

Dynamics of yellow pine chipmunk (*Tamias amoenus*) seed caches: Underground traffic in bitterbrush seeds¹

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Abstract: Fates of antelope bitterbrush (*Purshia tridentata*) seeds were monitored from the time the seeds were cached by yellow pine chipmunks (*Tamias amoenus*) until they germinated nine months later. One thousand seeds were numbered and then radioactively labelled with scandium-46 so that the histories of individual seeds could be followed. The labelled seeds were placed under a bitterbrush shrub in the morning and by that evening chipmunks had gathered most of the seeds and made 110 primary caches within 16 m of the source shrub. During the fall, chipmunks and other rodents visited many of these caches and removed some of the seeds. Thirty-one caches completely disappeared, 28 other caches had some but not all of the seeds removed, and 51 caches remained intact until the time of seed germination. Chipmunks recached about 30% of the seeds they took from primary caches during the late summer and fall at 12 secondary and two tertiary cache sites. The histories of seeds were often complicated. Seeds survived to the time of germination at 86 of the 124 cache sites (79 primary caches, six secondary caches, and one tertiary cache). The population of caches from a particular source plant is dynamic. Seed-hoarding animals frequently move seeds from one storage site to another, and this secondary dispersal has important consequences for the seeds being moved.

Keywords: secondary dispersal, seed caching, *Purshia tridentata*, radioactive labelling, scandium-46.

Résumé: Un suivi des graines de *Purshia tridentata* a été effectué à partir du moment où elles furent entreposées dans des caches de nourriture par le tamia amène (*Tamias amoenus*) jusqu'à ce qu'elles germent neuf mois plus tard. Mille graines ont été numérotées puis imprégnées d'un marqueur radioactif au scandium-46. Les graines marquées ont été placées sous un arbuste dans la matinée. En soirée, les tamias avaient prélevé la plupart des graines et entreposé ces dernières dans 110 caches d'ordre 1 à l'intérieur d'un rayon de 16 m de la source initiale de graines. Durant l'automne, les tamias et autres rongeurs ont visité plusieurs caches et retiré un certain nombre de graines. Les graines sont complètement disparues de 31 caches. Quelques graines ont été retirées de 28 autres sites d'entreposage. Dans les 51 caches restantes, la provision de graines est demeurée intacte jusqu'à la germination des diaspores. À la fin de l'été et durant l'automne, les tamias ont entreposé de nouveau environ 30 % des graines qu'ils avaient prélevées dans des caches de nourriture d'ordre 1, et ce dans 12 sites d'ordre 2 et 2 sites d'ordre 3. Le devenir de chaque graine est souvent fort complexe. Les graines ont survécu au temps requis pour leur germination dans 86 des 124 sites d'entreposage (79 caches d'ordre 1, 6 caches d'ordre 2 et 1 cache d'ordre 3). La population de caches associée à une source particulière de graines est dynamique. Les animaux entreposeurs de graines déplacent fréquemment ces dernières d'une cache à une autre. Cette dissémination secondaire a d'importantes conséquences sur les graines déplacées.

Mots-clés: dissémination secondaire, cache de nourriture, *Purshia tridentata*, marquage radioactif, scandium-46.

Introduction

Birds and mammals that scatter hoard seeds in soil are often important agents of dispersal for those seeds. The seeds of an individual plant go through two distinct phases between the time of seed maturation on the plant and seed germination within an animal cache months later. During the first phase, which is brief relative to the second phase, seeds are harvested and either eaten or transported to cache sites. During a period of days or weeks, animals establish numerous caches at varying distances from the source plant. These cache sites often vary greatly in their suitability as establishment sites for seedlings. During the second phase, which lasts until the time of seedling emergence, the scatter hoarder and other animals visit cache sites, excavate some or all of the seeds, and either consume or move them to new cache sites.

