Seed dispersal of western and Utah junipers: the role of scatter-hoarding rodents.

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ABSTRACT

The dispersal of Juniperus seeds is generally attributed to frugivores, both avian and mammalian. Junipers produce female cones with a husk enclosing the seeds that closely resemble fruit, thus they are often referred to as berries. These cones differ among juniper species with some species producing very fleshy, resinous cones such as those of western juniper, Juniperus occidentalis, while others are dry and leathery such as those produced by Utah juniper, J. osteosperma. Frugivorous birds and mammals have been found to disperse some juniper species through endozoochory by consuming juniper cones and passing intact seeds in their feces. However, seed dispersal in many other juniper species is not fully understood. Scatter-hoarding rodents have been recorded removing seeds and/or cones of several juniper species but have mostly been considered seed predators.

In this study I documented harvest and caching of western and Utah juniper seeds, showing that scatter-hoarding rodents should be considered seed dispersal agents for these two juniper species. I also compared removal of western and Utah juniper cones and seeds and observed that removal of seeds from seed and cone stations of both species by scatter-hoarding rodents was nearly equal. However, the removal rate of cones was very different. Frugivores were recorded removing western juniper cones at Shinn Peak, while no frugivores were recorded removing Utah juniper cones at either site. Kangaroo rats, Dipodomys spp., removed Utah juniper cones at both sites but never removed western juniper cones.

Results of this study suggest that scatter-hoarding rodents play a role in the dispersal of western and Utah juniper seeds. My study confirms that there is very little evidence of frugivores dispersing the seeds of Utah juniper, and I suggest that scatter-hoarding rodents are the primary dispersal agents of this species. Drier, less nutritious cones and larger seeds could be signs of
adaptation in Utah juniper to dispersal by scatter-hoarding. The cones of western juniper appear
to be more rewarding for frugivores and consumption of western juniper cones by frugivorous
birds and mammals has been previously described. This study is the first to document caching of
western juniper seeds by scatter-hoarding rodents. There is evidence to suggest that western
juniper seeds are dispersed in a two-phased dispersal process, diplochory, where scatter-hoarding
rodents cache seeds that have been initially dispersed through endozoochory by birds. Scatter-
hoarding rodents could play a role in the dispersal of other Juniperus species where their ranges
overlap and should not be regarded strictly as seed predators.
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Chapter 1: Seed dispersal of western and Utah juniper by scatter-hoarding rodents

INTRODUCTION

Dispersal of seeds away from the parent plant is an important component of plant population dynamics influencing gene flow and genetic variation (Howe & Miriti 2004; Karubian et al. 2010; Calviño-Cancela et al. 2012; Vander Wall & Beck 2012). Dispersal helps seeds and seedlings escape high density-dependent mortality that occurs under the parent canopy due to higher levels of seed predation and/or herbivory and an increase in pathogens (Janzen 1970; Connell 1971; Harms et al. 2000). Trees produce thousands of seeds to yield few seedlings (Terborgh et al. 2014), so processes that increase seedling survival can be important for plant demographics (Howe & Miriti 2004). Biotic seed dispersal can give seedlings advantages that are less likely attained through abiotic dispersal (Chambers & MacMahon 1994). Some important benefits of biotic dispersal include long distance dispersal and seed burial which can allow seeds to escape predation and desiccation on the soil surface (Chambers & MacMahon 1994). Directed dispersal is another potential benefit of biotic dispersal, where seeds are non-randomly dispersed to microsites that enhance seedling establishment and recruitment (Wenny & Levey 1998; Briggs et al. 2009; Hirsch et al. 2012; Yi et al. 2013; Salazar et al. 2013).

Two mechanisms of biotic seed dispersal include endozoochory and scatter-hoarding. Endozoochory occurs when an animal, usually a frugivorous bird or mammal, consumes a fruit reward and regurgitates the seeds or passes them intact through their gut. Several taxa of granivorous rodents and a smaller number of birds disperse seeds by storing them in scattered, superficially buried caches (Vander Wall 1990). Granivorous rodents have been found to be important dispersers of many plant seeds including grasses (Longland et al. 2001), herbaceous perennials (Barga & Vander Wall 2013), shrubs (Vander Wall 1994; Roth & Vander Wall 2005;
Hollander & Vander Wall 2009; Beck & Vander Wall 2011) and trees (Vander Wall 1992; Hollander & Vander Wall 2004; Waitman & Vander Wall 2012; Steele et al. 2013). Although many seeds are eaten, some cached seeds are forgotten or surplus and are left in the ground to germinate (Longland et al. 2001; Vander Wall 2002; Beck & Vander Wall 2011). The sacrifice a plant pays in eaten seeds for the service of dispersal and burial can payoff in more effective dispersal and should not be considered more costly than the excessive seeds lost during abiotic dispersal processes such as wind (Janzen 1986; Vander Wall 1993). Although the relationship between plants and granivorous dispersal agents fluctuates between antagonism and mutualism across spatial and temporal scales (Burns 2004), a review and analysis of published seed dispersal studies has shown the benefits tend to outweigh the costs (Zwolak & Crone 2012).

The female cones of junipers (*Juniperus* spp.) have been modified into a fruit-like structure that bears seeds and attracts both frugivores and granivores. The degree to which these cones, commonly referred to as juniper “berries,” resemble true fruits differs among juniper species. Previous studies have revealed the dependence of some frugivorous birds on the pulpy cones of western juniper (*J. occidentalis*) during winter months (Poddar & Lederer 1982), and the capacity of birds to be important dispersers for many other juniper species (Adams 2010); however, only herbivorous lagomorphs have been documented eating the cones of Utah juniper (*J. osteosperma*) which are drier and more fibrous (Schupp et al. 1999). Chambers et al. (1999) suggested that even though birds have long been regarded as primary dispersal agents of juniper seeds, this is not likely the case for all junipers species, and rodents are likely to play a role. A study of seed and sapling distribution in one-seed juniper (*J. monsperma*) found that most seeds were located under productive trees, while seedlings were more common away from trees (Salomonson 1978). Despite some observational and anecdotal evidence indicating that scatter-
hoarding rodents consume as well as cache several species of juniper in the western United States (Schupp et al. 1999; Vander Wall 1990), rodents have mostly been considered seed predators of juniper (Chavez-Ramirez & Slack 1993; Garcia 2001; Horncastle et al. 2004; Salomonson 1978).

