent studies (e.g., Vander Wall and Joyner 1988; Vander Wall 2002; Hirsch et al. 2012), a better understanding of such strategies may be important for understanding how rodents manage caches and how such cache management strategies in turn influence patterns of seed dispersal. In addition, we emphasize that several factors, other than density-dependent pilferage (optimal spacing), are likely

to interact to influence cache placement, cache dynamics, and seedling establishment.

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