The first phase of this process, the establishment of an array of cache sites in space, has received a fair amount of study. The distances that scatter hoarders carry seeds to

cache sites, the number of seeds in caches, cache depths, and the microsites where animals cache seeds have been carefully documented for a number of plant species (Abbott & Quink, 1970; Stapanian & Smith, 1978; Sherry, Avery & Stevens, 1982; Jensen, 1985; Hallwachs, 1986; Jensen & Nielsen, 1986; Forget, 1991; Vander Wall, 1992; 1993; 1994). The second phase, the modification of existing populations of caches over time, has received much less attention. The disappearance of caches has been described in several studies (Cahalane, 1942; Sherry, Avery & Stevens, 1982), but reduction in the number of seeds in caches over time and establishment of new caches using seeds taken from existing caches has received little attention. Abbott & Quink (1970) documented the consumption and removal of white pine (*Pinus strobus*) seeds from rodent caches, and Vander Wall (1994) documented the removal and recaching of antelope bitterbrush (*Purshia tridentata*) seeds previously scatter hoarded by yellow pine chipmunk (*Tamias amoenus*). DeGange *et al.* (1989) observed that Florida scrub jays (*Aphelocoma coerulescens*)

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recache more than 90% of the acorns retrieved from caches during the fall. This secondary dispersal, the movement of seeds after they leave the parent plant and arrive on a substrate (Chambers & MacMahon, 1994), although little studied, has potentially important consequences for both the food hoarder and the seeds being reshuffled.

The objective of this contribution was to permit a yellow pine chipmunk to establish an array of caches around a source shrub and then observe those caches over time to determine how rodents and other animals alter that distribution of seeds. I selected antelope bitterbrush, a widely distributed and economically important shrub in the western United States, as the source plant because this shrub owes virtually all of its establishment to the activities of chipmunks and other rodents that scatter hoard the seeds in numerous shallow caches in the soil (Vander Wall, 1994).

Study area

I conducted this study at the University of Nevada's Whittell Forest and Wildlife Area in Little Valley, Washoe County, Nevada (39°15'10" N, 119°52'35" W, elevation 1990 m) between August 1993 and May 1994. The research area is on the east slope of the Sierra Nevada, 30 km south of Reno and 5 km northeast of Lake Tahoe. I studied the dynamics of antelope bitterbrush seed caches in mixed-age stands of bitterbrush with scattered Jeffrey pines (*Pinus jeffreyi*). Further details concerning this study site can be found in Vander Wall (1994).

Methods

I selected 1000 plump, healthy bitterbrush seeds (mass ≈ 25 mg each) and numbered them from 0 to 999 with black indelible ink. I also labelled the seeds with scandium-46, which has a half life of 84 days, by soaking lots of 100 seeds in petri dishes containing ≈ 1 mL solution of ScCl_3 in distilled water until seeds had absorbed nearly all the solution. Each seed absorbed about $1 \mu\text{Ci}$ of scandium-46 onto the seed coat. I dried the seeds at ambient temperature for 2 days and then packaged the seeds. I could detect these seeds from about 30 cm in the air and through more than 10 cm of soil using a portable Eberline ASP-1 counter with an SPA-3 probe.

I deployed the radioactive seeds at a bitterbrush "source" shrub (canopy diameter ≈ 150 cm) at dawn on 20 August 1993 in three petri dishes half filled with soil. At dusk of that day, I returned to the source shrub to find most of the seeds gone or consumed. I retrieved unharvested seeds and seed fragments from the petri dishes. The next morning I began searching the area around the source shrub for radioactive seed caches. I searched the area within 25 m of the source shrub. When I found a cache, I covered it with a wire mesh screen ($\approx 20 \text{ m} \times 20 \text{ cm}$) and placed a rock on it to prevent rodents from removing the seeds. After I had located all labelled caches (≈ 6 hours later), I began excavating the caches to determine their contents. I counted radioactive seeds and recorded the number on each. If the cache contained unlabelled, indigenous seeds I also counted them. I then returned all seeds to the cache site at approximately the

same depth, attempting to leave each site as it was before I disturbed it. I recorded the distance from the cache to the center of the nearest bitterbrush shrub and the diameter of that shrub canopy. I recorded the substrate as bare mineral soil, or soil covered with light plant litter (< 5 mm deep) or heavy plant litter (> 5 mm deep). I recorded the Cartesian coordinates of each cache site using the source shrub as the origin and the cardinal directions as axes.