Life history and seed characteristics of western and Utah juniper appear to have the appropriate qualities that stimulate scatter-hoarding behavior such as spatial and temporal synchrony in seed production, or masting, having seeds with a handling cost (a thick, hard seed coat), and the production of fairly large seeds (Vander Wall 2010). Seed morphology may not reflect the entire suite of agents important in dispersal. For example, although Jeffery pine seeds are obviously adapted to dispersal by wind with their winged seeds, rodents have been found to be crucial for seedling recruitment (Vander Wall 1992). Rodents have also been recognized as important seed dispersers of many plants that were previously thought to only be dispersed through frugivory, whether as secondary dispersers (Beck & Vander Wall 2011; Enders & Vander Wall 2012) or as primary dispersers in plants that have adapted to more xeric environments (Beck & Vander Wall 2010; Hollander et al. 2010). Most plants have complex dispersal systems with more than one disperser, and most vertebrate dispersal agents disperse more than one plant (Nathan 2007); however, some dispersers are more effective than others (Schupp et al. 2010). Scatter-hoarders and frugivores can both be effective seed dispersers (Hollander & Vander Wall 2004; Speigel & Nathan 2007). Effectiveness is measured quantitatively by dispersal distance, the number of visits a disperser makes to a plant and seeds dispersed per visit, while qualitative measures include how seeds are treated in the mouth or gut and the likelihood of germination and survival in the microsite where it is deposited (Schupp et al. 2010). The consequences and advantages of seed dispersal through endozoochory and scatter-
hoarding are distinguishable once movement away from the parent plant occurs. Some secondary metabolites in fruit can inhibit germination, so fruit consumption and defecation or regurgitation of seeds by frugivores can be an important component of the dispersal process for some plants (Cipollini & Levey 1997). Frugivores can disperse seeds much further than granivorous rodents sometimes allowing plants to colonize new environments, but this can leave seeds clumped in fecal piles or under popular perches (Vander Wall & Beck 2012). Chavez-Ramirez & Slack (1994) looked at dispersal patterns in Ashe juniper, \textit{J. ashei}, and found an average 22,250 seeds/m$^2$ under perches of Cedar waxwings, 30 seeds/m$^2$ beneath American robin perches, and 5 seeds/m$^2$ in open sites. Scatter-hoarders disperse seeds shorter distances, but they often bury seeds in beneficial microsites (Vander Wall & Beck 2012). Seed burial can be vital for relatively larger seeds that are less likely to be buried in abiotic processes, and can also allow seeds to escape desiccation and predation on the soil surface (Chambers & MacMahon 1994). Some plants seem to be able to take advantage of both frugivores and scatter-hoarders in a two-phased dispersal syndrome known as diplochory (Forget & Milleron 1991; Vander Wall & Longland 2004; Vander Wall et al. 2005; Enders & Vander Wall 2012). In western juniper, the dispersal of seeds by frugivorous birds would represent the first phase, and subsequent dispersal by scatter-hoarding rodents that collect seeds from bird feces and bury them in caches would represent the second phase. Johnsen (1962) found that the seeds of one-seed juniper buried from 6.4 mm to 25.4 mm deep had higher seedling emergence than those buried at 50.8 mm, and all seeds placed on the soil surface or buried at 50.8 mm failed to emerge. The removal of the husk increased one-seed juniper seed germination when compared to seeds left husks (Johnsen 1962), so removal of the husk and burial at intermediate depths appeared to increase germination and seedling establishment. Establishment of western juniper seedlings is also enhanced by seed
burial and by removal of the husk, whether through manual de-pulping or by frugivorous birds, although the latter also resulted in enhanced establishment relative to manually cleaned seeds (Longland & Dimitri 2016). Diplochory, and rodent dispersal in general, could be an important but overlooked dispersal mode for some Juniperus.

For this study I sought to understand the role that granivorous rodents play in the dispersal of juniper whether the cones are fleshy and resinous or dry and leathery. I studied two closely related juniper species with different fruit morphology: Juniperus occidentalis, western juniper, and J. osteosperma, Utah juniper. Trees in the genus Juniperus have modified female cones with fused scales that are convergent with fleshy fruit or berries that enclose their seeds. The cones of western juniper are resinous and juicy containing 1-5 seeds; whereas, those of Utah juniper are dry and fibrous containing 1-2 seeds. These two species may represent opposite ends of the spectrum in terms of juniper berry water content. Seed size differs between the two species (Chapter 2, Table 3). Western juniper has smaller seeds with thinner seed coats, and Utah juniper seeds are larger with a thicker seed coat, hence the species name ‘osteosperma’ or bone seed. I conducted field experiments to understand if scatter-hoarding rodents collect and cache western and Utah juniper seeds from below juniper canopies (Figure 1). Some rodent species might be more effective dispersers than others depending on quantitative and qualitative aspects of their interactions with seeds. In order to understand the role rodents play in the dispersal of western and Utah juniper seeds, I first tested individual rodent species in enclosures, monitoring the movement of radio-labeled seeds at two sites. Secondly, I tracked removal and dispersal under more natural circumstances (unconstrained by enclosures) by placing radio-labeled seeds under juniper canopies across two sites.
METHODS

Field sites

Due to restrictions in permitting for the use of radioactive material, only two field sites were used for this study: Shinn Peak and the Pine Nut Mountains. Shinn Peak is located in northeastern California in Lassen County (40°42’015"N, 120°17’399"W, elevation 1678 m). Western juniper is the only tree at this site and the understory is predominantly occupied by big sagebrush, *Artemesia tridentata* ssp. *tridentata*, and antelope bitterbrush, *Purshia tridentata*. The site consists of fairly open juniper forest adjacent to a large burned area with scattered junipers that were able to survive the fire in rock outcrops. Scatter-hoarding rodent species at this site include: yellow-pine chipmunks, *Tamias amoenus*, California kangaroo rats, *Dipodomys californicus*, deer mice, *Peromyscus maniculatus*, piñon mice, *Peromyscus truei*, and Great Basin pocket mice, *Perognathus mollipilosus*. The Pine Nut Mountains site is located in western Nevada, east of Carson City in Carson County (39°06’142"N, 119°38’211"W, elevation 1861 m). In the Pine Nut Mountains, Utah juniper co-occurs with single-leaf piñon, *Pinus monophylla*, and has a more patchy distribution. The dominate understory shrubs include big sagebrush, antelope bitterbrush, and green ephedra, *Ephedra viridis*. Several species of perennial bunchgrasses such as *Acnatherum hymenoides* are common, but *B. tectorum* is much less common than at Shinn Peak. At the Pine Nut Mountains site, scatter-hoarding rodents include: Panamint kangaroo rats, *Dipodomys panamintinus*, least chipmunks, *Tamias minimus*, deer mice, piñon mice, Great Basin pocket mice, and white-tailed antelope squirrels, *Ammospermophilus leucurus*.

Enclosure study
Caching trials were performed in two 15 m x 15 m enclosures constructed of ¼ inch (0.63 cm) mesh hardware cloth buried 18 inches below ground level to prevent rodents digging out and topped with aluminum flashing to prevent animals from climbing in and out. A 19 L bucket buried in the soil acted as an artificial burrow. It contained three levels and two 6 cm PVC pipes, one connecting the surface to the middle level, and the other connecting the top level to the soil surface allowing animals to enter and exit the bucket. For smaller rodents such as *Peromyscus* spp. and Great Basin Pocket mice, artificial burrows were constructed of 7.6 L buckets with two levels and two 3 cm PVC pipes. A partially buried can placed near the artificial burrows was kept full of water during trials. Many animals did not accept the artificial burrows, and several individuals uncovered and used old existing natural burrows that had been collapsed or were undetected. For each trial 200 seeds that had been labeled with Fe$^{59}$ were placed in a feeding tray with 3 black oil sunflower seeds (which tend to be a preferred food for granivorous rodents) and monitored for removal. If only sunflower seeds were consumed, I knew that the rodent in the trial was aware of the labeled juniper seeds even if they chose not to take them. Artificial burrows were also checked to confirm continued presence of test subjects. Feeding trays were covered with small wooden canopies to deter seed removal by birds. Sherman live traps were set in the corners of the enclosures and one in the center before each trial to ensure no other rodents other than the individual being tested were inside. Trials were checked within two days of deploying seeds. If over half of the seeds were removed, the trial was ended. Animals were left in enclosures for up to one week, with sunflower seeds sometimes replaced to further encourage juniper removal.

When over half of the juniper seeds were removed, or if the animal escaped, which happened in many trials, especially with deer mice, enclosures were searched with a portable
Geiger counter (Eberline ASP-1 meter and SPA-3 probe; ThermoFisher Scientific, Santa, Fe, New Mexico, USA) to detect the radio-labeled seeds. When “hotspots” were found, caches were carefully excavated and the top and bottom depth (mm) of the cache were recorded as well as seeds per cache, microsite, substrate and cache locations within the enclosure were mapped. The distance to the closest shrub or tree canopy was recorded for caches in the open, and for caches under shrubs, shrub species and distance from the edge of the shrub canopy was recorded. Seeds larder-hoarded in the artificial burrows were counted, and those in naturally occurring burrow were excavated when possible and the number of seeds found stored within counted.

