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PLANT ANIMAL INTERACTIONS

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Seed-caching responses to substrate and rock cover by two *Peromyscus* species: implications for pinyon pine establishment

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Abstract We examined whether pinyon mice (*Peromyscus truei*) and brush mice (*P. boylii*) could act as directed dispersal agents of pinyon pine (*Pinus edulis*) through differential responses to soil particle size and rock cover. In field experiments, we allowed mice to either cache pinyon seeds or recover artificially cached seeds (pilfer) from quadrats containing large- or small-particle soils. Both species placed most (70%) seed caches in small-particle soil. Pilfering was the same from both particle sizes in the first year, while more seeds were pilfered from large-particle soils in the second year. In separate experiments, rock cover interacted with soil particle size, with both species placing over 50% of their caches in small-particle soil with rock cover. Overall, we found greater seed-caching in small-particle soils near rocks, with equal or lower pilfering from small-particle soils, suggesting more seeds would survive in small-particle soils near rock cover. Three lines of evidence supported the hypothesis that mice could act as directed dispersers by moving pinyon seeds to beneficial microsites for germination and establishment. First, in greenhouse experiments, pinyon seed germination was 4 times greater in small-particle soil cores than in large-particle soil cores. Second, soils near rocks had significantly higher water content than areas of open soil at the driest time of the year, a critical factor for seedling survival in the arid southwestern USA. Third, 75% of juvenile pinyon trees were growing in small-particle soils, and 45% were growing near rock nurses.

Keywords Coexistence · Directed dispersal · Pilferage · *Pinus edulis* · Soil particle size

Introduction

Determining the consequences of animal-mediated seed dispersal for seedling recruitment is an important goal in understanding the dynamics of plant-animal interactions. Scatter-hoarding rodents can consume a significant proportion of seeds they handle, but may also act as seed dispersers by increasing the effective seed shadow (Vander Wall and Joyner 1998; Vander Wall 2002) or by moving seeds to specific microsites that enhance germination and seedling establishment, a form of directed dispersal (Howe and Smallwood 1982; Wenny 2001). Several studies have tested the directed dispersal hypothesis in frugivorous birds (Reid 1989; Sargent 1995; Wenny and Levey 1998; Tewksbury et al. 1999) and ant-dispersed systems (Rice and Westoby 1986; Hanzawa et al. 1988; Passos and Oliveira 2002). Fewer studies have examined the possibility of directed dispersal by seed-caching rodents (but see Vander Wall 1993, 1997, 1998b; Hoshizaki et al. 1999), despite their prevalence in a majority of seed-dispersal systems.

Directed dispersal may be most important for plant species that depend upon a narrow range of microsite characteristics for germination and establishment (Harper 1977). Pinyon pines (*Pinus* spp.) are widely distributed in arid habitats of the southwestern USA and are dependent on seed-caching corvid birds (jays and nutcrackers) (Vander Wall and Balda 1981; Lanner 1996) and rodents (chipmunks and mice) (Vander Wall 1997) to disperse the heavy, wingless seed by caching them during periods of high seed production for later use. Microsites chosen for seed caching may influence pinyon regeneration because pinyon seedlings require relatively high soil moisture, shade, and protection from browsers (Chambers 2001). In many areas, nurse shrubs provide seedlings with these characteristics (Calloway et al. 1996; Chambers 2001); however, other structures, such as downed logs and rocks, potentially offer similar benefits. In addition to nurse structures, soil characteristics such as particle size could affect germination and survival by influencing soil water potential and nutrient dynamics (Everett et al. 1986;

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Chambers 2001). Seed-caching rodents have been shown to disperse seeds under nurse plants (Vander Wall 1993, 1997; Giannoni et al. 2001), and some studies have examined dispersal to other nurse structures (Iida 1996), but there is an absence of studies that have examined directed dispersal based on soil properties.

Foraging behavior of rodents may be influenced by a number of environmental characteristics that could lead to non-random seed dispersal patterns. Substrate qualities such as soil density and texture can affect the ability of rodents to find and recover seeds (Price and Heinz 1984; Price and Podolsky 1989; Morgan and Price 1992; Hughes et al. 1995; Kotler et al. 2001), and could likewise affect seed germination and survival. Similarly, rodents may preferentially forage and/or cache seeds in areas near cover (Brown et al. 1988; Longland and Price 1991; Vander Wall 1997) thereby altering the rate of seed arrival and removal from these sites.