I monitored the labelled caches at ≈ 2 -week intervals during the fall to determine the fate of the seeds. When a cache site appeared disturbed or when the radioactivity at a cache site was noticeably reduced, I excavated the site to confirm the seed fate. I counted seed fragments to determine the number of seeds that rodents had eaten. During each visit to the study area, I resurveyed the area within 25 m of the source shrub to find new (secondary) caches. When I found new caches, I excavated them and recorded the numbers on the seeds to determine their cache site of origin. I then recorded the same set of microhabitat and position information that I had recorded for the primary caches. I checked and excavated all remaining caches the following spring (10 May 1994) to determine which had surviving seeds.

I trapped small mammals on 27-30 September 1993 around the source shrub. I used 25 Sherman live traps in a 5×5 grid with 10-m spacing, centering the trapping grids on the source shrub. I baited traps with peanut butter and rolled oats. I recorded the species, sex, age, and mass of each individual and marked them for individual identification. I checked each animal for traces of radioactivity using the gamma radiation detector.

Results

At the end of the day on which I deployed seeds under the source shrub, I found 12 intact seeds and 57 eaten seeds in and near the petri dishes under the source shrub. I found an additional one intact and 22 eaten seeds at several scattered feeding sites within 10 m of the source shrub. I found a total of 863 labelled seeds in 110 primary caches. Combining eaten, unharvested, and cached seeds, I relocated 955 seeds or 95.5% of the 1000 seeds that I put out.

All primary caches were within 16 m of the center of the source shrub (Figure 1). Median dispersal distance was 6.3 m (mean \pm SD = 6.21 ± 3.98 m). Caches contained one to 25 seeds (median = 7, mean \pm SD = 8.1 ± 5.9 seeds), including 28 unlabelled, indigenous seeds found in four of the caches. Chipmunks made 44 caches under bitterbrush shrub canopies, 43 caches at the edge of bitterbrush shrub canopies, and 23 caches in the open. They cached primarily in mineral soil (60 caches), and less frequently where there was plant litter (35 caches in light litter and 15 caches in heavy litter). Dispersal distances, number of seeds per cache, and cache microhabitats were similar to those observed at seven other source shrubs at this study site (Vander Wall, 1994).

I captured 16 yellow pine chipmunks and three deer mice (*Peromyscus maniculatus*) in the vicinity of the source shrub. None of these animals had any trace of radioactivity, but contamination from the seeds is transient and may have