Source tree study

Due to slow seed removal and difficulty retaining animals in enclosures, I began trials outside enclosures under mature, cone producing source trees. One hundred juniper seeds were placed under or at the edge of a mature juniper tree where seeds would naturally be found, except for the first trial at each site where two hundred seeds were used. Source trees for each trial were at least 80 m apart to decrease the likelihood of the same individual participating in more than one trial. I used trail cameras recording 30 second videos to identify species removing seeds and observe dispersal behavior. The videos were watched before searching in order to inform the size of area to be searched as larger rodents have larger home ranges than smaller species. Seeds were checked until more than half were removed for up to 30 days, after which trials were terminated if there was no removal. As in the enclosure trials, a portable Geiger counter was used to find caches, eaten seeds and larder-hoarded seeds by searching in concentric circles around the source tree out to around 50 m. When a kangaroo rat was recorded removing seeds, trials often went beyond 50 m focusing on visible burrow mounds. The same cache measurements were taken as discussed in the enclosure study in addition to distance to the seed station (dispersal distance).
Larder-hoarded seeds were again recovered when possible. All procedures involving animals were conducted in accordance with University of Nevada, Reno IACUC approved protocols (#00026).

A principal component analysis (PCA) was used to compare variation among cache characteristics such as seeds per cache (cache size), distance from the cache to the seed station (dispersal distance), and top depth. Species was overlaid to look for differences among rodent species for the cache characteristics listed. I looked at the mean proportion of caches placed in four different microsites by rodent species at Shinn Peak and the Pine Nut Mountains using a means test (PROC MEANS, SAS 2012), and a mixed model analysis of variance (PROC MIXED, SAS 2012) was used to test whether proportional caching frequencies differed among microsites and rodent species. The four microsites where caches were found included beneath shrub canopies (shrub), beneath the canopy of the source tree (source), under the canopy of a non-source juniper or single-leaf piñon at the Pine Nut Mountains (tree), and out in the open (open).

In order to understand the effectiveness of different dispersers during this study, I examined trail camera videos and counted the number of visits made by individual dispersers. I also monitored seeds removed over the trial, which was used together with the counts of visits to calculate average number of seeds removed per visit. Trials were only used if seed removal could be attributed to a single species, as I could not unmistakably accredit how many seeds were removed by different dispersers by watching videos. Only trials where trail cameras captured most removal events were used, as sensitivity settings caused some cameras to miss removal events on infrequent occasions (e.g., seeds were visible in one video and gone in the next).

RESULTS


Enclosure study

Among 66 trials run at both sites, only 19 caches were found inside enclosures (Table 1). Despite the small sample sizes, caches that were made are useful for characterizing cache attributes of four species, Great Basin pocket mice, piñon mice, Panamint kangaroo rats, and California kangaroo rats, which are summarized in Table 2. In the Pine Nut Mountains, one Panamint kangaroo rat cache was found with 5 seeds buried just below the soil surface under a shrub. All eight Great Basin pocket mouse caches were found in the open at a mean depth (± SD) of 17.9 ± 5.2 mm, and were fairly large (mean ± SD = 24.9 ± 15.4 seeds/cache). The relatively small standard deviation for cache depth and consistent caching in open microsites suggest that these are typical cache characteristics for this species.

At Shinn Peak, three individuals of three species cached (Table 2). Great Basin pocket mouse caches were all under shrub canopies with a mean (± SD) 30 ± 4.6 seeds per cache and a mean (± SD) top depth of 21.5 ± 5.0 mm. The small standard deviation of these cache attributes could indicate that this is typical for Great Basin Pocket mice at this site. Caches made by a California kangaroo rat were mostly in open microsites, and the one cache that was not completely recovered contained at least 23 seeds. The piñon mouse made both caches under a dead shrub canopy just below the soil surface.

Source tree study

Trials outside of enclosures resulted in considerably more caches (Table 3). At Shinn Peak, removal of 100 radioactive western juniper seeds (200 were used in trial 1) from 20 trees was monitored during fall of 2014 and spring of 2015 (total seeds, n=2100). There was no removal in 3 trials after 30 days, so trials were ended. Of the seeds that were removed (n=1736), I recovered 40.5%, 23.9% of which were found in 82 caches and 11.8% had been eaten. I did not
recover any larder-hoarded seeds, which was due to the difficulty in finding and excavating larders or burrows at this site, which has many large rock outcroppings that both shielded radiolabel signals and made excavation impractical.

Three rodent species were responsible for all but one cache at both sites. At Shinn Peak, piñon mice made 72 caches, deer mice made 6 and California kangaroo rats made 3 (Table 4). Piñon mouse caches had on average 4 or 5 seeds with a mean (± SD) top depth of 7.3 ± 4.7 mm and a mean dispersal distance of 6.4 ± 5.6 m away from the source tree. Deer mice were recorded removing seeds in one trial and made 6 caches with approximately 5 (SD = ± 1.1) seeds per cache that had a mean (± SD) top depth of 7.8 ± 5.0 mm and an average (± SD) dispersal distance of 7.3 ± 4.6 m. Only 3 caches were attributed to California kangaroo rats. These caches were larger and shallower than those made by Peromyscus spp., with just over 9 seeds per cache (SD = ± 2.9) and a mean top depth of 6.3 ± 2.6 mm, and were moved further from the source with a mean dispersal distance of 8.4 ± 5.9 m.

Since piñon mice made the vast majority caches at Shinn Peak, not many conclusions can be drawn about deer mouse and California kangaroo rat caches due to the small sample sizes. PCA produced two primary axes of variation in cache attributes. Factor 1 which is represented by seeds per cache and top depth explained 42% of the variation, while factor 2 represented by dispersal distance explained 30% of the variation (Table 5). When looking at the PCA plot (Figure 2) there is little separation among species, but deer mice seem to have deeper caches that are dispersed farther.

Rodent use of four microsite types was examined at Shinn Peak (Figure 3). Piñon mice cached mostly under source tree and shrub canopies. All 6 deer mouse caches were found under a shrub canopy and California kangaroo rat caches were under the source tree and in the open. A
mixed model ANOVA found no significant differences for the main effects of species ($df = 32, f\ value = 0.22, P = 0.8$) and microsites ($df = 32, f\ value = 2.23, P = 0.1$), but the interaction between species and microsite was significant ($df = 32, f\ value = 2.6, P = 0.04$).

At the Pine Nut Mountains, 21 trials were completed with 2200 radioactively labeled Utah juniper seeds of which 2045 were removed, and 1 recovered 1160 (56.7%) of those removed by rodents (Table 3). Of the seeds recovered, 39.5% were cached in 127 caches, 3.1% were found eaten and 26.9% were found in larders. Larder-hoarded seeds were probably much higher than reported, as many seeds were inaccessible because they were too deep, under a larger shrub or in rocky soil. Both Panamint kangaroo rats and piñon mice larders were found and excavated. One piñon mouse larder of 43 seeds was found in the branch of an Artemesia sp. 53 cm above the ground, while Panamint kangaroo rat larders were always in large burrows mostly found in sandy areas with some located at least partially beneath shrubs.

Two species, piñon mice and Panamint kangaroo rats, made all but one cache at the Pine Nut Mountains (Table 4). The most prolific scatter-hoarders were piñon mice, which made 115 of the 127 caches found during this study. Caches averaged approximately two seeds per cache ($1.9 \pm 0.74$) with a mean dispersal distance of $5.23 \pm 3.74$ m and a top depth of $6.7 \pm 5.0$ mm. In contrast, Panamint kangaroo rat made larger ($21 \pm 15.8$ seeds/cache), deeper ($14.4 \pm 6.4$ mm) caches and dispersed seeds farther from the source ($8.36 \pm 6.92$ m). One Panamint kangaroo rat cache was located 27.5 m from the seed station and placed under an Artemesia sp. canopy. A single cache was attributed to least chipmunk, which was recorded in three 30-second videos taking approximately 4 seeds. The cache had been recovered by rodents and 4 seeds lay eaten next to a small excavation that was 8.57 m from the seed station with a bottom depth of 8.0 mm.
At the Pine Nut Mountains, cache characteristics of piñon mice and Panamint kangaroo rats were examined, and the single cache made by a least chipmunk was left out of the principal components analysis (PCA). Seeds per cache and top depth (factor 1) explained 51% of the variation, and factor 2 (dispersal distance) explained 31% of the variation (Table 5). When looking at the PCA plot (Figure 4) there is separation among species, with Panamint kangaroo rat caches being larger and deeper than those of piñon mice. There is considerable variation in dispersal distance for both species.

