

## Cache site selection by chipmunks (*Tamias* spp.) and its influence on the effectiveness of seed dispersal in Jeffrey pine (*Pinus jeffreyi*)

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**Abstract.** The effectiveness of Jeffrey pine (*Pinus jeffreyi*) seed dispersal performed by seed-caching yellow pine chipmunks (*Tamias amoenus*) and lodgepole chipmunks (*Tamias speciosus*) was compared to that of wind dispersal in the Sierra Nevada of western Nevada. Wind-dispersed seeds typically fall under or near the parent tree. Chipmunks removed 90 and 97% of 1064 radioactive seeds from each of two simulated wind-dispersed seed shadows in less than 24 h. “Wind-dispersed” seeds were deployed within 12 m of the two “source” trees, but chipmunk caches were found from 2–69 m from the trees. Chipmunks carried nearly all seeds away from source trees, greatly reducing the density of seeds under and near source trees. Caches contained from 1–35 seeds and most were buried 7–21 mm deep. Chipmunks cached in open bitterbrush shrubland with mineral soils much more than expected and cached in closed-canopy Jeffrey pine and lodgepole pine forests with thick needle litter much less than expected. Many Jeffrey pine seedlings and saplings grow in the bitterbrush habitat and few grow in the pine forests. Ten and 20% of the original caches survived until April, the time of seed germination, at the two sites. The movement of wind-dispersed seeds is random relative to environmental variables important in seedling survival, and the wind in coniferous forests cannot quickly bury seeds. The quality of seed dispersal rendered by chipmunks was superior to that provided by the wind because the chipmunks quickly harvested seeds on the ground, moved them away from source trees, and buried them in the ground in habitats and microhabitats where they were more likely to establish new seedlings. The increased quality of seed dispersal provided by animals relative to the wind may help explain why over twenty species of pines have evolved seeds and cones that are adapted for dispersal by seed-caching animals.

**Key words:** Caching – Chipmunks – Jeffrey pine – Seed dispersal – Bitterbrush

Howe and Primack 1975; McKey 1975; Howe 1977, 1980; Herrera and Jordano 1981; Malmborg and Willson 1988; Murray 1988; Reid 1989; 1991). Schupp (1993) defines disperser effectiveness as the contribution a disperser makes to the future reproduction of a plant. Disperser effectiveness has two components: (1) the quantity of dispersal, which is determined by the number of visits a disperser makes to a plant and the number of seeds dispersed each visit, and (2) the quality of dispersal, which is determined by how the disperser treats seeds and the quality of the sites where the disperser deposits viable seeds. Much of the work on disperser effectiveness (reviewed in Schupp 1993) has been conducted on frugivorous birds and mammals, but these definitions apply equally well to other types of seed dispersers and to physical processes (e.g., wind, gravity).

The objective of this paper is to describe the effectiveness of dispersal of Jeffrey pine (*Pinus jeffreyi*) seeds provided by seed-caching rodents and compare it to that likely from wind dispersal. Over twenty species of pines (including pinon pines [*Pinus edulis* and *Pinus monophylla*], whitebark pine [*Pinus albicaulis*], limber pine [*Pinus flexilis*], and southwestern white pine [*Pinus strobiformis*]) are dispersed by seed-storing birds and rodents (Vander Wall and Balda 1977; Hutchins and Lanner 1982; Lanner 1982b; Tomback 1982; Miyaki 1987; Hayashida 1989; Vander Wall 1992a, b). These pines have evolved seed and cone traits (i.e., large, wingless seeds that are retained in relatively poorly defended cones) that attract seed-storing animals. These animals recover only a portion of the seeds they scatter hoard, and many of the overlooked seeds establish new plants. It is generally acknowledged that these animal-dispersed pines have evolved from ancestors with winged seeds and strikingly different seed and cone traits, and that these ancestral seeds were wind dispersed (e.g., Lanner 1982b).