We examined the influence of soil substrate and rock cover on the seed-caching and pilfering behaviors of two mouse species, *Peromyscus truei* and *P. boylii*, that are closely associated with pinyon-juniper woodlands (Holbrook 1978; Hoffmeister 1986). In order to examine the effects of these parameters on rodent behavior and subsequent pinyon establishment, we addressed the following three questions:

1. How do differences in soil particle size and rock cover affect the caching and pilfering behaviors of the two mouse species?
2. How do differences in soil particle size influence pinyon seed germination rates?
3. Are established juvenile pinyon pine trees found in microsites with soil particle sizes and nurse structures consistent with patterns of rodent seed dispersal?

Study site

This study was conducted in a pinyon-juniper woodland near Sunset Crater National Monument in the San Francisco volcanic fields, northern Arizona (approximately 6,500 feet elevation). Sunset Crater is one of the youngest scoria cones in the US, last erupting around 1064 A.D. for a period of 200 years. These eruptions eventually covered over 2,000 km^2 with cinders, leaving the site barren of vegetation, and creating a hotter, drier environment, less hospitable to plant growth (Krutch 1974). The area now supports pinyon-juniper woodlands growing in early successional cinder soils. These soils have low water holding capacity, low nutrient content, and are highly variable in particle size, ranging from ash to volcanic boulders (Cobb et al. 1997). Shrub cover is widely spaced and interspace environments offer harsh conditions for seedlings due to high soil temperatures and vulnerability to browsers (Everett et al. 1986; Calloway et al. 1996), therefore the abundant large volcanic boulders may be important protective structures for both foraging mice and pinyon seedlings.

Materials and methods

Particle-size effects on pilfering and caching behaviors

To address the effects of varying soil particle sizes on seed-dispersal behaviors, we allowed mice, *P. boylii* and *P. truei*, to cache or pilfer pinyon seeds in field enclosures containing two different soil particle sizes. Soil for these experiments was collected from naturally occurring patches that consisted of either predominately small particles (<1.0 mm in diameter) or large particles (>2 mm in diameter). Each experimental enclosure (2×2.5 m) consisted of 1-m-high wooden-framed walls covered with hardware cloth. A hinged top, also of wood frame and hardware cloth, prevented mice from climbing out while allowing us to access the inside of the enclosure. The bottom of the enclosure was set on a plastic tarpaulin covering the natural soil beneath. The floor of the enclosure was divided into five sections. The middle section (0.5×2 m) was covered with a wooden plank on which an open live trap containing cotton batting served as a nesting site. The outer two sections on either side were each divided into two quadrats (1×1 m each) and were filled to a depth of 4 cm with either large- or small-particle-sized cinder soils. Small, artificial "shrubs" were constructed by tying together branches of naturally occurring shrubs from nearby areas. One artificial shrub was placed in each quadrat to provide mice with protective cover. Four of these field enclosures were placed in open areas at the study site, all at least 2 m from the nearest shrub or tree.

The night before each trial, mice were live-trapped using Sherman traps within the 1-ha area surrounding the enclosures. The following morning, an apple slice was added to each of the traps containing mice to be used in the trials (to provide food and moisture) and traps were placed in the shade of dense shrubs for the rest of the day. That evening one mouse was placed in each enclosure and remained there overnight, with the trap it had been housed in acting as the nest site. The next morning, mice were removed from the enclosure and released back at their original trap location.

Caching and pilfering behaviors were observed separately in two different types of trials. For both types of trials, short pieces of thread (10 cm) were first tied and then glued to uniquely numbered pinyon seeds. Thread tails allowed detection of seeds cached beneath the soil surface, while uniquely numbering the seeds allowed the fate of individual seeds to be followed through successive movements. All trials were conducted between the months of May and August 2001.

In caching trials, 40 seeds were placed on the wooden plank surface. After each trial period, cache site locations were identified by locating thread tails protruding from the soil and by searching each quadrat until all seeds were accounted for. Seed fates were categorized as: (1) cached in small-particle soil, (2) cached in large-particle soil, (3) cached in nest box, (4) eaten, and (5) left on wood plank.