I looked at the use of four main microsites by both species at the Pine Nut Mountains (Figure 5). Most piñon mouse caches were found under shrub canopies, whereas a larger proportion of Panamint kangaroo rat caches per trial were found in the open. There were no significant differences for the main effects of species ($df = 52, f\ value = 1.14, P = 0.3$) and microsites ($df = 52, f\ value = 1.26, P = 0.3$), but the interaction between species and microsite was again significant ($df = 52, f\ value = 4.2, P = 0.01$).

Quantifying seed removal

Ten trials at Shinn Peak and 9 at the Pine Nut Mountains fit the requirements for calculating average number of seeds removed per visit. Mice had to make more visits than kangaroo rats to remove 100 seeds (Table 6). Piñon mice and deer mice had average load sizes of approximately 3-8 seeds per visit, while Panamint kangaroo rats and California kangaroo rats took approximately 40-50 seeds per visit.

DISCUSSION

Results of this study clearly indicate that scatter-hoarding rodents disperse western and Utah juniper seeds. Although frugivores may indeed represent a primary pathway from parent plant to seedling establishment (Adams 2010) for juniper species with more fleshy cones, scatter-
hoarding rodents should be considered as an additional or alternate pathway to seedling recruitment for these juniper species and perhaps others. Most of the caches found in my source tree study were made by piñon mice at both Shinn Peak (76.5%) and the Pine Nut Mountains (90.6%). Both *Peromyscus* spp. observed are known scatter-hoarders that have been shown to be effective dispersers for other tree species (Vander Wall et al. 2001; Hollander & Vander Wall 2004). Great Basin pocket mice made most of caches in enclosures at both sites. California kangaroo rats made a handful of western juniper caches in the enclosure and source tree studies at Shinn Peak, and at the Pine Nut Mountains, Panamint kangaroo rats made 11 caches in my source tree study and 1 in my enclosure study. These scatter-hoarding rodents can be an important pathway for western and Utah juniper to escape the parent plant and the predation seeds experience on the soil surface.

Most *Peromyscus* spp. caches found at both western and Utah juniper sites were under shrub canopies, which is where the majority of seedling recruitment has been found for western (Burkhardt & Tisdale 1976) and Utah juniper (Schupp et al. 1999). Juniper canopies and open areas were also frequently used caching microsites in my study that can be conducive to seedling recruitment (Burkhardt & Tisdale 1976; Schupp et al. 1999). Barney & Frischknecht (1974) found that Utah juniper seedlings sampled post fire were under or adjacent to canopies of trees that had burned, suggesting they survived the fire in the seed bank. Solar radiation decreased seedling survival but increased growth for established western juniper seedlings (Burkhardt & Tisdale 1976). Open microsites mostly used by Panamint kangaroo rats and Great Basin pocket mice at the Pine Nut Mountains in this study are likely more suitable during cooler or wetter years when desiccation is not as limiting. Seedling emergence of Utah juniper was found to vary from one year to the next, with some years having higher emergence under shrubs while in other
years emergence was higher in interspaces (Chambers et al. 1999). This suggests that juniper can establish in open microsites when environmental conditions are ideal, but might need nurse plants in drier years. Having a diverse array of dispersers that cache in a variety of microsites could allow juniper to take advantage of variable weather conditions or landscape altering events over long time periods.

The mean distance Panamint kangaroo rats dispersed seeds was farther than that of piñon mice, with one cache being found under an *Artemesia* sp. 27.5 m from the source. Although only 3 caches made by California kangaroo rats were found at Shinn Peak, the average dispersal distance was again farther than that of piñon mice. However, mean dispersal distances were not considerably greater for kangaroo rats than for piñon mice and were in fact less than for deer mice at Shinn Peak. The main quantitative difference in caches made by species in these two genera is in cache sizes, with kangaroo rat species making caches ranging from approximately twice the number of seeds of those made by *Peromyscus* spp. (at Shinn Peak) to more than an order of magnitude more seeds per cache (at Pine Nut Mountains). This probably occurred because kangaroo rats also took larger average loads of seeds than *Peromyscus* spp. Like all species in the family Heteromyidae, kangaroo rats have external cheek pouches that can hold larger seed loads than other rodents (Vander Wall et al. 1998, Vander Wall & Longland 1999). Another heteromyid species that occurred at both sites, Great Basin pocket mice, made the majority of caches in enclosure experiments, and their caches (approximately 25-30 seeds/cache) were even larger than most of those made by kangaroo rats in source tree experiments. Although most seed removal by *Dipodomys* at both sites resulted in larder-hoarding and thus seed predation, kangaroo rats may be important for less frequent, longer distance dispersal.
Although the larger caches made by heteromyids could increase seedling competition and be less beneficial for seedling recruitment than smaller caches, many juniper seeds are parthenocarpic and have unfertilized or aborted seeds that still develop and appear to be normal externally. Therefore, multi-seeded caches might not be as detrimental for seedling establishment in western and Utah juniper as it appears. Many of the seeds I collected were empty, where the seed coats developed normally but the embryo inside was either dry or never formed, so floating seeds in a saline solution to remove the empty seeds that rose to the top was necessary. Samples of seeds cached in enclosure trials were cut open revealing that some empty seeds had escaped my detection. Thus, it is likely that rodents cache some percentage of empty juniper seeds that cannot germinate. Juniper seeds often have very low rates of seedling emergence (Young et al. 1988, Longland and Dimitri 2016). Regardless of whether the underlying reason for this is due to empty seeds or other factors, such low establishment would be expected to greatly reduce the chance that large seed caches would result in significant seedling competition.

The depth at which scatter-hoarding rodents cache seeds is an important factor for cache recovery by naïve rodents and for seedling germination (Vander Wall 1993b). Very few studies have been conducted on seed burial depth and germination in Juniperus, but Johnsen (1962) found that depths from 6-13 mm were suitable for seedling emergence of J. monosperma while seeds on the surface and buried just over 100 mm did not emerge. A planting depth of 10 mm was used in two studies examining the influence of stratification on western and Utah juniper seeds and the influence of burial (Young et al. 1988; Longland & Dimitri 2016). Longland and Dimitri (2016) showed that removal of western juniper husks and burial at 10 mm increased seedling emergence when compared to seeds placed on the soil surface and those left within whole cones. In my studies, the mean top depths of caches by all species at Shinn Peak fell
within the range of 6-13 mm, but at the Pine Nut Mountains only piñon mouse caches and the one cache made by a least chipmunk fell in that range. Panamint kangaroo rat caches had a slightly deeper mean top cache depth of 14.4 mm, but cache depth was highly variable. Cache discovery by a naïve forager decreases with cache depth (Vander Wall 1993b), so deeper caches made by kangaroo rats might be more likely to persist in the ground.

Juniper seeds are fairly small with a thick, woody seed coat which could make them a lower preference food item. Removal rates were slower for many trials compared to those of more preferred seeds like Jeffrey pine (Vander Wall 1992) and piñon pine (Hollander & Vander Wall 2004). Nonetheless, juniper seeds are abundant in mast years and available early in the spring when other seeds are not yet available. If they are a lower preference food item, juniper seeds could have low recovery rates after being cached by rodents allowing the seeds to germinate and establish (Chambers et al. 1999). Most dispersal studies focus on seeds that are highly preferred and are removed at a high rate, but rodents can still be important dispersers for less preferred seeds (Barga & Vander Wall 2013). In addition to the possibility that rodents prefer other seeds to juniper, thick seed coats may make juniper seeds difficult to detect by olfaction, potentially reducing recovery of seed caches by rodents.