I selected Jeffrey pine for this study because it is adapted for wind dispersal; it has large seeds with functional wings that are released from well-armored cones at maturity. Most Jeffrey pine seedlings, however, establish from animal caches (Vander Wall 1992a, b). Consequently, Jeffrey pine represents a character state through which many animal-dispersed pines appear to have passed; a pine morphologically adapted for wind dispersal

The propagules of many plants are dispersed by a variety of vertebrates as well as physical processes, and these agents of dispersal vary greatly in their effectiveness (e.g.,

but which owes much of its establishment success to seed-caching by animals. Animals that scatter hoard Jeffrey pine seeds in the soil at my study area include yellow pine chipmunk (*Tamias amoenus*), lodgepole chipmunk (*T. speciosus*), golden-mantled ground squirrel (*Spermophilus lateralis*), deer mouse (*Peromyscus maniculatus*), Clark's nutcracker (*Nucifraga columbiana*), and Steller's jay (*Cyanocitta stelleri*). Only the chipmunks appear to have played a role in seed dispersal in the experiment reported here.

### Study area

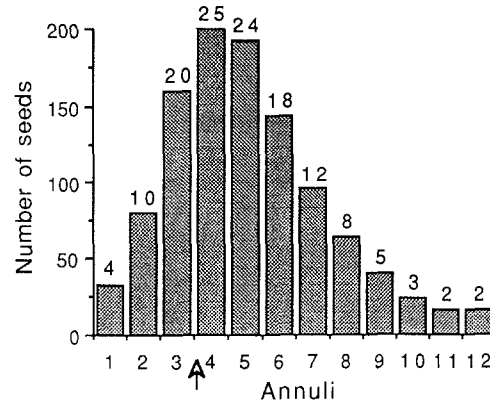
The data reported here were collected in Little Valley, Washoe Co., 30 km south of Reno, Nevada during late September 1991 through April 1992. Four vegetation types dominate the lower portions (1960–2100 m elev) of Little Valley: meadows of grasses, sedges, and forbs, lodgepole pine (*Pinus contorta*) forests, Jeffrey pine forests, and antelope bitterbrush (*Purshia tridentata*) shrublands with scattered Jeffrey pines. I studied the dispersal and survival of Jeffrey pine seeds at two sites located at the Jeffrey pine forest-antelope bitterbrush shrubland edge and about 30 m from lodgepole pine forests. The bitterbrush habitat had bare soils of decomposed granite with relatively thin (generally <2 cm) accumulations of plant litter under shrubs. The forest habitats has closed canopies with little or no shrub understory and relatively thick (>5 cm) deposits of needle litter. At each site, the experiment centered around a Jeffrey pine "source" tree located at the Jeffrey pine forest edge. Source trees were approximately 18 m tall with 80 cm basal diameters and canopy radii of about 3 m. Jeffrey pines produced a small and patchy seed crop in the study area during fall 1991.

### Methods

I created seed shadows around source trees following the procedure described in Vander Wall (1992b). Each seed shadow consisted of 1064 Jeffrey pine seeds placed at various distances from source trees so as to mimic a pattern expected from wind dispersal under conditions of a slight wind. I arranged the seeds at 133 stations each with 8 seeds marked with a pin flag 50 cm away. The stations were arranged in concentric circles at the midpoints of twelve 1-meter wide annuli centered on the source tree (i.e., 0.5, 1.5, . . . 11.5 m from the trunk). I numbered seeds with indelible ink 1 through 12 representing the annuli where I initially deposited them. I also labelled seeds with scandium-46, a gamma-emitting radionuclide, so that I could later locate cache sites. Each Jeffrey pine seed received a label of approximately 75–100 kBq.

The distribution of seeds (and stations) around source trees is illustrated in Fig. 1. Consistent with theoretical and experimental studies of wind dispersal, the greatest number of seeds per annulus were deployed just beyond the tree canopy (annulus 4), and the greatest density of seeds occurred just inside the tree canopy (annulus 3). Over 74% of the seeds were deployed beyond the perimeter of the tree canopies.

