

Jennifer L. Hollander · Stephen B. Vander Wall

Effectiveness of six species of rodents as dispersers of singleleaf piñon pine (*Pinus monophylla*)

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Abstract The effectiveness of six species of rodents as dispersers of singleleaf piñon pine (*Pinus monophylla*) was investigated in field enclosures. The rodent species were Panamint kangaroo rat (*Dipodomys panamintinus*), Great Basin pocket mouse (*Perognathus parvus*), pinyon mouse (*Peromyscus truei*), deer mouse (*Peromyscus maniculatus*), least chipmunk (*Tamias minimus*), and white-tailed antelope ground squirrel (*Ammospermophilus leucurus*). Five measures of seed harvesting and caching behavior were assessed and used to calculate the effect of species on the probability of effective dispersal (i.e., movement of seeds to potential establishment sites) of piñon pine seeds. These measures were proportion of seeds harvested, proportion of harvested seeds that were scatter hoarded, relative dispersion of scatter-hoarded seeds, seedling emergence and seedling establishment. To evaluate the effects of the last two variables, a 2-year study of seed germination and seedling establishment was conducted in the field. Seedling survival was 72–90% for seedlings emerging from 1–4 cm deep but was markedly lower from surface caches and for depths >4 cm. All seedlings in the open microsite perished before the end of the first year, whereas 38–97% of seedlings under shrubs survived. Cache size did not affect seedling survival over the 2 years, but large caches reduced the total number of potential establishment sites. All six species harvested over 90% of the piñon seeds presented and scatter hoarded from 31% (pocket mouse) to 66% (chipmunk) of the seeds they harvested. Piñon mice and deer mice distributed seeds to more caches sites (i.e., put fewer seeds in caches) than the other species and, consequently, created more potential establishment sites. All species scatter hoarded seeds at depths suitable for seedling emergence, but pocket mice and piñon mice cached under shrubs more than the other species, the microhabitat where seedlings had the greatest

probability of establishing. Factors that had the greatest effect on the probability of effective dispersal were microhabitat selection and cache size.

Keywords Food hoarding · Granivory · Seed caching · Seed dispersal · Seedling establishment

Introduction

Many plants are dispersed by animals (e.g., birds, mammals, ants) that consume or handle fruits or seeds. In many cases, plants engaged in these relationships appear to have evolved fruits and seeds specifically adapted to attract these agents of dispersal. However, careful analysis of these plant-animal interactions reveals that few are tightly coevolved relationships between one plant species and one animal species (Janzen 1970; Herrera 1982, 1985; Reid 1991). Instead, nearly all of these “mutualisms” appear to be the sum of numerous, diffuse interactions involving dozens of species. Generally, a number of unrelated vertebrate taxa can be found consuming and dispersing the propagules of a particular plant species, and these animal species consume fruits of a variety of plant species, providing dispersal services as an unintended consequence of their foraging. In most cases, seed dispersal occurs by the combined effect of a seed-consuming guild. However, within these guilds, animal species differ in the contribution that they make to the future reproduction of a plant. These differences depend on the quantity of seeds that an animal handles and on the quality of dispersal or the extent to which seeds are deposited in situations conducive to seedling establishment (Herrera and Jordano 1981; Schupp 1993). Some seed consumers have no beneficial effect on the plant (exclusive seed predators), whereas other species inadvertently provide some benefit to the plant (seed predators and dispersers). How species differ in their effectiveness as dispersers is a question that is central to the evolution of seed dispersal (Howe 1977; Hutchins and Lanner 1982; Wheelwright and Orians 1982; Sun et al. 1997), because

J. L. Hollander (✉) · S. B. Vander Wall
Department of Biology and the Program in Ecology, Evolution
and Conservation Biology, University of Nevada,
Reno, NV, 89557, USA
e-mail: jlmcknig@scs.unr.edu

foragers have important effects on seed fates and, consequently, the evolution of fruit traits.

In this paper, we examine the relative effectiveness of six rodent species in dispersing the seeds of singleleaf piñon pine (*Pinus monophylla*). These six species include two murid rodents [deer mouse (*Peromyscus maniculatus*; 18.0±1.2 g) and piñon mouse (*Peromyscus truei*; 21.0±3.7 g)], two heteromyid rodents [Great Basin pocket mouse (*Perognathus parvus*; 19.0±1.6 g) and Panamint kangaroo rat (*Dipodomys panamintinus*; 65.8±10.5 g)], and two sciurid rodents [least chipmunk (*Tamias minimus*; 42.0±7.9 g) and white-tailed antelope ground squirrel (*Ammospermophilus leucurus*; 99.0±5.1 g)]. All of these species are common in piñon woodlands in western Nevada. Relatively little is known about their scatter-hoarding behavior. We define scatter hoarding as the burying of seeds in the soil surface (i.e., potential establishment sites) and larder hoarding as the deposition of seeds in underground burrows and chambers where they could not possibly establish seedlings.