Junipers with moist, fleshy cones like western juniper, are initially dispersed by frugivores, such as birds, to microsites away from the parent plant. Burial could be another important factor for seedling recruitment. At Shinn Peak during years with increased, synchronous cone production, seeds passed by birds not only cover the ground beneath cone producing trees but cover boulders and pile up under perches such as large shrubs and juniper snags (personal observation). This clumping of seeds after bird dispersal has also been observed in Ashe juniper and can vary depending on bird species (Chavez-Ramirez & Slack 1994).
Rodents take western juniper seeds defecated by frugivorous birds (Longland and Dimitri 2016), and we have often observed chipmunks and ground squirrels utilizing this abundant and predictable food source. Secondary dispersal by rodents and burial of seeds that have been primarily dispersed by frugivores is likely important for seedling recruitment in western juniper. Junipers with drier, leathery cones like Utah juniper that are not attractive to frugivores, are likely primarily dispersed by scatter-hoarding rodents, which can easily husk seeds from cones. Piñon mice and Panamint’s kangaroo rats removed both seeds and cones at the Pine Nut Mountains (Ch.2), and whole cones were found in a Panamint kangaroo rat cache and within their larders (Figure 4).

Plants that are dispersed by scatter-hoarding rodents often have traits that can increase the likelihood that cached seeds are not recovered (Vander Wall 2010). Seed production varies annually in most junipers, including western and Utah juniper, with many species going 2-5 years between large crops (Bonner & Karafeldt 2008). This inter-annual variation can be synchronous at the population level similar to masting in other plants, but is not consistent on a smaller spatial scale. Some juniper trees are consistently productive while others rarely produce seeds and only produce male cones (Chambers et al. 1999; unpublished data). During years with large seed crops, mast years, it is likely that rodents make more caches than they can consume, which could lead to more seedling recruitment when excess caches are left in the ground (Jansen et al. 2004; Vander Wall 2002; Vander Wall & Beck 2012; Zwolak et al. 2015) Another way in which plants have adapted to dispersal by scatter-hoarders is by increasing handling costs. Vander Wall (2010) argues that traits such as thick seeds coats increase handling costs and encourage scatter-hoarding. Juniper species in general have very hard seeds. Utah juniper gets its
name *osteosperma*, “bone seed,” from its hard, thick seed coat, so this could be a potential adaptation to promote dispersal by scatter-hoarding rodents.

In this study I did not follow the fate of seeds after initial caching, but many cached seeds are pilfered and re-cached (Vander Wall & Jenkins 2003) or re-cached by the initial disperser (Vander Wall & Joyner 1998; Roth & Vander Wall 2005; Jansen et al. 2012). Re-caching can result in a reduction in the number of seeds per cache, further movement from the source, the evening out of cache distribution, and more caches being moved under shrub canopies, thus increasing the chance of seedling establishment (Vander Wall & Joyner 1998; Roth & Vander Wall 2005; Jansen et al. 2012). If re-caching occurs frequently in western and Utah juniper dispersal as well, my study only provides insight into part of the pathway a seed may take from the parent plant to an established tree.

Although I did not measure all quantitative and qualitative subcomponents of disperser effectiveness outlined by Schupp et al. (2010), my studies can provide insights into the quantity and quality of dispersal provided by the two main groups of scatter-hoarding rodents at my sites. Quantity is the product of the number of visits made by a disperser and the number of seeds that are dispersed during each visit, and quality is determined by the likelihood a seed survives handling in the mouth or gut and the probability of survival in the microsite to which the seed is dispersed. Kangaroo rats clearly can move more seeds than *Peromyscus* spp. Although piñon mice were capable of removing all experimental seeds in a single night by making multiple visits, they removed fewer seeds per visit than kangaroo rats, which only needed to make two visits to remove all seeds. It is likely that kangaroo rats would have made many more visits if more seeds had been available, so their potential in pure quantitative aspects of dispersal exceeds that of piñon and deer mice. However, kangaroo rats also deposited more seeds per cache, and
while the relative benefits and costs of larger versus smaller caches is not clear, as discussed above, *Peromyscus* species make more caches from a given number of seeds than kangaroo rats. *Peromyscus* species may also often have larger population densities than larger-sized kangaroo rats, as was true at my sites (see chapter 2), so it is likely that they are superior dispersers on a quantitative basis. Qualitatively, seeds that were not eaten and were cached were undamaged by handling or treatment in the mouths of rodents, and many of the cache microsites where seeds were deposited in my study are microsites that have been found suitable for establishment of juniper seedlings. Although species did show some differences in caching microsites, the favorability of these different microsites for seedling establishment is likely to vary with environmental conditions, such as precipitation. Species that cache seeds in open areas, as kangaroo rats and pocket mice often did in my experiments, may be qualitatively superior dispersers in more rare wet years, while those that cache under shrubs or tree canopies may be superior under dry conditions.

My study sites were located near the edge of both juniper species ranges. The Pine Nut Mountains site is located on the western edge of Utah juniper’s range. Throughout the full extent of its range, Utah juniper coexists with other species of scatter-hoarding rodents that could be potential dispersers. Rodhouse et al. (2010) found that *Tamias dorsalis* selected habitats with old growth juniper woodlands, so this species could also be a potential disperser of Utah juniper in the extensive area that their ranges overlap. Shinn Peak is located in the southeastern corner of western juniper’s range, so it likely overlaps with other scatter-hoarding species across its range as well. It is also likely that across the range of these two juniper species seed dispersal mutualisms vary, with coevolution between juniper and scatter-hoarders being stronger and more important for seedling recruitment in some areas and weaker and less significant in others.
(Thompson 1999). An individual juniper that lives within the home range of a rodent that tends to larder-hoard more seeds than it scatter-hoards will experience a more antagonistic relationship. In contrast, juniper trees within the home range of an individual that is a prolific scatter-hoarder will have a more mutualistic relationship with the rodents that disperse their seeds. Zwolak & Crone (2012) evaluated 14 plant-granivore studies and their model suggested that overall interactions between rodents and the plants studied were weakly mutualistic.

The dispersal of *Juniperus* seeds through endozoochory in North America is well documented for several juniper species (Adams 2010). However, seed dispersal systems in other juniper species have been overlooked and dispersal by frugivores is assumed in the absence of direct evidence. Piñon mice overlap with many *Juniperus* species across their extensive range, and are likely important dispersers for more than just western and Utah juniper given the amount of caching I observed at both sites. Several other *Dipodomys* species across western North America overlap in range with *Juniperus*, and *Dipodomys* spp. vary in their propensities to cache seeds in scatter-hoards versus larderhoards (Jenkins & Breck 1998), so this genus could represent important seed dispersers for other juniper species. Although *Tamias* spp. did not appear to be important dispersers in my study, other species within the genus also overlap with western and Utah junipers as well as other North American *Juniperus*. Rodhouse et al. (2010) found that cliff chipmunks, *Tamias dorsalis*, preferred old growth Utah juniper and single-leaf piñon forests, so this species could be another overlooked dispersal agent.