I deployed the seed shadows on 17 September at site 1 and on 7 October at site 2. On the next days, after most seeds had been harvested by animals, I visited each release station to collect unharvested seeds. From 18–20 September at site 1 and from 8–10 October at site 2, I located caches around the source trees using an Eberline model ASP-1 gamma radiation counter with SPA-3



**Fig. 1.** Allocation of 1064 Jeffrey pine seeds to twelve 1-m wide annuli around "source" trees to simulate a wind-dispersed distribution. The numerals above the bars are the numbers of release stations (8 seeds per station). The arrow marks the edge of the tree canopy

detector. When I located a cache site, I covered it with a 20 × 20 cm piece of coarse wire mesh weighted with a rock to prevent removal of the seeds by animals. I searched the study areas thoroughly to a radius of 40 m from the source trees. Beyond this perimeter, I thoroughly searched at least 10 m beyond and around the most distant cache discovered in any particular direction.

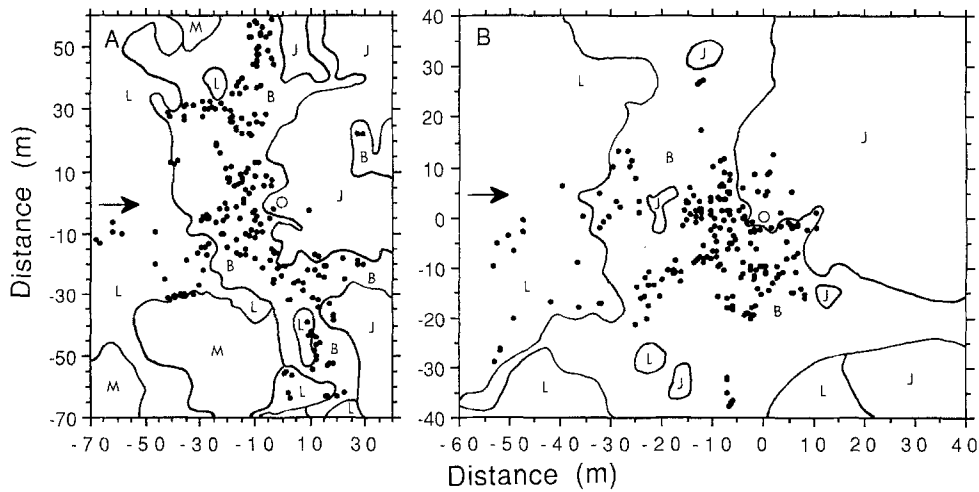
When searches of the areas were completed, I immediately began mapping and excavating caches. I determined the depth of burial at the top and bottom of seeds. I counted the seeds and recorded the numbers on the seeds that represented the annulus from which they originated. Then I measured the straight line distance from the source tree to the cache and determined the x- and y-coordinates of each cache using the source tree as the origin of a graph space and the cardinal directions as axes. Finally, I returned the radioactive seeds to the cache site at the same depth, leaving the cache in as undisturbed a condition as possible. Later in the fall (30 October at site 1 and 7 November at site 2) and again just as seeds began to germinate in the spring (21 April), I checked all cache sites to determine whether seeds had been removed by animals. Where caches had been removed during the fall survey, I resurveyed the surrounding area to a radius of ≈3 m with the radiation detector to find new (secondary) caches. Although the radioactive scandium at the concentration used does not appear to have any effect on seed viability, I recorded a cache as surviving to germination if it contained one or more edible (apparently viable) seeds.

To determine the amount of recent establishment of Jeffrey pine seedlings and saplings in the three vegetation types, I established four 10 × 10 m plots in each habitat type. The plots were selected in early spring before seedling emergence about 1 km from the two experiment sites and at sites with similar conditions: forests with nearly closed canopies and litter >5 cm deep and open bitterbrush shrubland with mineral soil. On 10 June 1992, I surveyed the plots and counted the number of healthy new seedlings (from the fall 1991 seed crop), 3-year old seedlings (from the fall 1988 seed crop), and saplings <1 m tall.