We focus primarily on the quality of deposition of dispersed seeds. The most effective seed dispersers among food-storing species are those that scatter-hoard at depths (Vander Wall 1993) and in microsites (Chambers and MacMahon 1994) that intersect conditions necessary for the plant to establish (Price and Jenkins 1986; Vander Wall 1990). Furthermore, those species that make relatively small caches are likely to be better dispersers than those that make large caches, because they are likely to make more caches and emergent seedlings are likely to experience less competition (Howe 1989). These three factors: cache size (or relative seed dispersion), the effect of cache depth on seedling emergence, and the effect of microsite on seedling survival, are among the most important factors in the quality of deposition for plants dispersed by food-hoarding animals. We also examine the proportion of seeds taken from a feeder and the proportion of those seeds that were scatter hoarded. These measures are somewhat artificial (seeds are taken from a feeder and cached inside an enclosure) but because all subjects were tested under the same conditions, we believe that they are valid measures of the relative propensity of subjects to harvest and scatter hoard seeds.

Our goal was to estimate the effect of each rodent species on the probability of effective dispersal of piñon pine seeds. We did this by calculating the product of the five independent components (proportions) of the dispersal process (Fig. 1), following a method similar to that proposed by Price and Jenkins (1986) and used by Rey and Alcantara (2000). Multiplying the proportions accounts for interactions among aspects of dispersal. For example, if one behavioral attribute of a species resulted in zero potential for seedling establishment (e.g., caching seeds too deep for seedlings to emerge), but all other behaviors were generally beneficial for the seedlings, the product of the five variables would estimate the true potential for seedling recruitment (i.e., zero). This method does not assume that the five behavioral attributes be of equal "weight" but only that they be independent

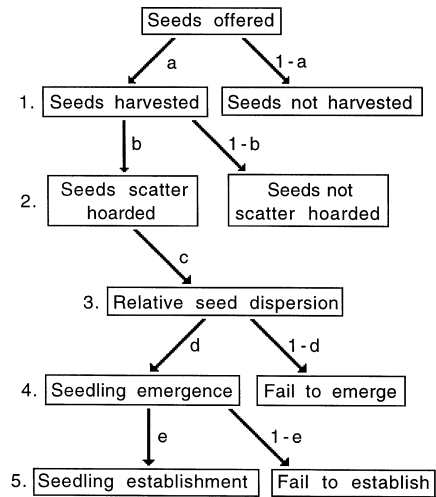


Fig. 1 Possible seed fates of piñon pine seeds offered to subjects. Five aspects of seed fates were measured and are described in the text. The product of $a-e$ for each subject was used as an estimate of its dispersal effectiveness

components of seed fate pathways. Our measure of the impact of rodent species on the probability of effective dispersal of piñon seedlings is also incomplete because there are other factors that influence seedling establishment that we do not consider (i.e., cache recovery). Consequently, our estimates of the effects of species on potential seedling recruitment are intended to serve as a means of ranking the beneficial effects of the six species, not to estimate actual seedling recruitment in a given year.

Materials and methods

This study was conducted in the Pine Nut Range in Carson City County, Nevada, 12 km southeast of Carson City. Vegetation at the site (39°5'10"N, 119°39'0"W; elevation 1,920 m) consists of singleleaf piñon pine and Utah juniper (*Juniperus osteosperma*), and Great Basin Desert shrubs, including big sagebrush (*Artemisia tridentata*), rubber rabbitbrush (*Chrysothamnus nauseosus*), antelope bitterbrush (*Purshia tridentata*), desert peach (*Prunus andersonii*), plateau gooseberry (*Ribes velutinum*), and Mormon tea (*Ephedra viridis*). Precipitation at Carson City (elevation 1,433 m) during the water years (1 October–30 September) 1998–1999, 1999–2000 and 2000–2001 was 215, 175 and 84 mm, respectively.

To determine the rodent community composition of this piñon-juniper woodland, we established two trapping grids, each containing 50 Sherman live traps. Traps were 15 m apart, were baited with mixed bird seed, and were open for 4 days and 4 nights. We recorded rodent species, gender, and mass, and tagged each rodent with a numbered ear tag. Trapping dates were 19–22 August 1999, 24–27 August 2000, and 16–19 August 2001.

We collected singleleaf piñon pine seeds in the fall of 1998, 1999, and 2001 to use in seedling emergence studies and caching trials. The piñon pine cone crop in 2000 was very small throughout the region.