Future studies should include germination/seedling emergence experiments as a function of cache sizes and microsites found in my study and with whole cones for Utah juniper. Juniper germination studies in nature are difficult and require long-term monitoring, since seeds can remain viable for almost 50 years (Johnsen 1959). Nevertheless, in order to truly understand the
current expansion of juniper, having a complete understanding of seedling recruitment and survival is vital. Cutting junipers with many seeds cached under the canopy and leaving shrubs and open microsites with seeds intact in the soil seed bank, is not likely to be an effective long-term management strategy for converting expanding woodlands back to sagebrush-steppe habitat. It might be more efficient to focus on cone producing trees along woodland ecotones where small mammal diversity is highest and junipers are encroaching into the sagebrush-steppe habitat that is currently highly valued.
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Zwolak, R., Bogdziewicz, M., and A. Wrobel (2015). Advantages of masting in European beech: Timing of granivore satiation and benefits of seed caching support the predator dispersal hypothesis. Ecological Society of America annual meeting, Baltimore, MD, COS 18-6
Table 1. Summary of enclosure trials at Shinn Peak and Pine Nuts sites. For each trial, 200 radio-labeled juniper seeds were placed in a seed box that permitted rodents but deterred birds with 4 sunflower seeds placed next to the pile of juniper seeds. If sunflower seeds were consumed, then I knew that rodents had encountered the juniper seeds. The values are total numbers for each species.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>No. Trials</th>
<th>No.</th>
<th>No.</th>
<th>Sunflower seeds removed</th>
<th>Larder-hoarded</th>
<th>Juniper eaten</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Trials</td>
<td>Individuals</td>
<td>Caches</td>
</tr>
<tr>
<td>Pine Nut Mts</td>
<td>Panamint kangaroo rat</td>
<td>9</td>
<td>9</td>
<td>2</td>
<td>9</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Deer mouse</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Great-Basin pocket mouse</td>
<td>4</td>
<td>4</td>
<td>8</td>
<td>3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Piñon mouse</td>
<td>5</td>
<td>5</td>
<td>0</td>
<td>5</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Least Chipmunk</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>23</td>
<td>23</td>
<td>10</td>
<td>21</td>
<td>12</td>
</tr>
<tr>
<td>Shinn Peak</td>
<td>California kangaroo rat</td>
<td>12</td>
<td>9</td>
<td>5</td>
<td>8</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Deer mouse</td>
<td>5</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Great-Basin pocket mouse</td>
<td>11</td>
<td>8</td>
<td>3</td>
<td>6</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Piñon mouse</td>
<td>8</td>
<td>6</td>
<td>2</td>
<td>6</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Yellow-pine chipmunk</td>
<td>7</td>
<td>7</td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>43</td>
<td>40</td>
<td>11</td>
<td>39</td>
<td>8</td>
</tr>
</tbody>
</table>
Table 2. Enclosure study caching summary for Pine Nut Mountains and Shinn Peak.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>No. of caches</th>
<th>Eaten</th>
<th>Larder hoarded</th>
<th>Cached</th>
<th>Missing</th>
<th>Left</th>
<th>Seeds/cache Mean ± SD</th>
<th>Top depth (mm) Mean ± SD</th>
<th>Cache Microsites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pine Nut Mountains</td>
<td>Panamint kangaroo rat</td>
<td>2</td>
<td>0</td>
<td>195</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>1</td>
<td>shrub canopy</td>
</tr>
<tr>
<td></td>
<td>Great Basin pocket mouse</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>199</td>
<td>1</td>
<td>0</td>
<td>25 ±15.4</td>
<td>17.9 ±5.2</td>
<td>open</td>
</tr>
<tr>
<td>Shinn Peak</td>
<td>California kangaroo rat</td>
<td>5</td>
<td>1</td>
<td>127</td>
<td>NA</td>
<td>11</td>
<td>33</td>
<td>22*</td>
<td>4 open, 1 shrub canopy</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Great Basin pocket mouse</td>
<td>3</td>
<td>0</td>
<td>107</td>
<td>90</td>
<td>3</td>
<td>0</td>
<td>30 ±4.6</td>
<td>21.5 ±5.0</td>
<td>shrub canopy</td>
</tr>
<tr>
<td></td>
<td>Piñon mouse</td>
<td>2</td>
<td>15</td>
<td>0</td>
<td>2</td>
<td>13</td>
<td>170</td>
<td>1 ±0</td>
<td>5 ±0</td>
<td>dead shrub canopy</td>
</tr>
</tbody>
</table>

*4 out of 5 *D. californicus* caches were recovered and larderhoarded, so total seeds cached, median seeds/cache and median cache depth were unknown for most caches. The 4 caches recovered had a total of 4 seeds that were left in or next to the cache mixed in with the displaced soil.
Table 3. Summary of source tree caching trials for Shinn Peak and Pine Nuts. For all but the first trial at both sites where 200 seeds were used, 100 seeds were placed below the canopies of junipers with a trail camera placed above the seed station to identify species removing seeds. Percentages are calculated from the number of seeds removed.

<table>
<thead>
<tr>
<th>Site</th>
<th>Trials</th>
<th>Total seeds</th>
<th>Seeds removed</th>
<th>Seeds recovered</th>
<th>Seeds cached</th>
<th>Mean seeds/Cache (SD)</th>
<th>Caches</th>
<th>Eaten</th>
<th>Found in larders</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shinn peak</td>
<td>20</td>
<td>2100</td>
<td>1612</td>
<td>659 (40.9%)</td>
<td>415 (25.7%)</td>
<td>5.1 (±1.9)</td>
<td>82</td>
<td>205</td>
<td>0</td>
</tr>
<tr>
<td>Pine Nut Mts</td>
<td>21</td>
<td>2200</td>
<td>2045</td>
<td>1160 (56.7%)</td>
<td>458 (39.5%)</td>
<td>3.62 (±7.2)</td>
<td>127</td>
<td>57</td>
<td>497 (26.9%)</td>
</tr>
</tbody>
</table>
Table 4. Summary of cache characteristics from Shinn Peak and Pine Nut Mountains from source tree study. The number of caches is given with the means for three cache variables.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Caches</th>
<th>Seeds/cache (± SD)</th>
<th>Dispersal distance (m) (± SD)</th>
<th>Top Depth (mm) (± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Shinn peak</strong></td>
<td>Piñon mouse</td>
<td>72</td>
<td>4.9 (±1.7)</td>
<td>6.05 (±5.29)</td>
<td>7.1 (±4.6)</td>
</tr>
<tr>
<td>(Western juniper)</td>
<td>Deer mouse</td>
<td>6</td>
<td>5.0 (±1.1)</td>
<td>12.62 (±0.44)</td>
<td>10.8 (±5.5)</td>
</tr>
<tr>
<td></td>
<td>California kangaroo rat</td>
<td>3</td>
<td>9.3 (±2.9)</td>
<td>8.37 (±5.93)</td>
<td>6.3 (±2.6)</td>
</tr>
<tr>
<td><strong>Pine Nut Mts</strong></td>
<td>Piñon mouse</td>
<td>115</td>
<td>1.9 (±0.7)</td>
<td>5.23 (±3.74)</td>
<td>6.7 (±5.0)</td>
</tr>
<tr>
<td>(Utah juniper)</td>
<td>Panamint kangaroo rat</td>
<td>11</td>
<td>21.4 (±15.8)</td>
<td>8.36 (±6.92)</td>
<td>14.4 (±6.4)</td>
</tr>
<tr>
<td></td>
<td>Least chipmunk</td>
<td>1</td>
<td>4</td>
<td>8.57</td>
<td>8.0*</td>
</tr>
</tbody>
</table>

* The one cache attributed to *T. minimus* at the Pine Nuts was recovered, and 4 seeds were found eaten next to the digging, only bottom depth was measured.
Table 5. The Variable loads of three factors (principal components) of the principal component analysis.