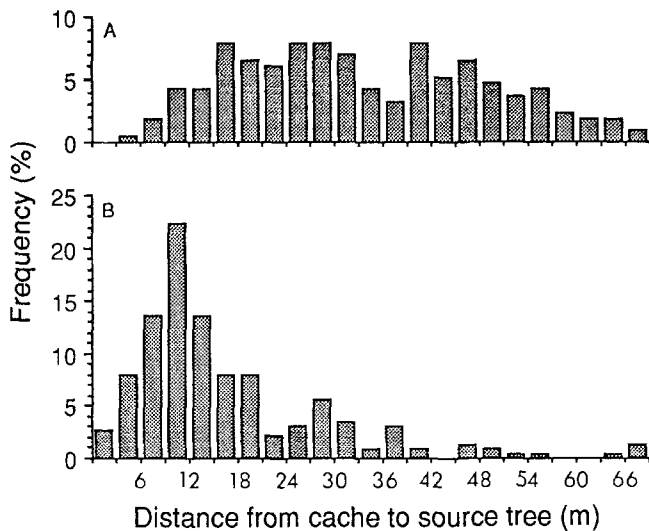
### Results

#### *Fate of "wind-dispersed" seeds*

After I deployed the two Jeffrey pine seed shadows, I observed the area from a distance of about 50 m for 1 h. I saw yellow pine chipmunks and golden-mantled ground squirrels near site 1, but these rodents had apparently not discovered the seeds by the time I left the site. At site 2,

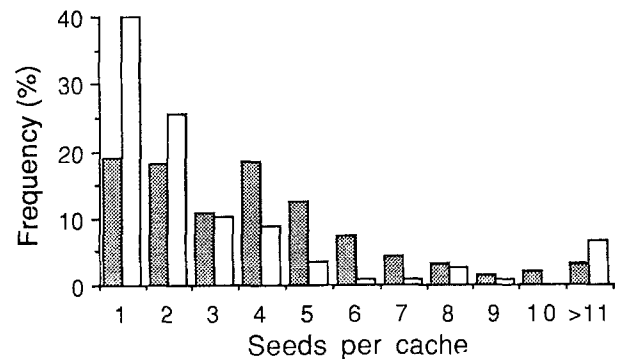


**Fig. 2A, B.** Cache site locations (filled circles) around two "source" trees (open circle) located at the edge of the Jeffrey pine forest; (A) source tree 1 and (B) source tree 2. The arrow indicates the direction of the prevailing winds. Habitat types are: *B*, bitterbrush shrubland; *J*, closed-canopy Jeffrey pine forest; *L*, closed-canopy lodgepole pine forest; *M*, meadow



**Fig. 3A, B.** Frequency distribution of distances from source trees to cache sites at source tree 1 (A) and 2 (B)

I observed yellow pine and lodgepole chipmunks harvest and cache seeds. I returned to the sites the next day (24 and 20.5 h after seed arrays were established at site 1 and 2, respectively) and found 34 intact seeds at site 1 and 104 intact seeds at site 2. Most of these unharvested seeds were at 4 and 11 completely overlooked stations. Chipmunks has harvested 97 and 90% of the seeds at the two sites. I found the fragments of only 8 seeds near (within 12 m) source tree 1 and 49 seeds near source tree 2, suggesting that most of the harvested seeds had been carried off intact. At greater distances (13–45 m), I found the fragments of 6 and 20 additional seeds. During the next several days, I found and mapped 216 caches containing 857 seeds at site 1 and 228 caches containing 752 seeds at site 2. Considering unharvested, eaten, and cached seeds, I accounted for 85 and 87% of the seeds that I had deployed at the two sites. The remainder had probably been carried to larders deep underground or out of the search area.



**Fig. 4.** Frequency distribution of cache sizes at site 1 (shaded) and site 2 (open)

Caches were scattered at distances ranging from 3.25–68.22 m at source tree 1 and 1.90–68.94 m at source tree 2 (Fig. 2). The distributions of cache site-to-source tree distances (Fig. 3) at the two sites were significantly different (Chi-squared test pooling some data to avoid cell values less than 5,  $\chi^2 = 148.07$ ,  $df = 11$ ,  $P = 0.0001$ ) with dispersal distances being much shorter at site 2. Of particular interest, I found only 14 caches at site 1 (6.5%) within a radius of 12 m from the source tree where the initial seed shadow was deployed, but at site 2, I found 106 caches (46.5%) within this area. Mean ( $\pm$ SD) minimum dispersal distances (the shortest distance between the cache site and the annuli where a seed originated) were  $28.67 \pm 15.68$  m at site 1 but only  $12.48 \pm 13.32$  m at site 2. Only 2 of 343 seed movements (i.e., annulus-to-cache measurements) at site 1 and 14 of 292 seed movements at site 2 were toward the source trees.