We examined the ways that different rodent species cache singleleaf piñon pine seeds by conducting caching trials in two 15×15-m enclosures. The enclosures were constructed of 12-mm wire mesh hardware cloth supported by a wooden frame 80 cm high and extending 40 cm below ground. Metal flashing lined the top of the enclosures to prevent rodents from leaving or entering. The habitat in the enclosures was similar and typical of the area, consisting of a variety of shrubs and herbaceous plants (but lacking trees).

Although enclosures encompassed <5% of the home range area of subjects, they included a diversity of microhabitats that subjects could select for caching.

Each enclosure contained an artificial burrow, which consisted of a plastic 20-l bucket buried in the ground with the lid level with the ground surface. The inside of the nest bucket was partitioned into three levels by two plywood dividers. Each divider had a 4-cm diameter hole to allow rodents access to all levels. Two segments of PVC pipe (60 cm long) connected the upper and middle levels to the ground surface. We adjusted the diameter of the entrance to accommodate large rodents (5 cm diameter) and smaller rodents (2.5 cm diameter). We placed 2 cm of soil in the bottom chamber of the nest bucket, and a small amount of cotton for a nest.

Each enclosure also contained a small feeder box in which we placed 100 radioactively-labeled singleleaf piñon seeds. The feeder box was wooden and measured 40×30×10 cm with an opening on two sides to allow rodents access to the seeds, but to exclude birds.

Seeds to be used in caching trials were labeled with scandium-46, a biologically inactive, gamma-emitting radionuclide with a half life of 84.5 days. We labeled seeds at the University of Nevada, Reno, by soaking lots of seeds in sealed, plastic containers with sufficient ScCl_3 dissolved in distilled water to moisten the seeds. After moisture was absorbed, we allowed seeds to dry for 2 days.

We conducted all caching trials from late August to mid-November, in 1999, 2000, and 2001. To characterize the caching behavior of all members of the local rodent community, we tested five individuals of each of the six species. No subject was tested more than once. Animals were treated according to protocols approved by the University of Nevada-Reno's Institutional Animal Care and Use Committee. Subjects were not tested in random order because we had difficulty trapping some species in some years. However, ANOVA of the effects of year and month using number of seeds scatter hoarded as the dependent variable were not significant ($P > 0.15$ for both), suggesting that the order of testing was unimportant.

To conduct trials, we placed 100 labeled seeds in the feeder box and placed a subject in the artificial burrow. We provided water in a container partially buried in the ground. Trials lasted 48 h unless all of the seeds had been removed from the feeder in the first 24 h (only 2 of 30 subjects). After terminating a trial, we searched the nest bucket for larder-hoarded seeds and the hulls of eaten seeds. We removed all of these seeds, along with any unharvested seeds left in the feeder box from the enclosure. We then searched the enclosure for caches and hulls of eaten seeds using a Eberline model ASP-1 gamma radiation counter and SPA-3 detector. We carefully excavated each cache and recorded the cache depth (top and bottom) and the number of seeds per cache. We recorded the location of each cache within the enclosure, along with the distance from the base and edge of the canopy of the nearest woody plant. We identified the microsite in which the rodents made caches as either in the open or under a shrub canopy.

We analyzed differences in the caching behavior of rodent species using a Kruskal-Wallis test (Zar 1997) on averaged parameter values of individual subjects. We analyzed the differences in the top depths of caches using a one-way ANOVA, with the mean top cache depth of each subject as the dependent variable ($n = 5$ for each species) and rodent species as the independent variable. We tested for differences among species in the percentage of caches placed under shrubs (the only microsite in which seedlings survived) by using a Kruskal-Wallis test.

To characterize the probability of seedling emergence and establishment conditions for singleleaf piñon pine, we planted fresh seeds in rodent-proof cages at the study site in the autumn of 1998 and 1999 to simulate actual rodent caches. Cages were constructed of 12-mm wire mesh and measured 46×46 cm, with walls extending 14 cm above ground and 10 cm below ground, to keep rodents from entering. We covered each cage with a wire mesh lid to prevent pilfering by rodents or birds. We placed 15 cages under shrubs and 15 in the open in the fall of 1998, and 13 additional cages under shrubs and 12 in the open in the fall of 1999. Because cages sometimes extended beyond shrub canopies, we covered cages under shrubs with shade cloth to ensure that seedlings

in the shrub microsite received more shade than did seedlings in the open.

We planted piñon seeds at eight depths, at 1-cm intervals ranging from 0 cm (on the surface) to 7 cm deep. The seeds at 0 cm simulated abiotic dispersal. We used three cache sizes: 1 seed, 3 seeds, and 10 seeds, to represent the range of cache sizes made by different rodent species. Twenty-four caches were made in each enclosure, each cache with a different combination of the three cache sizes and eight cache depths arranged randomly in a 5×5 grid (one of the 25 positions was unassigned).