<table>
<thead>
<tr>
<th>Site</th>
<th>Variable</th>
<th>Factor 1</th>
<th>Factor 2</th>
<th>Factor 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shinn Peak</td>
<td>Distance to station</td>
<td>0.613686</td>
<td>0.681575684</td>
<td>0.3985525</td>
</tr>
<tr>
<td></td>
<td>Seeds per cache</td>
<td>0.6169966</td>
<td>-0.669389505</td>
<td>0.413803</td>
</tr>
<tr>
<td></td>
<td>Top depth</td>
<td>0.7011148</td>
<td>-0.007505785</td>
<td>-0.7130089</td>
</tr>
<tr>
<td>Pine Nut Mts.</td>
<td>Distance to station</td>
<td>0.6189201</td>
<td>0.711220807</td>
<td>0.333321</td>
</tr>
<tr>
<td></td>
<td>Seeds per cache</td>
<td>0.8505061</td>
<td>-0.008810714</td>
<td>-0.5258914</td>
</tr>
<tr>
<td></td>
<td>Top depth</td>
<td>0.6568104</td>
<td>-0.658782608</td>
<td>0.3668863</td>
</tr>
</tbody>
</table>
Figure 1. A simplified seed fate diagram for western and Utah juniper displaying potential dispersal pathways. Red lines depict biotic dispersal by frugivores and/or scatter-hoarding rodents that could lead to seedling establishment, whereas black lines depict abiotic movement.
Figure 2. Principal components analysis for three cache variables: dispersal distance, seeds/cache and top depth, at Shinn Peak.
Figure 3. Bar graph showing the proportion of caches made by each species in four microsites per trial for Shinn Peak.
Figure 4. Principal components analysis for three cache variables: dispersal distance, seeds/cache and top depth, at the Pine Nut Mountains.
Figure 5. Bar graph showing the proportion of caches made by each species in four microsites per trial for the Pine Nut Mountains.
Chapter 2: Seed and Cone removal of western and Utah juniper: implications for seed dispersal

INTRODUCTION

Fruit, cone and seed traits can be influenced by both biotic and abiotic dynamics experienced by plants (Siepielski & Benkman 2007, Jordano 1995). Coevolutionary processes resulting in mutualisms can be important biotic interactions driving adaptive traits that encourage pollinators or seed dispersers (Thompson 1999). The dispersal of seeds away from the parent plant has many potential benefits (Schupp et al. 2010) including escaping increased seed and seedling mortality that exists under or near the parent canopy (Janzen 1970; Connell 1971), the colonization of new habitats (Howe & Smallwood 1982), directed dispersal of seeds to specific, beneficial microsites (Wenny & Levey 1998; Briggs et al 2005), and increasing genetic diversity (Calviño-Cancela et al. 2012). Coevolution between plants and animals has resulted in a wide array of dispersal syndromes, including endozoochory in which animals consume fruits and pass seeds through their guts intact (van der Pijl 1969). Frugivores are utilized by a wide array of plants in many different environments to disperse seeds (Jordano 2000). The production of fruit to attract vertebrate dispersers is possibly the ancestral condition in angiosperms (Corner 1949). However, in xeric environments, fewer plants produce fruit likely due to water and nutrient constraints (Bronstein et al 2007). Some lineages of plants that disperse seeds through frugivory in mesic environments have adapted to xeric environments by producing dry fruits and attracting scatter-hoarding granivores to disperse their seeds instead (Hollander & Vander Wall 2009; Beck & Vander Wall 2010).

Trees and shrubs in the genus Juniperus produce female cones with fused scales that enclose their seeds. These female cones closely resemble fruit or berries and function as an
attractive reward for frugivores. Throughout the literature *Juniperus* is described as being dispersed by endozoochory, where frugivorous birds and mammals consume the female cones and pass the seeds through their guts intact. Juniper seeds have been found to pass through the guts of frugivorous birds and mammals not only intact and unharmed, but often with increased germination (Philips 1910; Johnsen 1962; Holthuijzen & Sharik 1985; Longland & Dimitri in press). Frugivory has been studied in multiple species of juniper including *J. virginiana* (Livingston 1972; Holthuijzen & Adkisson 1984; Holthuijzen & Sharik 1985; Holthuijzen et al. 1987; Horncastle & Hellgren 2004), *J. monosperma* (Johnsen 1962; Salomonson 1978), *J. occidentalis* (Poddar & Lederer 1982; Schupp et al. 1997b), *J. communis* (Garcia 2001), *J. ashei* (Chavez-Ramirez & Slack 1993, 1994), *J. cedrus* (Rumeu et al. 2009), and *J. osteosperma* (Schupp et al. 1997a). However, little attention has been paid to the potential role of scatter-hoarding in the dispersal of juniper seeds (but see Schupp et al. 1999). Horncastle and Hellgren (2004) observed removal of eastern red cedar cones from under the canopy, but they considered removal by rodents to be strictly seed predation. Chambers et al. (1999a) acknowledged that seed dispersal systems in juniper are likely more complex, and birds are probably not the primary dispersers for all juniper species.

The distributions of western (*J. occidentalis*) and Utah juniper (*J. osteosperma*) are largely contiguous, although they overlap in some locations (Adams 2011). Utah juniper is found in fairly xeric habitats throughout the Great Basin desert in Nevada, Utah, northern Arizona, southeastern Idaho, and western Colorado, where it often co-occurs with piñon pine. Western juniper occupies more mesic habitats in northeastern California, eastern Oregon, southeastern Oregon, western Idaho and the extreme northwestern corner of Nevada. Despite being closely related and readily hybridizing (Terry 2010; Adams 2011), the female cones, of western and
Utah juniper are very different. Production of mature cones in both species takes almost two years, maturing in their second fall. An individual tree can simultaneously have both ripe second year cones and unripe first year cones. Unripe western and Utah juniper cones are very similar, but after ripening the pulp of Utah juniper is leathery and fibrous, whereas the pulp of western juniper is soft and resinous. Utah juniper cones become so dry during periods without precipitation, that they must be cracked open like a hard shell to remove the seed inside, unlike the soft pulp of western juniper cones that can easily be crushed. Another area of differentiation between the two species is in the number of seeds contained in each cone with Utah juniper only having 1 or 2, while western juniper cones have anywhere from 1 to 5 seeds per cone (Bonner and Karrfalt 2008; Adams 2011).

In North America, both western and Utah juniper have been reported to be migrating northward, expanding in range and infilling during the Holocene (Miller & Wigand 1994; Weisburg et al 2007; but see Lanner 1977). Grazing, changing fire regimes and climate change (Burkhardt & Tisdale 1976; Miller & Rose 1999; Van Auken 2000; Weisburg et al 2008) have been cited as potential factors fueling this expansion. Land managers have spent millions of dollars to counteract this expansion. A better understanding of the ecology of these junipers, particularly factors which influence seedling recruitment such as seed dispersal, is vital to inform management decisions.

I sought to explore the differences in dispersal vectors and dispersal modes between Utah and western juniper by observing removal of seeds and cones of both species from under tree canopies. Dispersers at two sites were first offered local seeds and cones to determine background removal rates and record potential dispersers. Subsequently, removal of both local and non-local juniper seeds and cones was observed in order to understand if potential dispersers
show local adaptation or conditioning by recognizing differences between western and Utah
juniper seeds and cones, and if there are implications for different dispersal modes as a result. I
also examined the morphological and nutritional differences between the cones and seeds of
Utah and western juniper that might influence or attract potential dispersers.

**METHODS**

*Field sites*

I used two field sites for this study: Shinn Peak and the Pine Nut Mountains. Shinn Peak
is located in northeastern California in Lassen County (40°42′015″N, 120°17′399″W, elevation
1678 m). At this site western juniper is the only tree species. Understory shrubs consist of mainly
*Artemesia tridentata* ssp. and *Purshia tridentata* along with scattered *Ribes velutinum* and
*Ephedra viridis*. Native perennial bunchgrasses and introduced annual grasses (*Bromus tectorum,
*Taeniatherum caput-medusae*) dominate the herbaceous understory. The site consists of semi-
open juniper forest adjacent to a large burned area with scattered junipers that were able to
survive the fire in rock outcrops. The Pine Nut Mountains site is located in western Nevada, east
of Carson City (39°06′142″N, 119°38′211″W, elevation 1861m). At this site, Utah juniper is
distributed in a patchy fashion with *Pinus monophylla*. Understory shrubs include *Artemesia
tridentata, Purshia tridentata, Ephedra viridis, Ribes velutinum, Chrysothamnus nauseosus*, and
*Prunus andersonii*. Several species of native perennial bunchgrasses are common, but *B.
tectorum* is much less common than at Shinn Peak.