Cache sizes ranged from 1 to 17 seeds at site 1 and 1 to 35 seeds at site 2. The distributions of cache sizes at the two sites (Fig. 4) were significantly different (Chi-squared test lumping cache sizes 6–10 seeds and 11–35 seeds to avoid small cell values,  $\chi^2 = 56.38$ ,  $df = 6$ ,  $P < 0.001$ ). The most frequent cache size at both sites was one seed: 19% of caches at site 1 and 40% of caches at site 2. Median cache size was 4 and 2 seeds, respectively. Only seven caches at site 1 and 15 caches at site 2 contained 11 or more seeds.

Mean depth of the top of caches at site 2 was  $12.7 \pm 7.4$  mm, significantly deeper than the mean top depth of  $6.7 \pm 4.3$  mm at site 1 ( $t$ -test,  $t=8.017$ ,  $df=249$ ,  $P<0.0001$ ). The mean bottom depth of caches at site 2,  $20.7 \pm 10.5$  mm, was also significantly deeper than at site 1 ( $14.2 \pm 5.0$ ;  $t=6.479$ ,  $df=249$ ,  $P<0.0001$ ). These differences were probably due to the deeper, more friable soils in the bitterbrush habitat at site 2. For caches made in mineral soil, depth of the top of a cache was not significantly correlated with number of seeds in the cache at site 1 ( $r=-0.16$ ,  $df=89$ ,  $P>0.05$ ) but this relationship was significant at site 2 ( $r=0.51$ ,  $df=63$ ,  $P<0.001$ ). Number of seeds in a cache was strongly correlated with the bottom depth of the cache at both sites (site 1:  $r=0.46$ ,  $df=89$ ,  $P<0.001$ ; site 2:  $r=0.74$ ,  $df=63$ ,  $P<0.001$ ).

#### Distribution of caches among habitat and microhabitat

The chipmunks did not distribute caches around the source trees uniformly (Fig. 2). I tested whether chipmunks had any preference for habitats within 40 m of the source trees, the areas that I had searched completely and uniformly, by comparing the observed number of caches per habitat with the expected number of caches assuming that an animal caching at random would use each habitat type in proportion to habitat area. The comparison showed that the bitterbrush habitat received nearly twice as many caches as expected and the Jeffrey pine habitat had less than one-sixth the expected number of caches (Table 1; Chi-squared test,  $\chi^2=64.3$ ,  $df=2$ ,  $P<0.001$  for site 1;  $\chi^2=136.2$ ,  $df=2$ ,  $P<0.001$  for site 2). The lodgepole pine forest at site 2 also received fewer caches than expected but this may have been partially because the closest lodgepole pine forest was 30 m from the source tree.

In the bitterbrush habitat, 53 and 56% of the caches at the two sites were in the open ( $>10$  cm from a bitterbrush shrub). Twelve and 16% of the caches were well under the canopy of bitterbrush shrubs, and the remainder of the

caches (35% at site 1 and 28% at site 2) were at the edges of bitterbrush canopies (within 10 cm of the edge of the canopy). At site 1, 73% of the caches were in mineral soil, 24% were in thin plant litter ( $<5$  mm thick), and 3% were in thick plant litter ( $>5$  mm thick). Comparable values at site 2 were 66%, 27%, and 7% respectively. In the Jeffrey pine forest, most caches were under the canopies of mature trees (75 and 86%) and in thick (often 5–10 cm deep) accumulation of plant litter (63 and 100%). Conditions of cache sites in the lodgepole pine forest were similar: 87 and 47% of caches were under tree canopies and 83 and 71% of caches were in thick accumulations of plant litter. Consequently, conditions experienced by seeds in caches and any seedlings that might result from those caches in the bitterbrush and forest habitats were very different. In the bitterbrush habitat, seedlings generally experience open sun or light shade and become rooted in mineral soil. In the forest habitats, on the other hand, seedlings typically experience deep shade and their roots must often penetrate relatively thick mats of decomposing forest litter before reaching the mineral soil.