We recorded the emergence and survival of singleleaf piñon seedlings the following spring and summer (1999 and 2000). We analyzed data on seedling emergence and cache survival (i.e., at least one seedling per cache surviving to the end of the first or second growing season) using logistic regression performed by the statistical software Statistica. To determine the advantage or disadvantage of a seedling being a member of a multi-seed cache, we examined the percentages of seedlings that survived after emerging from 1-, 3- or 10-seed caches at 1–4 cm depths (the depths at which rodents buried most seeds). We followed survival for two growing seasons, and we analyzed the differences in percent survival among cache sizes using a one-way ANOVA on arcsine transformed data, with percentage of seedlings surviving as the dependent variable. We used the characteristics of the caches from which the highest proportion of seedlings survived two growing seasons to characterize favorable establishment sites.

We estimated the potential impact of the six species on various aspects of seed dispersal by calculating proportionate scores for each of the following five aspects of seed dispersal (Fig. 1).

1. The proportion of seeds harvested from the feeder of the 100 seeds presented.
2. The proportion of seeds scatter-hoarded of those harvested from the feeder.
3. How subjects distributed seeds to cache sites, determined by dividing the number of cache sites by the number of seeds cached. The potential of a subject to disperse seeds is lower if they clump seeds in large, multi-seed caches, because large caches mean fewer total caches (i.e., fewer establishment sites) and possibly more seedling competition (i.e., greater mortality) within clumps of seedlings. For example, if a subject placed 50 seeds in 25 caches, it would reach half as many potential establishment sites as hypothetically possible ($25/50=0.5$).
4. Seedling emergence from cache sites. We did this across a range of cache depths because depth influences the probability of seedling emergence. We determined the proportion of caches with a top depth in a given range of depths ($0.0 \leq 0.5$ cm, $0.5 \leq 1.5$ cm, $1.5 \leq 2.5$ cm, etc.) for each subject, multiplied that proportion by the proportion of seedlings emerging from that depth in the seedling study, and then summed these values to obtain the final proportion for each subject.
5. Seedling establishment in the microsities in which subjects made caches. We determined the value for this attribute by multiplying the proportion of caches that each subject placed in each microsite (in the open or under shrubs) by the probability that a seedling would survive for two growing seasons in that microsite based on results from the seedling survival study and summing the products.

We averaged each of the proportionate dispersal attribute values for subjects within species to determine the dispersal attribute value for each species. To calculate the proportion of seeds likely to be dispersed to favorable situations by each species of rodent, we multiplied the five separate attribute values together (Price and Jenkins 1986; Fig. 1). We analyzed differences among species in the five seed harvesting and caching attributes, by arcsine transforming the proportional data and performing one-way ANOVAs on the six dependent variables. Finally, we ranked the relative effectiveness of each species as a disperser of piñon pine seeds by using the least effective species as a reference, and dividing the proportion of seeds dispersed to favorable sites by each of the remaining species by that of the least effective species.

Table 2 Top depths, and coefficients of variation (*CV*) of piñon pine seed caches made by six species of rodents in enclosures in the field

Species	Number of caches	Top of cache (cm)	
		Mean \pm 1 SD	CV (%)
Pinyon mouse	228	0.74 \pm 0.25	33.8
Deer mouse	200	0.86 \pm 0.41	47.7
Least chipmunk	233	0.67 \pm 0.22	32.8
Antelope ground squirrel	176	1.70 \pm 0.75	44.1
Panamint kangaroo rat	33	1.58 \pm 0.41	26.0
Great Basin pocket mouse	35	1.45 \pm 0.94	64.8

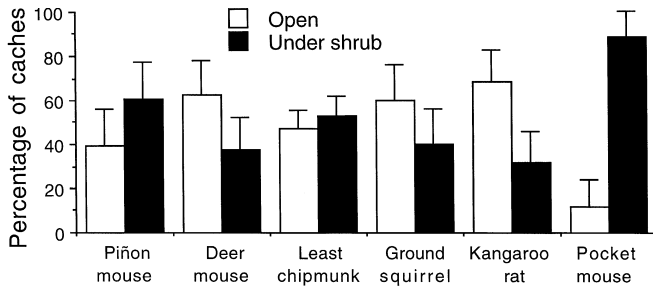


Fig. 3 Microsite placement of caches made by six species of rodents. Values are means \pm 1 SE ($n=5$ of each species)

=716). By 23 October 1999, all of the emerged seedlings in the open ($n=138$ caches and 448 seedlings) had perished. Under shrubs, 97% of the clumps of seedlings that had emerged ($n=170$ clumps and 530 seedlings) were represented by at least one survivor, and by the end of the second growing season for the 1999 cohort, 93% ($n=521$ seedlings) were still alive. By 15 October 2000, all seedlings that had emerged in the open ($n=96$ caches and 265 seedlings) had perished. Under shrubs, 74% of the seedlings that had emerged ($n=223$ seedlings) were still living, and by the end of the second growing season, only 32% of the 2000 cohort ($n=97$ seedlings) were still alive.