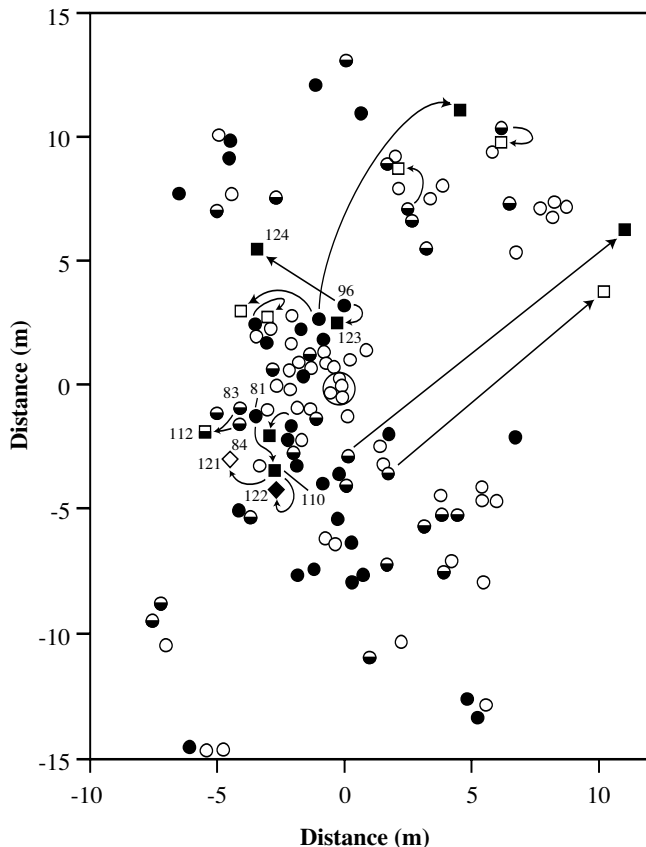


FIGURE 1. The arrangement of primary (circle), secondary (square), and tertiary (diamond) caches around the source shrub (large circle). Arrows indicate the movement of seeds from primary to secondary and tertiary cache sites. Open symbols represent caches that survived intact until the time of seed germination in spring, half shaded symbols represent caches where some (but not all) of the seeds survived until the time of seed germination, and shaded symbols represent caches with all seeds removed or eaten. The numbers refer to cache sites that are mentioned in the text.

been lost during the week that elapsed between seed handling and rodent trapping. Chipmunks were very likely responsible for all of the initial seed caching because the seeds were presented during the day, precluding access by the nocturnal deer mice.

Between the time of cache establishment and seed germination in April of 1994, 31 of the 110 primary caches completely disappeared (Figure 2). The seeds of 21 caches were eaten, seeds from three caches were moved to new sites, and at seven caches rodents ate some of the seeds and moved the rest to new sites. Eleven of the caches disappeared before winter snow began to accumulate and the rest (20 caches) disappeared during the winter and early spring before seeds germinated. In addition to the 31 caches that completely disappeared, rodents discovered 28 of the 110 primary caches and ate or removed some of the seeds. Initially, these 28 caches contained 11.0 ± 6.0 seeds (median = 11, range = 3-25), but at the time of seed germination in spring they contained only 3.9 ± 2.7 seeds (median = 4, range = 1-14). Of the 491 seeds that rodents took from primary cache sites, they ate 373 (76%).

During the fall, rodents removed 81 intact seeds from 17 primary caches. I was able to relocate 53 of these seeds

in 12 secondary caches (Figures 1 and 2). One of these secondary caches was subsequently emptied and the seeds moved to two tertiary caches. The 14 secondary and tertiary caches contained a mean (\pm SD) of 7.9 ± 6.7 seeds (median = 6, range = 1-18), significantly fewer than the primary caches from which they originated (mean \pm SD = 12.1 ± 5.9 seeds, median = 11, range = 4-23) (Wilcoxon paired-sample test, $p < 0.001$). Secondary and tertiary caches were 3.6 ± 4.5 m (range = 0.2 to 14.3 m) away from their cache of origin. Only four of the secondary and tertiary caches were moved toward the source shrub (all < 0.5 m), and 10 caches were moved away from the source shrub (range = 0.6 to 9.5 m). This is not significantly different from the expected pattern of one half of the secondary caches moved toward and one half moved away from the source shrub ($\chi^2 = 2.57$, $df = 1$, $p > 0.05$). The microhabitats (shrub cover and substrate type) where chipmunks recached seeds were similar to those used for primary caches.