In pilfering trials, 40 seeds (ten in each quadrat) and their thread tails were completely buried under the soil surface. Seeds were buried in a grid pattern with approximately 30 cm between each seed and were at least 5 cm from the edge of the enclosure frame. Each seed was uniquely numbered and the original quadrat and grid location where the seed was buried was recorded. One seed in each quadrat was left on the soil surface to stimulate searching behavior by the mice. At the end of each trial, seeds either remained unrecovered, were recovered and eaten, or were recovered and reburied (recached). Recached seeds were detected when seed identification numbers indicated a buried seed had been moved from its original location. Final seed locations were recorded and seed fates categorized as one or more of the following: (1) pilfered from small-particle soil, (2) pilfered from large-particle soil, (3) recached in small-particle soil, (4) recached in large-particle soil, (5) recached in nestbox, (6) eaten, and (7) unrecovered.

Roughly equal numbers of both male and female mice were used for the trials. Only individuals that cached or pilfered three or more seeds were considered in the analysis of the effects of particle size on caching and pilfering behavior. As a result, ten *P. boylii* and ten *P. truei* were analyzed for caching trials and nine *P. boylii* and 12 *P.*

truei were analyzed for pilfering trials. In eight cases, the same individual was used for both types of trials, but in each case, whether the caching trial or pilfering trial was presented first was randomized based on a coin toss. The percentages of seeds cached or pilfered in small-versus large-particle soils were normalized using a square root transformation and were compared using ANOVA.

Interactive effects of particle size and rock cover

To address the interactive effects of soil particle size and the presence or absence of rock cover on seed-dispersal behaviors, mice were allowed to cache and pilfer 40 seeds in enclosures containing two different soil particle sizes as before. However, in this experiment, cover was also manipulated by presenting rocks as cover in two of the four quadrats, while the other two quadrats lacked cover of any kind. The placement of rocks in a particular quadrat was randomly determined for each trial to avoid site effects. To avoid the possibility that the wooden frame of the enclosure unintentionally affected caching behavior by providing mice with cover, seeds that were cached within 5 cm from the frame edges were excluded from the analysis. These trials were conducted between May and August 2002.

For both caching and pilfering trials, seed locations were recorded and their fates categorized as one or more of the following: (1) cached, pilfered or recached in small-particle soils without rock cover, (2) cached, pilfered or recached in small-particle soils with rock cover, (3) cached, pilfered or recached in large-particle soils without rock cover, (4) cached, pilfered or recached in large-particle soil with rock, (5) eaten, (6) cached in nest box, or (7) left on the surface of a wooden plank or unrecovered.

As in the first experiment, roughly equal numbers of both male and female mice were used for the trials and only individuals that cached or pilfered three or more seeds were considered in the analysis. Ten *P. boylii* and ten *P. truei* were analyzed for both caching and pilfering trials. Eleven individuals were used for both types of trials, and in each case the type of trial (pilfer or cache) first encountered was randomized. Two of the 11 individuals used in both trials cached and pilfered in the same microhabitat selected in the first trial, while the remaining nine showed no pattern, suggesting that previous experience did not strongly influence behavior in the subsequent trial.

The percentage of seeds cached and pilfered for the four different treatment types was normalized using square root transformation and analyzed using ANOVA with soil particle size and rock cover as fixed factors.

To determine whether the two mouse species differed in their propensity to cache seeds versus eat them, we combined trials from both years and compared the ratio of seeds cached to those eaten using a *t*-test. Likewise, to test whether the species differed in their ability to detect experimentally cached seeds, we combined trials across years and compared the number of seeds pilfered by each species.

Soil moisture

Because soil moisture has been shown to affect the ability of rodents to detect seeds (Vander Wall 1995), soil samples were collected from each enclosure to determine whether soil moisture differed between soil particle sizes and across years. Samples were taken at 3 times each year, during early, mid and late June when the majority of experimental trials were conducted. We used repeated measures ANOVA to test for differences between large- and small-particle soils within each year and a paired *t*-test to test for differences in soil moisture across years, with samples paired by enclosure, soil particle size and time of year. In addition, to test whether soil moisture differed between microsites near natural rock outcrops and nearby open areas, in late June (the driest period of the year) we haphazardly selected 20 rock outcrops in our study area where we collected soil: (1) from within 5 cm of the base of the rock, and (2) from an open area of soil approximately 2 m away. Soil samples (approximately 50 ml) were sealed in plastic ziploc bags, taken to the laboratory, weighed, oven-dried at 105°C for 24 h and then reweighed. Percent soil moisture was calculated by dividing the difference between wet and dry soil mass by the dry soil weight. We tested for differences in soil moisture between rock cover and open sites using a paired *t*-test.