There were significant differences in seedling emergence (Wald = 88.79, $df=1$, $P < 0.001$; Fig. 4), and survival (Wald = 11.39, $df=1$, $P < 0.001$; Fig. 5) among the different depths at which we planted seeds. The greatest emergence occurred at intermediate depths (1–4 cm at top of seeds). Cache size had a significant effect on emergence of seedlings (Wald = 115.59, $df=1$, $P < 0.001$; Fig. 4) and survival of at least one seedling per cache through the first growing season (Wald = 14.98, $df=1$, $P = 0.0001$; Fig. 5). This indicates that larger caches are more likely to have at least one seedling survive simply because they have more members to start with. However, single seedlings did not exhibit significantly higher survival than seedlings emerging in clumps (either three- or ten-seed caches; one-way ANOVA $F_{2,12}=0.10$, $P = 0.905$; Table 3). There was no significant interaction between cache depth and cache size for emergence or survival. However, seeds placed on the surface (0 cm) and at the deepest depths (6–7 cm) had slightly greater emergence and survival if they were members of larger caches.

There were significant differences among species in their effect on the overall probability of seedling recruitment ($F_{5,24}=6.35$, $P = 0.0006$). Rodent species did not

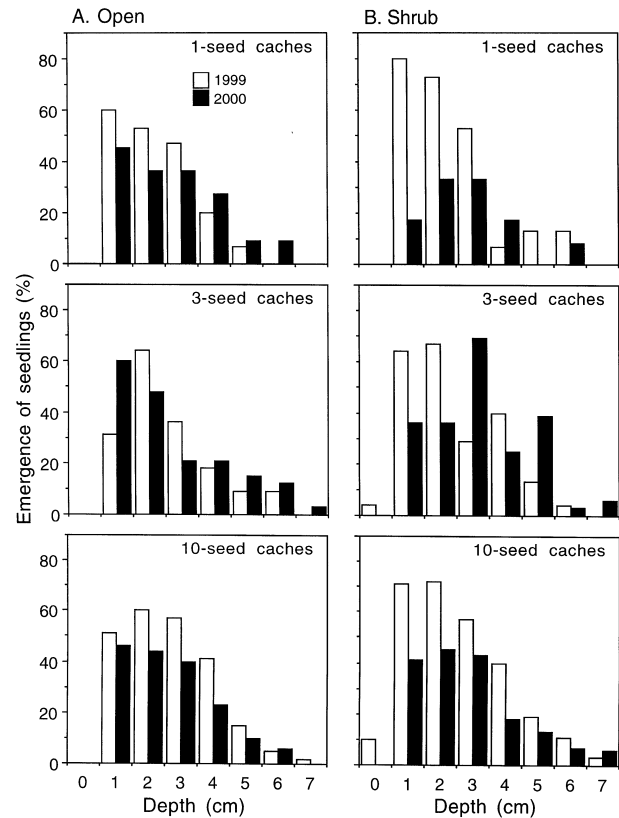


Fig. 4 Emergence of seedlings (%) planted in three cache sizes (one, three, and ten seeds per cache) in the open (A) or under shrubs (B) in 1999 (open bars) and in 2000 (closed bars) and at eight depths (0–7 cm)

differ significantly in three of the five attributes: proportion of seeds harvested ($F_{5,24}=1.003$, $P = 0.437$), proportion of harvested seeds scatter-hoarded ($F_{5,24}=1.63$, $P = 0.19$), and depth at which they cached seeds ($F_{5,24}=0.479$, $P = 0.787$). However, there were significant differences in the microsite in which rodents cached seeds ($F_{5,24}=5.76$, $P = 0.001$) and in the number of seeds per cache ($F_{5,24}=44.85$, $P < 0.001$). There was considerable individual variation among piñon mice, least chipmunks and deer mice, but the behavior of Great Basin pocket mice, Panamint kangaroo rats, and especially white-tailed antelope ground squirrels, was much more consistent.