#### Cache survival

Many of the caches made by the chipmunks in late September and early October disappeared during the weeks leading up to the initiation of winter snowfall in November. When I checked cache sites in the fall, there were 131 intact caches (61%) at site 1 and 66 intact caches (29%) at site 2 (Fig. 5). Only a few of the empty caches had seed fragments nearby (2.4 and 3.1% of the sites), indicating that animals had carried many of the cached seeds away intact. When I searched the vicinity of cache sites that had been emptied, I found 18 and 17 new caches at the two sites. These secondary caches usually contained fewer seeds than the original caches (mean  $\pm$  SD =  $1.8 \pm 1.0$ ,  $n=18$ , range 1 to 4 seeds at site 1; I did not excavate secondary caches at site 2). It was clear that secondary caches had been made with the seeds from the emptied caches because they were usually located only a couple of

**Table 1.** The distribution of Jeffrey pine seed caches among habitat types within a radius of 40 m of two Jeffrey pine source trees compared to the expected distributions of caches based on caching in proportion to habitat area. The differences between the expected and observed distributions are significant (Chi-squared test,  $\chi^2 = 64.3$  and  $136.2$ ,  $df = 2$ ,  $P < 0.001$  for both source trees)

Habitat	Source tree 1				Source tree 2			
	Total caches	Caches $\leq 40$ m from source tree	Habitat area (m <sup>2</sup> )	Expected caches <sup>a</sup>	Total caches	Caches $\leq 40$ m from source tree	Habitat area (m <sup>2</sup> )	Expected caches <sup>a</sup>
Jeffrey pine forest	8	7	1812	50.8	14	14	1935	83.2
Lodgepole pine forest	30	9	416	11.7	17	5	501	21.5
Bitterbrush shrubland	176	125	2724	76.4	197	197	2591	111.3
Meadow edge	2	0	75	2.1	0	0	0	0
Total	216	141	5027	141	228	216	5027	216

<sup>a</sup>Number of caches expected if all caches within 40 m of the source tree are allocated to habitats in proportion to habitat area (i.e., uniformly distributed)

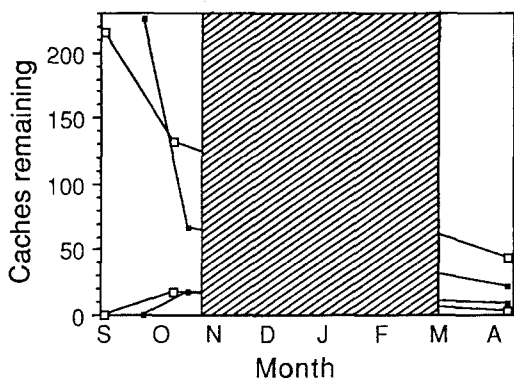


Fig. 5. Changes in the number of caches at site 1 (open squares) and site 2 (closed squares) during fall and winter. The upper set of lines refers to primary caches, and the lower set of lines refers to secondary caches. The shaded area is the period of winter snow pack

meters away and they contained numbered seeds that were the same as those missing from the raided caches. Both the number of secondary caches made and the distances these seeds were dispersed should be considered minimum estimates because only a small portion of each study area was searched. Chipmunks and other rodents may have moved many of the excavated seeds to underground larders (Broadbooks 1958), but this idea could not be tested.