Pinyon pine germination

To address how soil particle size affected pinyon pine germination, 140 soil cores, 70 of small- and 70 of large-particle soils, were collected from the study site. Soil was collected with a plastic soil corer (0.5 cm in diameter) and cores were immediately placed into planting pots. The planting pots were transported to a greenhouse and pinyon seeds were placed approximately 2 cm below the surface. Prior to planting, pinyon seeds were tested for viability using a pentane test. Seeds were watered daily and the number of seeds that germinated after 45 days were recorded. The total number of seeds germinating in small- versus large-particle soils was compared using a χ^2-test.

Soil particle size and rock cover variability

To address whether our experiment accurately represented caching and pilfering choices *Peromyscus* would have in the natural environment, we recorded soil particle size and rock cover availability along haphazardly selected, non-overlapping transects across our study area. To assess soil particle size variability, we collected four, 50-ml soil samples (to a depth of 3–4 cm below the surface) at 10-m intervals along a 100-m transect. Within a 5-m radius of each collection point, we selected two samples in the open (>2 m from a rock) that visually appeared to represent the extremes in soil particle size available at that site. We then did the same to obtain two samples of soil particle size extremes from within 1 cm of a rock. Each sample was sifted into small- (<2 mm) and large-particle (>2 mm) size classes using Tyler soil sieves. The percentage (by weight) of each sample made up of each particle size was used to determine the dominant soil particle size. A particle-size class was considered dominant if it contributed >65% to the weight of the sample. If neither size class contributed >65%, then the sample was considered mixed. To assess rock cover availability, we determined the distance to the nearest rock at 10-m intervals along two 100-m transects. The distance to the nearest rock was categorized as <2, 2–5, 5–10 and >10 m from the sample point.

Soil particle microsite and nurse association of juvenile pinyon pines

To address whether established juvenile pinyon pines were associated with particular microsites, four 1,000-m transects were haphazardly chosen and all pinyons under 1 m in height growing within 50 m of either side of transect lines were located. Measurements taken for each pinyon included height, nurse association and particle size of soil at the base of the stem. Particle size was determined based on a categorical designation.

Results

Overall, mice cached some seeds in 80% of the trials and pilfered some seeds in 100% of the trials. Of the caching trials in 2001 where three or more seeds were cached, mice cached between 23 and 37% of the available seeds (Fig. 1a). *P. boylii* ate approximately the same percentage of seeds as were cached, whereas *P. truei* ate more seeds than were cached, but the ratio of cached to eaten seeds did not differ significantly between species (t=1.63, df=44, P=0.11). In the pilfering trials of 2001, approximately 40% of the available seeds were pilfered (Fig. 1b) and there was no significant difference between species in the number of seeds pilfered (t=0.52, df=38, P=0.60). Of the seeds pilfered, both species ate more of the pilfered seeds than were recached, with *P. boylii* recaching a greater percentage of the seeds than *P. truei* (t=2.34, df=19, P=0.01).

Particle-size effects on pilfering and caching behaviors

Soil particle size affected the caching behavior of both species of mice (Fig. 2a, Table 1), with approximately 40% more seeds cached in small-particle soil compared to the percentage cached in large-particle soil. Recaching behavior showed the same pattern. Of the seven *P. boylii* that recached seeds, all placed more seeds in the small-particle soils [mean number in small=4.0±2.1 SE (96%) vs. 0.4±0 (4%) in large]. Five of the seven *P. truei* that recached seeds placed more in small-particle quadrats [mean number of seeds recached in small=1.1±0.4 (79%) vs. 0.4±0.3 (21 %) in large]. In contrast, particle size did not affect the pilfering behavior of either species, as mice pilfered similar proportions from both small and large soil particles (Fig. 2b, Table 1).