Seedlings began to germinate in April, a couple weeks after snow melt. Eighty-six of the 124 caches that chipmunks made during the fall (69%) had one or more seedlings or intact seeds in early May (I use intact seeds to estimate potential germination because the radioisotope may have reduced seed viability). Seventy-nine of these caches were primary caches, six were secondary caches, and one was a tertiary cache (Figure 2). From another perspective, 51 of the 86 caches with surviving seeds (59.3%) were primary caches that had not been disturbed by rodents or other animals since they had been established, 28 surviving caches (32.6%) were primary caches that had been revisited by rodents that had eaten or removed some but not all of the seeds, and 7 surviving caches (8.1%) were secondary or tertiary caches. The mean number of seeds that survived to the time of germination was 4.3 ± 3.0 ($n = 79$) in primary caches and 3.0 ± 1.6 ($n = 7$) in secondary and tertiary caches. This difference was not significant (unpaired t -test, $t = 1.131$, $df = 84$, $p = 0.13$).

CACHE HISTORIES

Here I describe the histories of three groups of caches to help illustrate the dynamics of seeds after they have been initially cached. The locations of the caches mentioned are shown in Figure 1.

Cache 96 initially contained 23 bitterbrush seeds. Between 2 and 18 October, a chipmunk opened the cache, ate one seed, and removed one other seed before reburying the remaining seeds. The chipmunk buried the single removed seed 0.6 m away at site 123. Sometime between 18 and 29 October, a chipmunk reopened cache 96, ate 3 seeds, and carried 18 seeds away. I found 17 of these seeds along with one unlabelled indigenous seeds in a cache 4.3 m away at site 124. During this period, the single seed cached at site 123 disappeared. Sometime in early April, a chipmunk emptied cache 124 and ate all the seeds.

Cache 83 initially contained 19 seeds, and cache 84 (0.5 m away) 7 seeds. A chipmunk opened cache 83, ate one seed, removed six seeds, and reburied 12 seeds. The same chipmunk also visited cache 84, removed two seeds, and covered the remaining five seeds. This chipmunk carried the eight labelled seeds to site 112, 1.5 m away and buried

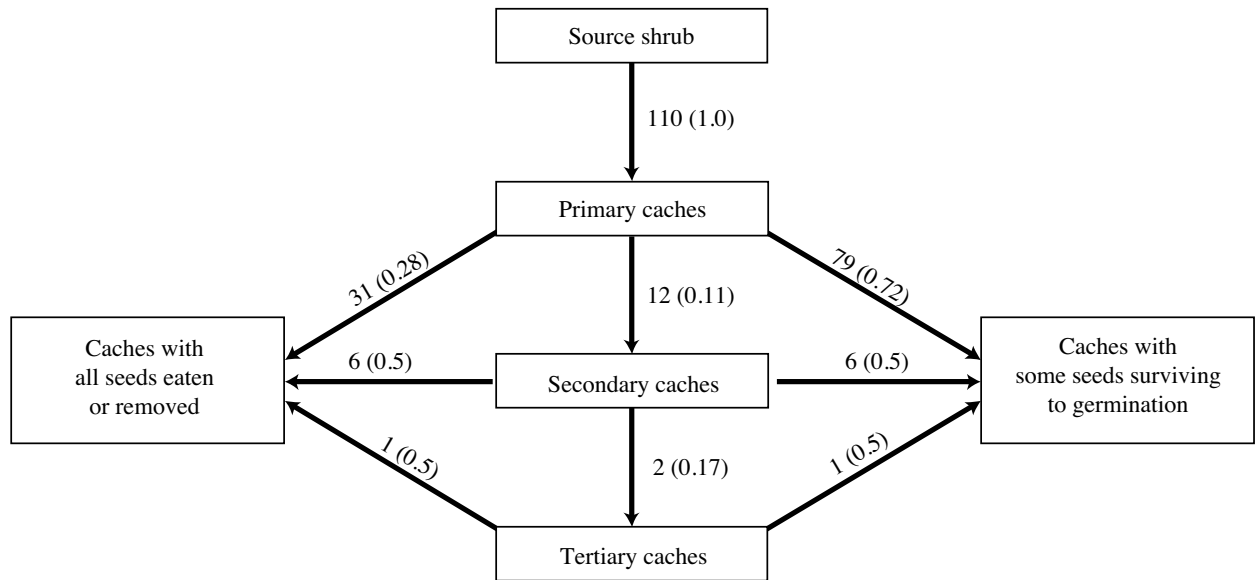


FIGURE 2. The fates of bitterbrush seed caches. The arrows indicate the movement of seeds from one state to another, the number beside the arrow indicates the number of caches involved, and the number in brackets is the proportion of caches involved. The numbers (or proportions) along the arrows emanating from primary and secondary caches sum to more than the input (or one) because the seeds of some caches had two or more fates.