On 21 April, about four weeks after snowmelt, I checked the sites again and found 43 original and 3 secondary caches still intact at site 1 and 22 original and 8 secondary caches intact at site 2. Of these sites, 26 and 27 had one or more emerging seedlings and the rest had healthy, edible seeds that had not yet germinated. Survival rate (including both germinated and ungerminated seeds) of the original caches was 19.9% at site 1 and 9.7% at site 2. Most of the original caches that survived were in the bitterbrush habitat (34 at site 1 and 16 at site 2), but the proportions of caches surviving in the bitterbrush and forest habitats were not significantly different (Chi-squared test with forest habitats combined at each site to avoid small cell values,  $\chi^2 = 0.15$ ,  $df = 1$ ,  $P > 0.05$  for site 1 and  $\chi^2 = 2.80$ ,  $df = 1$ ,  $P > 0.05$  for site 2).

#### Suitability of habitats for establishment of Jeffrey pine

The 10 × 10 m plots in the bitterbrush habitat had far more total seedling and sapling stems than the plots in the forest habitats (Table 2; Kruskal-Wallis test,  $H_{4,4,4} = 8.33$ ,  $P < 0.01$ ). Even though the lodgepole pine

forest had more total seedling and sapling stems than the Jeffrey pine forest, this difference was not quite significant (Mann-Whitney test,  $U_{4,4} = 13$ ,  $P = 0.10$ ). With regard to the amount of recent establishment and early survival of Jeffrey pine, the habitats can be arranged in the following sequence: bitterbrush shrubland > lodgepole pine forest ≥ Jeffrey pine forest.

#### Discussion

As defined in the introduction, the effectiveness of a seed disperser depends on the quantity of seeds it removes from a parent plant and the quality of its handling and deposition of those seeds. The quantity of seed dispersal performed by chipmunks in this experiment was high. Chipmunks removed nearly all of the 1064 seeds from around each of the two source trees in less than 1 day, and they ate very few of those seeds. Most of the overlooked seeds would very likely have been removed by seed-caching animals by the next day. This high rate of removal was no doubt facilitated by placing the seeds in clumps and marking the clumps with pin flags. However, in a separate study in the same area (Vander Wall, ms), widely-spaced, unmarked, winged Jeffrey pine seeds also disappeared quickly, having a half life (the time for half of the extant seeds to be removed by animals) ranging from 53 to 119 hours depending on the microsite where a seed was placed. This is very rapid seed removal for a wind-dispersed seed that must survive for five to seven months until germination. The rapid removal of seeds by scatter-hoarding animals is also important because this affords less time for ground-foraging seed predators (e.g., deer, quail, black bear) to discover seeds.

The quality of Jeffrey pine seed dispersal is largely dependent on the distance seeds are transported, depth of seed burial, and the habitat and microhabitat to which they are transported. Because of the scatter hoarding activities of chipmunks, mean minimum dispersal distances increased by 28.7 m at site 1 and 12.5 m at site 2 relative to initial seed placement. Chipmunks made only 6 caches under (< 3 m from) source trees (Fig. 3). There were only 16 instances ( $n = 635$  at the two sites combined) of chipmunks moving seeds toward the source trees, reaffirming the findings of Vander Wall (1992b) that dispersal is predominantly away from the concentrated distribution of seeds under source trees. The caching activity of chipmunks resulted in a relatively uniform (Fig. 3) and less dense distribution of seeds compared to the initial seed arrays. In contrast, the wind may disperse a few seeds very great distances, much greater distances than in the

Table 2. Number of healthy Jeffrey pine seedlings and saplings (mean ± SD) found on four 10 × 10 m plots in each of three vegetation types in Little Valley, Nevada, on 10 June 1992

Vegetation type	1992 seedlings	1989 seedlings	Saplings < 1 m tall	Total stems
Closed Jeffrey pine forest	0.00	0.25 ± 0.50	0.25 ± 0.50	0.50 ± 0.58
Closed lodgepole pine forest	0.00	2.25 ± 2.06	0.50 ± 1.00	2.75 ± 2.22
Open bitterbrush shrubland	5.50 ± 5.07	37.75 ± 48.53	7.75 ± 2.50	51.00 ± 48.35

“wind-dispersed” seed array deployed in these experiments, but theoretical and experimental studies (e.g., Greene and Johnson 1989) indicate that most wind-dispersed seeds fall under or near the source plant. This is even more likely to be the case in large-seeded species like Jeffrey pine and for trees growing in closed-canopy forests where wind velocity is reduced.