The overall probability of effective dispersal for rodent species ranged from a low of 0.007 for kangaroo rats to a high of 0.114 for piñon mice (Table 4). According to this measure, piñon mice are 16.3 times more effective as

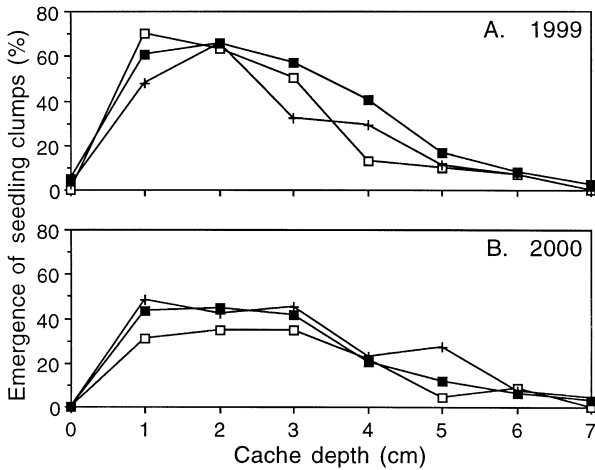


Fig. 5 Emergence of seedling clumps (%; at least one seedling per cache emerging) in 1999 (A) and 2000 (B) for caches planted at eight depths (*open squares* one-seed caches, *crosses* three-seed caches, *closed squares* 10-seed caches)

dispersers of piñon pine seeds than Panamint kangaroo rats. Least chipmunks ranked second in relative effectiveness as dispersers, and white-tailed antelope ground squirrels and deer mice had similar effectiveness, intermediate to the other species. Great Basin pocket mice ranked just above kangaroo rats in relative effectiveness as dispersers of piñon pine seeds (1.9 times more effective than kangaroo rats).

Discussion

All six species investigated scatter-hoarded piñon seeds, and they all did so in a way that had a potential positive effect on plant recruitment. However, the behavior of species varied greatly, and certain attributes of caching behavior made some members of the rodent community much better dispersers of piñon pine seed than others.

All rodents readily harvested piñon pine seeds from the feeder. Five of the six species of rodents removed over 94% of the seeds presented, and the sixth species, deer mice, removed over 90% of the seeds. These data suggest that neither the enclosure nor the feeder box had a strong negative influence on the seed-harvesting behavior of subjects.

The percentage of seeds scatter-hoarded of those harvested is another important measure influencing the quantity of seeds dispersed. This attribute was much more variable than the proportion of seeds harvested, ranging from 31% (Great Basin pocket mouse) to 66% (least chipmunk). Three species larder-hoarded some seeds (Table 1). Seeds that are larder-hoarded are usually stored too deeply for seedlings to emerge. Pocket mice larder-hoarded the most seeds; all but one of five pocket mice larder-hoarded, and one did so exclusively. Pocket mice enter torpor in late autumn, so they may larder-hoard food more than other species because they cannot use surface caches during winter (Jenkins and Breck 1998). Least chipmunks also enter winter dormancy, however they did not larder-hoard any seeds, even though the caching trials were conducted in late autumn at a time when we suspect they begin to prepare winter larders. The rodents in this study did not have access to their own burrows, which could have affected the number of seeds that they larder-hoarded. However, three kangaroo rats and four pocket mice dug their own burrows while in the enclosure, and some made small larders in these burrows. Five of six larders that we found were in natural burrow systems, not the artificial burrow.

Rodents that made small caches likely had a greater effect on seedling establishment. Larger cache sizes may be unfavorable for the plant because fewer caches are made. For example, the average piñon mouse made 58 caches per trial (most with only one seed; Table 1). Although kangaroo rats cached nearly as many seeds (mean =54) they made an average of only 7 caches (~eight seeds per cache). Clearly, this results in a reduced potential for new establishment sites. Further, caches containing a

Table 3 Singleleaf piñon pine seedling emergence and survivorship in artificial caches containing one, three or ten seeds. Seedling survival was followed for 2 years for seeds planted in autumn of

1998 (15 sites per depth treatment) and 1999 (12 sites per depth treatment). Data from four depths (1–4 cm) were combined for this table

Year planted	Number of seeds per cache	Number of cache sites	Living seedlings		Living seedlings			
			Seedling emergence		after first year		after second year	
			Number	% ^a	Number	% ^b	Number	% ^c
1998	1	60	32	53.3	31	96.9	30	93.8
	3	60	90	50.0	84	93.3	84	93.3
	10	60	360	60.0	342	95.0	334	92.8
1999	1	48	12	25.0	10	83.3	5	41.7
	3	48	60	41.7	39	65.0	21	35.0
	10	48	177	36.9	128	72.3	51	28.8

^a Percent emergence; calculated as [number of seedlings that emerged/(number of seeds per cache × number of cache sites)]

^b Seedling survival (first year); calculated as (number of seedlings alive after first year/number of seedlings that emerged)

^c Seedling survival (second year); calculated as (number of seedlings alive after second year/number of seedlings that emerged)