them along with 10 unlabelled, indigenous seeds. After the initial visits, caches 83 and 84 remained undisturbed until spring when both produced seedlings. Rodents revisited cache 112 sometime during the winter or early spring and ate five seeds, carried two seeds away, and left one at the cache site. That seed germinated in April.

Cache site 81 contained 11 seeds. Between 21 August and 3 September, a chipmunk emptied the cache, eating four seeds and carrying seven seeds away. I found six of these seeds at site 110, 1.7 m away. Between 3 and 17 September, cache 110 disappeared. I found five of the seeds at site 121 and one of the seeds at site 122. These tertiary cache sites were 1.8 and 0.2 m away from cache 110, respectively. The single seed in cache 122 was eaten by a rodent (probably a deer mouse) sometime during the winter, but the five seeds in cache 121 produced healthy seedlings in April.

Discussion

Yellow pine chipmunks are very efficient at harvesting seeds from source shrubs, removing or eating in less than 12 hours nearly 99% of the seeds that I put out. I found most (92.7%) of the seeds that chipmunks removed from the source shrub in caches. I never located 45 of the 1 000 seeds offered. Chipmunks very likely transported these missing seeds outside the surveyed area where they either scatter hoarded or ate them. Or they may have transported them to their larders deep below ground where I could not detect them. Of the 110 primary caches of which I was aware, 51 (46%) survived to the time of germination without being further influenced by rodents and other vertebrates.

Although considerable, the amount of secondary caching around this source shrub was less than that observed at this site during an earlier study (Vander Wall, 1994). In that study, using unnumbered seeds and less thorough searches for secondary caches, I found from 17 to

55 primary caches and zero to 14 secondary caches around four source shrubs in 1989 and from 32 to 51 primary caches and 3 to 25 secondary caches around three source shrubs in 1990. Combining data for source shrubs within years, 15.9% and 20.3% of all caches were secondary caches in 1989 and 1990, respectively, compared to 11.3% for this study. Furthermore, the relative importance of secondary dispersal appeared to be greater in the earlier study. For example, at one site in 1990, rodents moved 31% of the seeds originally cached to secondary cache sites (compared to 6% for this study). Of the caches that survived until the time of seed germination, 45% were secondary caches (compared to 8% for this study). The causes for the lower percentages in this study are uncertain but may be related to the fact that chipmunks and other rodents exploited cached bitterbrush seeds less during this study than during the earlier study. For example, only 11.4% of cached seeds survived to the time of seed germination in 1989-90 compared to 45.5% for this study. Since chipmunks appeared to dig up primary caches relatively infrequently in this study (compared to Vander Wall, 1994) there was less opportunity for recaching.

One plausible explanation for the recaching of seeds by chipmunks (as well as other scatter hoarding birds and mammals) is that it helps them maintain or increase their knowledge of the stored food resource. Yellow pine chipmunks occupy broadly overlapping home ranges (Broadbooks, 1970), and caching appears to occur throughout the home range. Under favorable conditions, there could be thousands of caches prepared by dozens of chipmunks and other rodents and birds within a particular chipmunk's home range. Chipmunks are known to locate seed caches using at least three methods: spatial memory of cache sites, olfaction, and exploratory digging (Vander Wall, 1991). Memories of cache locations, which are possessed only by the hoarder, presumably give the individual an advantage over other animals when searching for caches (Andersson

& Krebs, 1978). Consequently, if a foraging chipmunk encounters a cache it did not make, it can increase its own knowledge of those seeds and reduce the knowledge of one of its competitors by moving the seeds to a new location. This knowledge may encompass both the placement and quality of the stored food (DeGange *et al.*, 1989). Any individual that does not engage in recaching of discovered seeds might gradually lose its competitive advantage for the seeds stored within its home range. This competitive "shell game" played by chipmunks results in a dynamic reshuffling of cached seeds from the time seeds are harvested in August to the time winter snows accumulate in November.