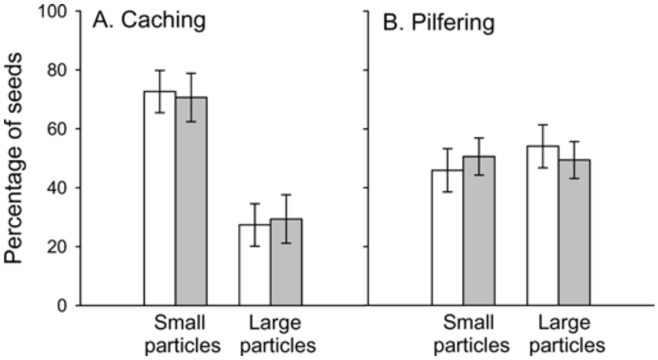

Fig. 2 **a** Mean percentage of pinyon seeds cached in large (>2.8 mm) vs. small (<2 mm) soil particles for *P. boylii* (*open bars*) and *P. truei* (*shaded bars*) with SE error bars. **b** Mean percentage of seeds pilfered by *P. boylii* and *P. truei* from the same two soil particle sizes

Table 1 ANOVA of the effects of soil particle size on the caching and pilfering behavior of *Peromyscus truei* and *P. boylii*

Source	*df*	MS	*F*	*P*
Caching				
Species	1	0.005	0.082	0.776
Particle size	1	1.401	25.390	0.001
Species×particle size	1	0.000	0.005	0.943
Error	36	0.055		
Pilfering				
Species	1	0.004	0.134	0.717
Particle size	1	0.013	0.458	0.503
Species×particle size	1	0.007	0.257	0.615
Error	38	0.029		

Interactive effects of particle size and cover

When both rock cover and soil particle size were varied, both species cached a greater percentage of seeds in small soil particles with rock cover (Fig. 3a, Table 2). However, there was a significant interaction between species and rock cover, with *P. boylii* showing no difference in caching behavior between large-particle size quadrats with rock cover and open treatments, while *P. truei* cached a greater portion (approximately 30%) of the remaining seeds in the large-particle quadrat with rock cover.

Both species of mice pilfered a greater portion of seeds from large-particle soils but were not affected by the presence or absence of cover (Fig. 3b, Table 2). *P. truei* was affected by particle size more than *P. boylii*, pilfering 50% more seeds from large-particle soils than from small-

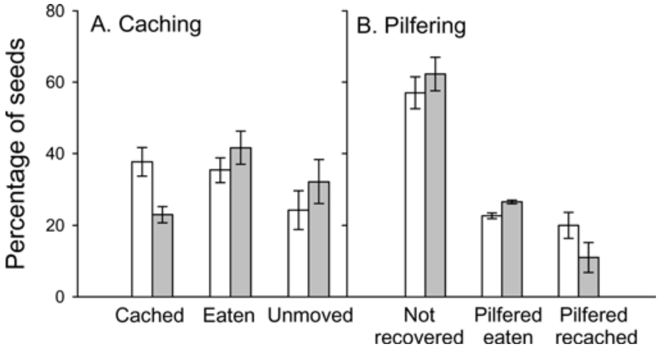

Fig. 1 **a** Mean percentage of available pinyon seeds that were cached, eaten, or left unmoved by *Peromyscus boylii* (*open bars*) and *P. truei* (*shaded bars*) in caching trials. **b** Mean percentage of pinyon seeds that were not recovered, pilfered and eaten, or pilfered and recached by *P. boylii* (*open bars*) and *P. truei* (*shaded bars*) in pilfering trials

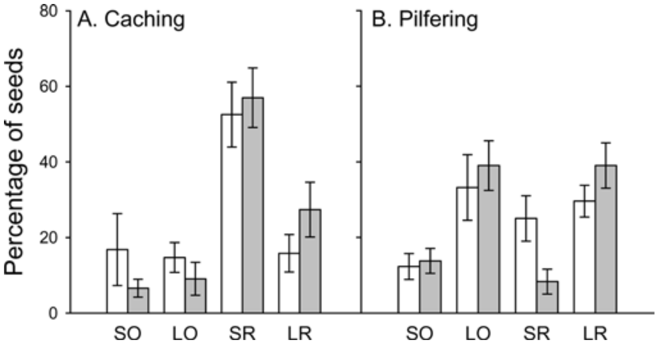

Fig. 3 **a** Mean percentage of pinyon seeds cached in four different treatments by *P. boylii* (*open bars*) and *P. truei* (*shaded bars*) with SE error bars. **b** Seeds pilfered by *P. boylii* and *P. truei* from the same combinations of rock cover and soil particle size. *SO* Small-particle soils (<2 mm) without rock cover, *LO* large-particle soils (>2.8 mm) without rock cover, *SR* small-particle soils with rock cover, *LR* large-particle soils