Table 4 Proportionate values for five stages of seed dispersal and seedling establishment for six species of rodents. The combined effects of these values on the probability of recruitment (*PR*) was obtained by multiplying the five attributes. Values were determined objectively based on results of caching trials and the seedling

emergence and survival study (see text for further details). Different letters within columns indicate statistically significant difference (ANOVA; $\alpha = 0.05$). There were no significant differences among species in the proportion of seed harvested, seed scatter hoarded or seedling emergence

Species	Seed harvesting and caching attributes					Probability of recruitment	Relative PR ^a
	Seeds harvested	Seeds scatter hoarded	Seed dispersion in caches	Effect of depth on seedling emergence	Effect of microsite on establishment		
Pinyon mouse	0.980	0.614	0.996a	0.359	0.530b	0.114a	16.3
Deer mouse	0.904	0.470	0.993a	0.390	0.283c	0.047c	6.7
Least chipmunk	0.970	0.664	0.760b	0.339	0.432b	0.072b	10.3
Antelope ground squirrel	1.000	0.608	0.600b	0.464	0.284c	0.048c	6.9
Panamint kangaroo rat	0.944	0.562	0.112c	0.403	0.297c	0.007d	1.0
Great Basin pocket mouse	0.998	0.310	0.182c	0.322	0.708a	0.013d	1.9

^a The probability of recruitment of rodent species relative to the lowest ranked species, Panamint kangaroo rat. The probability of recruitment of each species is divided by that of the Panamint kangaroo rat (0.007)

larger number of seeds may be more likely to be detected by foragers (Vander Wall 1993). Seeds and seedlings often suffer higher mortality when there are a large number clumped together (Howe 1989). Often only one or none of the seedlings survives. This is most likely because of competition for resources among seedlings (Howe 1989; McMurray et al. 1997). McMurray et al. (1997) found this to be true for clumps of cheatgrass seeds (*Bromus tectorum*). There are exceptions to this pattern however (Howe 1989; McMurray et al. 1997), especially in some species of pines (Tomback 1982; Saito 1983). There did not appear to be any advantage or disadvantage for seedlings emerging singly or in clumps in this study (Table 3), however, we were only able to follow seedling survival over 2 years. Singleleaf piñon pine seldom grows in clumps, which suggests that attrition among seedlings in clumps eventually eliminates all but one individual. Piñon mice and deer mice, which nearly always make one-seed caches, received the highest scores for this attribute.

The depth at which seeds are buried is also likely to be an important factor influencing the emergence of piñon seedlings. Seeds buried at 1–4 cm had fairly high seedling emergence (Figs. 4, 5). Seeds placed on the surface established poorly. However, during the fairly wet spring of 1999, 4% of three-seed surface caches and 9% of ten-seed surface caches had at least one seedling emerge and survive. Seedlings from depths of ≥ 5 cm did not fare as well either, exhibiting declining emergence with increasing depth. These results are consistent with the results obtained by Chambers (2001), in which emergence of seedlings was similar and relatively high from the 1 and 3 cm depths. Rodent cache depth broadly overlapped optimal seed burial depth for piñon pine. However, the values for this caching attribute are relatively low, ranging from 26% to 38% (Table 4). The reason is that the number of caches at each depth was multiplied by seedling emergence at that depth, and seedling emergence in the relatively dry years in which the study was conducted was generally low for all depths.

The factor that proved to be most important for survival of seedlings was the microsite in which they emerged. No seedlings that emerged in the open survived through the first autumn. Seedlings that emerged in the shade of shrubs in 1999 had 93% survival at the end of the second growing season (Fig. 5). Chambers (2001) found a similar result. Singleleaf piñon pine has a strong nurse plant requirement (Everett et al. 1986; Drivas and Everett 1988; Callaway et al. 1996). Callaway et al. (1996) found that removal of sagebrush shrubs from plots with singleleaf piñon pine seedlings decreased the efficiency with which the piñon seedlings used water. Other components that make the under shrub environment favorable for piñon pine seedling survival include soil temperature (lower under shrubs), soil moisture (higher under shrubs), soil surface attributes (e.g. presence of litter), and soil nutrient content (increased P and K; Chambers and MacMahon 1994; Chambers 2001).

Rodents that placed a large number of caches in the open spaces between shrubs had a negative effect on seedling establishment. Panamint kangaroo rats, antelope ground squirrels, and deer mice all placed most of their caches in the open (Fig. 2). The results for kangaroo rats are consistent with several other studies which have shown that bipedal kangaroo rats tend to forage and cache in the open (Munger et al. 1983; Price and Brown 1983; Reichman 1983; Daly et al. 1992). However, the results for deer mice contrast with the results obtained by Vander Wall et al. (2001) who reported that deer mice tended to avoid open areas, and cached near the edge of bitterbrush shrub canopies.