Because chipmunks and other seed-caching animals are among the most avid gatherers of Jeffrey pine seeds, a substantial portion of the seed crop is quickly buried. The rate of seed removal is much slower for cached seeds (Fig. 5) compared to wind-dispersed seeds on the ground surface. Cached seeds are also shielded from the harmful effects of hot sunshine and dry winds that reduce seed viability. Cache depths of scatter-hoarding animals are often within the range of depths suitable for plant establishment (Vander Wall 1993). While some burial may occur “accidentally” when seeds unmolested by animals fall into cracks in soil and plant litter, the most effective means of seed burial appears to be offered by chipmunks and other scatter hoarding animals. Without being buried, Jeffrey pine seeds are unlikely to germinate (Vander Wall 1992b).

The ability to disperse some seeds over great distances may be very important because it enables a plant to colonize new habitat patches, but for those seeds that move relatively short distances, the conditions at the site of seed deposition are more important than the distances travelled. A seed that is dispersed a long distance and lands under a tree of the same species has gained little compared to a seed that travels half that distance and lands in the open. The prevailing winds at both source trees used in these experiments (Fig. 2) probably carry most naturally-dispersed seeds into the Jeffrey pine forest. The deep shade and thick litter layer in these forests appear to create an inhospitable environment for young Jeffrey pine seedlings (Table 2) and other understory plants (e.g., Sherman and Chilcote 1972). Chipmunks in this experiment moved seeds into the bitterbrush openings, resulting in a highly nonrandom distribution of caches with regard to habitat availability. Furthermore, this redistribution of seeds was generally against the prevailing winds (Fig. 2). Chipmunks may reap several benefits by caching in the bitterbrush shrubland. The bitterbrush habitat provides excellent cover for foraging and caching rodents, presumably resulting in reduced risk of predation. Other activities of chipmunks are centered in the bitterbrush habitat, which, because of its diverse array of shrubs, forbs, and grasses, provides better foraging and nesting opportunities than the forest habitats. In addition, the chipmunks may prefer to cache in the friable mineral soils of the bitterbrush habitat compared to the thick mats of needle litter in the Jeffrey pine forest.

The bitterbrush habitat had the greatest number of recently established Jeffrey pine seedlings and saplings (Table 2). The density of these young pines is probably the result of two processes: a history of intensive seed caching in this habitat and suitable conditions for establishment and growth. Early successional habitats, such as the bitterbrush shrublands, have often been identified as important caching areas for seed-storing animals (Ligon 1978, Harrison and Werner 1984, Jensen and Nielsen 1986,

Stapanian and Smith 1986, Tomback 1986). The effect of cache site selection by chipmunks is to accelerate plant succession, causing open shrublands to be replaced by young Jeffrey pine forests. Within the bitterbrush habitat, chipmunks made about one-third of their caches under the canopies of bitterbrush shrubs. These microsites have been found to provide the greatest chances of Jeffrey pine seedling establishment at a nearby study site (Vander Wall 1992a). Some frugivorous birds are also known to disperse more seeds into habitat where they have a greater chance of establishing new plants (e.g., Herrera and Jordano 1981).

Animal-dispersed pines appear to have evolved several times (Lanner 1982b). This study helps to clarify why this evolutionary transition from wind to animal-dispersed seeds might have come about. Wind dispersal is random with respect to environmental variables important in seedling establishment. Although the quantity of dispersal provided by wind is high the quality of dispersal is low. Dispersal by seed-caching animals is more directional, moving a much greater proportion of seeds into habitats and microhabitats where they will find favorable conditions for establishment, and scatter hoarders provide a very effective means of seeds burial. This high quality seed dispersal performed by animals may have resulted in strong selection pressure acting on any characteristics of seeds and cones that facilitated animal harvest. This may have eventually produced the highly modified seeds and cones of pinon and stones pines we see today (Vander Wall and Balda 1977; Lanner 1982a).

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