Table 2 ANOVA test for effects of soil particle size and rock cover on the caching and pilfering behavior of *P. truei* and *P. boylii*

Source	*df*	MS	*F*	*P*
Caching				
Species	1	0.005	0.111	0.740
Rock	1	0.735	15.052	0.001
Particle size	1	0.583	11.943	0.001
Species×rock	1	0.522	10.690	0.002
Species×particle size	1	0.078	1.603	0.210
Rock×particle size	1	0.116	2.386	0.127
species×rock×size	1	0.001	0.021	0.886
Error	72	0.049		
Pilfering				
Species	1	0.000	0.000	0.984
Rock	1	0.002	0.038	0.847
Particle size	1	1.292	29.998	0.001
Species×rock	1	0.125	2.892	0.093
Species×particle size	1	0.139	3.231	0.076
Rock×particle size	1	0.000	0.003	0.953
Species×rock×particle size	1	0.101	2.350	0.130
Error	72	0.043		

particle soils. This pattern differed from that of 2001 where no significant difference in pilfering behavior was found between the two particle sizes (Fig. 2b).

Soil moisture

Soil moisture did not differ significantly between large- (mean=0.19%±0.01 SE) and small-particle soils (0.18% ±0.01) taken from within the experimental enclosures in 2002 (F=0.465, P=0.53). In 2001, there was a significant interaction, with soil moisture significantly higher in small-particle soils at one sampling period (small=0.79% ±0.02, large=0.56%±0.02) and higher in large-particle soils at the other two sampling periods (small=0.21% ±0.04, large=0.39±0.07, F=15.2, P=0.002). Soil moisture was approximately 50% lower in 2002 (mean=0.18% ±0.01) than in 2001 (mean=0.42%±0.05) due to a severe drought in the region. Soil moisture at the base of natural rock outcrops (0.16%±0.01) was significantly higher than at paired open sites (0.13%±0.01) in late June 2002, the driest period of the year (t=2.1, df=19, P=0.048).

Pinyon pine germination

Pinyon pine seeds were approximately 4 times more likely to germinate in small- vs. large-particle soil cores. Thirty-nine of the 70 seeds (56%) planted in small-particle soil cores germinated versus 11 (16%) in large-particle soil cores (χ^2=15.68, df=1, P<0.001).

Particle size and rock cover variability

The majority of the points surveyed (80%) showed some variability in soil particle size within the 5-m radius that was sampled. Both large- and small-particle patches were available at 30% of the sample points, small- and mixed or large- and mixed particle-size soil patches were available at 50% of the sample points, and 20% of the sample points had only one size class available. Rock cover was available at all of the sample points, with the nearest rock within 2 m in 55% of the sample points, within 2–5 m in 35%, within 5–10 m in 5% and >10 m in 5% of the sampling points.

Particle size, pinyon pine and microsite associations

Seventy-five percent of the 110 juvenile pinyon pines we surveyed were associated with small-particle soils. Forty-five percent were associated with rock nurses and all of these were in small-particle soils. Shrubs were associated with 35% of pinyons, with 68% of those in large- or medium-particle soils. Four percent of pinyons were associated with both a rock and a shrub. Relatively few pinyons were found beneath trees or near logs (7%) and the remaining 9% of pinyons were in small-particle soils in interspace environments.

Discussion

Soil particle-size effects

Across both experiments and mouse species, soil particle size had a significant effect on caching behavior, with more pinyon seeds cached in small-particle soils. Although recaching rates were relatively low, mice also recached seeds more often and in larger amounts in small-particle soils. In contrast, mice showed no difference in their tendency to pilfer seeds from soils of differing particle size, although *P. truei* pilfered significantly more from large-particle soils in the second year of the study.