Three species, Great Basin pocket mice, pinyon mice, and least chipmunks, placed most of their caches under shrubs. Quadrupedal heteromyids, such as pocket mice, have been shown to forage and cache beneath shrubs (Price and Brown 1983; Daly et al. 1992; Leaver and Daly 2001). Little has been reported on the caching behavior of least chipmunks, but a congener, the yellow pine chipmunk (*Tamias amoenus*) frequently caches seeds

beneath shrubs (Vander Wall 1995; Vander Wall and Joyner 1998).

Comparing the effectiveness of corvids (jays and nutcrackers) as dispersers of piñon pine seeds to that of rodents would be an interesting topic of future study. Nutcrackers and jays are considered to be important dispersers of piñon pine, but by some measures they may be less effective than previously thought. Jays and nutcrackers make many caches in open microsites (Ligon 1978; Vander Wall and Balda 1981; Vander Wall 1988), situations where the probability of seedling establishment is low. However, relative to rodents, corvids provide long-distance dispersal, which can be from one mountain range to another (Vander Wall and Balda 1981). Nutcrackers and jays were very likely responsible for the migration of piñon pines thousands of kilometers to their current range during the Holocene (Lanner 1981; Vander Wall and Balda 1981; Thompson 1990).

Our study does not consider the effects of cache recovery on seedling recruitment. Clearly, most caches are recovered by the cacher or found by other animals. The effect on recruitment can be negative or positive. Recovered seeds are exposed to predation (e.g., eaten or moved to a burrow larder), but many seeds are recached (Vander Wall and Joyner 1998; Vander Wall 2002), changing their microsite or depth with attendant consequences for the seeds. Seeds from multi-seed caches are often redistributed to several smaller caches (Vander Wall 2002), which is likely to benefit plants. If one species of rodent pilfers caches made by another species and recaches the seeds elsewhere, then the seeds could be exposed to markedly different conditions when they germinate. Pilfering of Panamint kangaroo rat caches by piñon mice, for example, might be highly beneficial to piñon pine. Corvids (Balda and Kamil 1989; Olson and Kamil 1995; Balda et al. 1997) and rodents (Jacobs 1992; Vander Wall 1991, 2000) use spatial memory to relocate their caches, but rodents can also use olfaction to locate their own caches and the caches of other animals (Vander Wall 1991, 1998, 2000; Vander Wall et al. submitted). Consequently, rodents are more likely to pilfer jay caches than the other way round. If jays are more inclined to cache piñon seeds in open (low quality) sites, as some limited data suggest, then pilferage of jay caches by rodents that cache under shrubs (high quality sites), may benefit plants. Clearly, the nature of interactions among rodent (e.g., Leaver and Daly 2001) and corvid species, which were beyond the scope of this study, could have a dramatic effect on the ultimate effectiveness of a species as a disperser of piñon pine. The last species to handle a seed has the greatest effect on the ultimate fate of that seed, but currently we do not understand these interactions sufficiently well to predict how the pine might be influenced. Future studies need to examine these cache dynamics so we can better understand how scatter-hoarding species effect each other, and how these interactions influence plant populations.

Our estimates of the relative effectiveness of rodent species as dispersers of piñon pine (Table 4) should be viewed tentatively, since there are a number of aspects of

our measures of the relative probability of recruitment that could be biased or imprecise. First, the unfamiliar and constrained conditions of the experimental enclosures could have caused subjects to behave abnormally. Seed harvest rates in the enclosures may have been different than those exhibited by unconfined animals, and some subjects may have larder-hoarded more seeds in their familiar home burrows than in our unfamiliar, artificial burrow. These and other factors could have changed subjects' propensity to scatter hoard seeds. Second, our estimates of the probability of effective seed dispersal make the unlikely assumption that the same proportion of caches of each species are recovered. The degree to which different species vary in their ability to recover stored food is poorly known and, as noted in the preceding paragraph, the extent and effects of interspecific pilferage on the dispersal effectiveness of species are not well understood. Because of cache recovery and pilferage, the percentage of seeds likely to establish is much lower than the probability of effective dispersal calculated in Table 4. Third, piñon pine, like many other plants in semi-arid and arid environments, probably establishes episodically, with large cohorts of seedlings occurring at infrequent intervals when heavy seed production and good conditions for establishment coincide. Short-term studies, such as ours, are unlikely to reveal these long-term patterns. Consequently, our calculations of the probability of effective dispersal are not meant to predict actual establishment in any 1 year but to serve as a first approximation of the relative impact of different rodent species in seed dispersal and seedling establishment. We expect that greater knowledge of rodent caching behavior and how species interact over stored seeds will help to evaluate and refine these predictions.

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