An observation, which is difficult to reconcile with this explanation of the adaptive significance of recaching, is that chipmunks left seeds at the primary cache site 28 times (of 59 primary caches that they excavated) and that, in most cases, the leaving of those seeds at the original cache site appeared to be intentional. There are two reasons for presuming that the leaving of seeds at cache sites was seldom accidental. First, the remaining seeds were usually covered with soil and the cache was well camouflaged. Second, at 19 of the 28 sites, rodents left three or more seeds (range = 1-14 seeds). Given the relatively large size of bitterbrush seeds, it seems unlikely that chipmunks simply overlooked these seeds.

Reshuffling of seeds may have several important implications for plant dispersal. First, the recaching of seeds means that the finding of a cache by a rodent does not necessarily mean death for all seeds in the cache. During the fall, rodents moved 27.5% of the seeds in caches they found to new cache sites. An additional 19.9% of the seeds continued to survive in the original cache ($n = 236$ seeds in 24 caches). As a consequence, 41% of all seedling emergence sites in spring were from secondary and tertiary caches and from primary caches that had been reduced in size. Second, the movement of seeds from cache site to cache site is likely to increase dispersal distances of some seeds from the source plant. Ten of 14 secondary dispersal movements were away from the source shrub. Most secondary dispersal distances (mean = 3.6 m) were fairly short relative to primary dispersal distances (mean = 6.2 m). But, I could not find 28 seeds taken from primary caches during the fall, and it is possible that rodents could have cached some of these outside the surveyed area (> 25 m from the source shrub). Third, secondary caches had fewer seeds than primary caches (means of 7.9 and 12.1, respectively), and visited caches were also reduced in size (means of 11.0 and 3.9 seeds before and after visitation). If rodents have more difficulty finding small caches (Reichman & Oberstein, 1977), then primary caches that have been reduced in size and smaller secondary caches may have a better chance of having some seeds survive to germinate.

Seed banks are often much more dynamic than they are portrayed (Chambers & MacMahon, 1994). The classical view of dispersal is a discrete spatial event occurring during a brief period of time. The modern view that is emerging is that dispersal is more often a series of steps that may occur intermittently during a long period of time between seed release from a plant and seed germination. Chambers and MacMahon (1994) define two phases in seed dispersal.

Phase I is movement from the parent plant to a substrate, and Phase II is any subsequent movement of the seed before it germinates. Phase II dispersal can be either horizontal across the substrate or vertical through the substrate. In the case of bitterbrush seeds handled by yellow pine chipmunks, all recaching is Phase II dispersal. This process creates smaller caches often farther from the source plant and thereby reduces the spatial patchiness of the cached seeds. Although the microhabitat distributions of primary and subsequent caches were similar, recaching creates more sites where seeds can potentially germinate. The detection of a cache by a forager is often equated with seed mortality, but in many cases it is just the beginning of the next step in the seed dispersal process. Even when rodents consume a portion of the seeds in large caches it may have a positive impact on the plant population because after germination seedling attrition from grazing and desiccation occurs within large seedling clumps, usually reducing the number of reproductive individuals in mature bitterbrush shrubs to fewer than five (Vander Wall, 1994, unpublished data). In other words, a certain amount of seed or seedling mortality in large caches is inevitable. The fragmenting of large caches into several smaller ones may over the long term actually reduce total mortality. As a consequence of these events, the patterns of establishment in plant populations are often more strongly affected by Phase II dispersal than by Phase I dispersal.

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