One hypothesis invoked to explain differences in caching and pilfering behavior is the pilfering avoidance hypothesis (MacDonald 1976), where cache strategy is determined by the likelihood of pilferage. For example, Merriam's kangaroo rats (*Dipodomys merriami*) reduced the number of scatterhoards and increased the number of larder hoards after seeds were pilfered by a conspecific (Preston and Jacobs 2001). Likewise, fox squirrels (*Sciurus niger*) were hypothesized to cache seeds far from the forest edge where predation threats decreased the likelihood of competitors searching for caches (Stapanian and Smith 1984). If this hypothesis held for mice in this study, we would have expected rates of pilfering to be lower in the small-particle soils where mice preferred to cache seeds and higher in large-particle soils that they avoided. The pilfering behavior in the first experiment and first year of this study did not support this hypothesis;

seeds were pilfered with equal likelihood regardless of soil type. However, in the second experiment and second year of the study, both species pilfered more from large-particle soils, though this pattern was stronger for *P. truei*. As a result, caching in soils with smaller particle sizes could potentially lower the probability of cache pilferage, but not at all times.

Because mice use olfaction to find buried seeds (Howard and Cole 1967; Howard et al. 1968; Vander Wall 1998a), differences in soil particle size could lead to differences in the ability of mice to detect buried seeds in these soils. Large-particle soils have greater macroporosity and therefore greater air movement (Brady and Weil 2000) and may consequently allow easier seed odor detection than the microporous, small-particle soils. Higher soil and seed moisture levels are also associated with greater seed odor detection, increasing the discovery of buried seeds by rodents (Johnson and Jorgensen 1981; Vander Wall 1993, 1995, 2000, 2003). In our experimental soils, soil moisture levels were relatively similar between small- and large-particle soils within a year. However, between years, moisture levels decreased from approximately 0.4–0.2% due to a regional drought. Interestingly, seed pilfering rates from both soil particle sizes were 20% lower in the second year compared to the first. These decreases are consistent with other studies showing 30–90% reductions in pilfering rates by deer mice between wet and dry soils (Vander Wall 1995, 2000). However, pilfering rates decreased more in small-particle soils, despite equally decreased soil moisture levels. This may have been due to the fact that smaller particle sizes have overall larger surface areas and therefore may lose water, and the odorants associated with it, at a slower rate than large-particle soils (Vander Wall 2003).

Several studies have shown that soil particle size and seed size can interact to affect the rate of seed recovery (Price and Heinz 1984; Price and Podolsky 1989; Hughes et al. 1995; Kotler et al. 2001). Generally, seed recovery is more rapid when seeds are larger than soil particles and recovery rates decline as seed size and particle size become more similar (Price and Podolsky 1989; Hughes et al. 1995). In our experiments, pinyon seeds were much larger than the soil particles in the small-particle treatment but approached the size of some soil particles in the large-particle treatment. Even so, pilfering rates did not differ between the two treatments, or when they did it was biased toward large particle sizes. This may have been due to the fact that recovery of large pinyon seeds depends more on simply uncovering the seed rather than sifting the seed from soil, as is the case for many of the heteromyids and jerboids in other studies.

Substrate could potentially affect the energetic cost of digging, and studies of heteromyid rodents found the energetic costs of scratch digging to be an important part of foraging cost, in some cases 5–10 times the cost of locomotion (Morgan and Price 1992). However, most studies failed to find a significant difference in energetic costs of digging among soils differing in either soil density (Morgan and Price 1992) or soil type (Vleck 1979). Unfortunately, we know of no studies that have examined the energetic costs of digging for soil particle sizes like those examined in this study.

Rock cover effects

Caching behavior was also affected by rock cover, with more seeds cached near rock structures in small-particle soils. Mice made 69% (*P. boylii*) and 84% (*P. truei*) of caches under or near rock cover, percentages similar to those of Vander Wall's (1993, 1995, and 1997) field studies where chipmunks, mice and kangaroo rats cached between 50 and 79% of seeds under or at the edge of shrub cover. This behavior could be the result of using rocks to aid in the recovery of seeds via spatial memory (McQuade et al. 1986). Alternatively, mice may have cached near rock cover because rocks afforded greater protection from predators. Several studies have documented higher rodent foraging activity near cover when predation risk was high (Abramsky et al. 1996; Kotler 1984). However, this hypothesis is not consistent with the lack of effect of rock cover on pilfering behavior, at least for *P. truei*, which apparently spent equivalent effort pilfering seeds from large-particle soils with and without rock cover. This trend contrasts with that from field studies in scrublands and desert ecosystems where seeds and seedlings incurred the greatest mortality under cover due to rodent predation (O'Dowd and Hay 1980; Hulme 1994; Chambers 2001). These studies suggest that rodents search for seeds where predation risk is low (Brown et al. 1988), and seed densities are typically high (Reichman 1984; Price and Reichman 1987). This inconsistency could be due to conditions unique to the design of the field enclosure. Both the enclosure frame and the short distance between open areas and rock cover may have affected how the rodents perceived predation vulnerability during the trials. However, if this were the case a similar pattern would have been expected in the caching trials.

Importance of soil particle size and cover for pinyon seed and seedling survival

Our data showed that pinyon seeds in small-particle soils were more likely to germinate than seeds in large-particle soils. Although microsite requirements for seedling survival may be different than for seed germination (Schupp 1995), the majority of small pinyons growing at our study site were associated with small-particle soils rather than large, suggesting seedling survival may also be greater in the small soil particle microsites. In sagebrush steppe habitats of southwestern Wyoming, Chambers (2000) documented both higher seed germination and 2-year seedling survival of several plant species in sandy soils compared to gravel soils despite a greater abundance of seeds entrapped in the gravel soils, and attributed this difference to less negative water potentials and overall greater soil water availability in sandy soils.

Small pinyons in our study site were associated with rocks (45%) as frequently as with shrubs (35%), suggesting that rocks may also serve as nurse structures. Several studies have indicated that nurse plants offer the best microsite for pinyon establishment (Calloway et al. 1996; Drivas and Everett 1988; Chambers 2001) and one documented higher soil moisture, decreased ambient temperatures and protection from browsers under nurse shrubs in west-central Nevada (Chambers 2001). Artificial shade alone can increase pinyon seedling survival (Meagher 1943) and rocks could act in a similar fashion. Red cedar (*Juniperus virginiana*) seedlings near rocks had higher survival than those farther from rock protection, presumably due to both protection from browsing and trampling by cattle and higher soil moisture from snowmelt and runoff during rains (Livingston 1972). Our data suggest that soils near rocks have higher moisture content than nearby open areas, a factor that may be especially important in arid ecosystems where rainfall is a major limiting factor and soils exhibit greater negative water potentials. One potential advantage of rock microsites over shrub microsites for pinyon regeneration is that there would no opportunity for the potentially negative effects of competition between pinyon seedlings and their shrub nurses (Bertness and Calloway 1994).

Mice as directed dispersers

Dispersal agents may be considered directed dispersers if a disproportionate number of seeds are deposited in suitable sites for seed germination and survival. Our survey of substrate variability indicated that both soil particle size and rock availability at our site varied at spatial scales (5 m radius around a point) relevant to those at which mice make choices among potential cache microsites. Caching patterns suggest mice could act as directed dispersers by moving pinyon seeds to suitable microsites in small-particle soils near rock nurses, and pilfering patterns suggest seeds would have equal or higher survival rates in those microsites. The pattern of seedling germination and natural seedling distribution documented in this study is consistent with the hypothesis that these microsites enhance early seedling establishment and survival.

The geographic ranges of the two *Peromyscus* species studied here (*P. boylii* and *P. truei*) overlap broadly with each other and with pinyon pines (Holbrook 1978; Hoffmeister 1986). Although pinyon pine in this study were growing entirely on relatively recently derived cinder soils, variation in soil particle sizes like those studied here occur across many different soil types and habitats (Chambers 2000), suggesting that the behaviors documented here could be important throughout the range of these trees. Finally, the strong similarity in caching and pilfering behavior of these sympatric mouse species suggests that differences in these behaviors are unlikely to act as a mechanism for species coexistence, as has been argued to be the case for some heteromyid rodents (Price et al. 2000; Leaver and Daly 2001). However, these species were not identical in their responses to rock cover, or in their tendency to cache seeds. *P. truei* cached fewer seeds overall, and placed more seeds in large-particle soils with rock cover, two behaviors that suggest it may be a slightly lower quality disperser than *P. boylii*.

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