*Morphological and nutritional properties of seeds and cones*

Morphological and nutritional traits of western and Utah juniper seeds and cones were
examined to understand differences that might influence potential dispersers. For fresh cone and
husk mass, cones were collected from Shinn Peak on November 2, 2012 and from the Pine Nut
Mountains on November 6, 2012 and immediately placed in sealed bags and frozen until analysis. On February 2, 2013 cones were removed from the freezer and 25 of each species weighed. Seeds were then removed, and the fresh husks were weighed to obtain the percentage of husk per cone (fresh husk mass/whole cone mass). I compared husk mass between juniper species with a t-test (PROC TTEST, SAS 2012). Western and Utah juniper cones used for nutritional analysis were collected from multiple trees across both sites during fall 2014/winter 2015 and placed in a freezer. Mature cones free of insect damage were selected, husks were removed from seeds, and cones were again placed in the freezer before 50 g of each species was sent to Ward Laboratories, Inc. (Kearney, NE) in September 2015.

Seeds were cleaned from cones of the same collection described above by hand and floated in a saline solution to remove empty or insect damaged seeds. After randomly selecting 25 seeds of each species, fresh mass, length and diameter at the widest point were measured. Seeds were then cracked open to ensure only filled seeds were used, dried in an oven (40°C for 48 h), and reweighed. The seed was then removed from the seed coat and seed coats were reweighed to obtain seed (embryo) size by subtraction. Seed size and mass were compared between juniper species with a t-test (PROC TTEST, SAS 2012).

Experiment 1

My aim in this study was to determine the rate of removal for seeds and cones at both sites and to identify which frugivores and/or granivores took them. I collected mature Utah and western juniper cones and placed them in the freezer. Seeds were cleaned by hand and floated in a saline solution to isolate and remove empty seeds that floated. Seeds were then thoroughly rinsed in water and dried at room temperature. Cones were examined for insect damage and maturity to ensure that ripe, healthy cones were selected for the experiment.
I placed 100 cones and 100 hand-cleaned seeds in petri dishes under juniper canopies at 10 stations. Stations were arranged in two parallel transects of 5 with ≥ 50 meters separating consecutive stations, and each station had a trail camera placed above the dishes to observe and record animals removing seeds and/or cones. At Shinn Peak, removal was monitored from January 19 – February 5, 2015, and at the Pine Nut Mountains from February 2 – 19, 2015. Seeds and cones were counted each day for the first 4 days, then again on days 7, 10 and 17. I assessed the differences in removal of seeds and cones at my sites using survival analysis (PROC LIFETEST, SAS 2012) and compared the survivor functions of two strata, seeds and cones, using the life-table method and the Wilcoxon test (Allison 1995). When seeds or cones were removed from one sampling day to the next, they were coded as failures and any seeds or cones left at the end of a trial were right censored (Allison 1995).

Experiment 2

To examine if potential dispersers recognize the differences between the cones and seeds of western and Utah juniper, I randomly selected 100 hand-cleaned seeds of both western and Utah juniper, and 100 cones of both species that had been collected and cleaned as previously described. These four types were placed in 8 x 8 cm wooden frames with partitions to separate all seed/cone treatments. The same 10 stations from the first experiment were used with trail cameras recording video to monitor removal. Starting on March 16, 2015 at Shinn Peak and March 31 at the Pine Nut Mountains, seeds and cones were counted each day for the first 4 days and then at days 7, 10 and 17. This experiment was repeated again beginning on October 13, 2015 at Shinn Peak and October 20, 2015 in the Pine Nut Mountains, and checked every day for the first 4 days, and on days 8, 10 and 17. Survival analysis was again used to compare removal
using survival functions; however, four strata were compared (western juniper seeds, western juniper cones, Utah juniper seeds, Utah juniper cones) instead of two as in experiment 1.

**Small mammal trapping**

I surveyed small mammals during the fall of 2015 at both sites in order to have an understanding of potential rodent dispersers. At both sites I set 80 folding Sherman live traps (Sherman Traps, Inc., Tallahassee, Florida) baited with mixed bird seed consisting of millet and black oil sunflower seeds. Traps were set in a 20 x 4 grid with adjacent stations 15 m apart for 3 consecutive days and nights. Animals were identified to species, sexed, weighed and given a numbered ear tag before release. The capture and handling of animals followed protocols approved by the Animal Care and Use Committee of the University of Nevada, Reno (protocol #00026). Trapping grids at both sites were near, but not overlapping, seed/cone removal transects.

**RESULTS**

**Morphological and nutritional properties of seeds and cones**

Fresh cone characteristics are summarized in Table 1. Whole fresh cone mass of Utah juniper and western juniper differed significantly ($t = 6.63$, $df = 48$, $P < 0.0001$) with western juniper cones having a larger mass than Utah juniper cones. The percentage of the whole cone accounted for by the husk differed between the two species ($t = 2.99$, $df = 48$, $P = 0.0044$), and fresh husks of western juniper cones accounted for a larger percentage of the whole cone than Utah juniper cones.

A summary of the cone nutritional analysis is given in Table 2. Western and Utah juniper husks had a similar percentage of protein and fat, yet western juniper cones contained more moisture and total digestible nutrients (TDN), a measurement that combines carbohydrates,
protein, fat and digestible fiber. Utah juniper cones had more starch and acid detergent fiber (ADF) which decreases the digestibility of a food.

Seed morphological characteristics are summarized in Table 3. Utah juniper seeds were significantly longer \((t = 11.33, df = 48, P < 0.0001)\) and wider \((t = 13.27, df = 48, P < 0.0001)\) than those of western juniper. Whole Utah juniper seeds had more mass \((t = 14.33, df = 48, P < 0.0001)\) as did the seed coats \((t = 14.2, df = 48, P < 0.0001)\) and edible portions of the seeds \((t = 3.81, df = 48, P = 0.0004)\).

**Experiment 1**

*Frequency of removal of local seeds and cones*

There was more removal for both Utah juniper cones and seeds at the Pine Nut Mountains than for western juniper cones and seeds at Shinn Peak (Figure 1). At the Pine Nut Mountains 96.8% of cones were removed and 90.6% of seeds, while at Shinn peak, 66.6% of cones and 50.3% of seeds were removed. These values also yielded significant differences in removal rate of cones versus seeds, with cones being removed at greater rates at both sites (Pine Nut Mountains: \(x^2 = 5.98, df = 1, P = 0.015\); Shinn Peak: \(x^2 = 8.77, df = 1, P = 0.003\)).

*Potential dispersers removing seeds and cones*

Trail camera video revealed that piñon mice, *Peromyscus truei*, were responsible for removing seeds and cones at the most stations at both sites (Table 4). At the Pine Nut Mountains, piñon mice removed Utah juniper cones and seeds from 9 of 10 stations. At Shinn Peak, piñon mice were recorded removing western juniper cones and seeds from 5 of 10 stations. Other species recorded at the Pine Nut Mountains included Panamint kangaroo rats (*Dipodomys panamintinus*), desert cottontails (*Sylvilagus audubonii*), and a juniper titmouse (*Baeolophus ridgwayi*). Removal of cones by desert cottontails did not always result in dispersal, as they often
consumed the cone husk leaving behind the seeds (Figure 4a). At Shinn Peak, additional species recorded removing western juniper cones included a Townsend’s solitaire (*Myadestes townsendi*) and a gray fox (*Urocyon cinereoargentus*).

**Experiment 2**

**Frequency of removal of local and non-local seeds and cones**

In spring 2015, removal rates of seeds and cones of both western and Utah juniper varied significantly among the four types at Shinn Peak ($\chi^2 = 1912.07$, $df = 3$, $P < 0.0001$) (Figure 2). Local cones (western juniper) were almost completely removed and non-local cones (Utah juniper) had much less removal overall, but total removal of seeds was almost identical (Table 5). Despite removal being equal for both seed types by the end of the 17 day trial, removal rate of local and non-local seeds differed significantly ($\chi^2 = 33.14$, $df = 1$, $P < 0.0001$). The local western juniper seeds were removed more rapidly prior to day 10 (Figure 2). Cone removal also varied between local and non-local types ($\chi^2 = 1210.20$, $df = 1$, $P < 0.0001$) with local western juniper cones having higher removal (Table 5).

At the Pine Nut Mountains site, the local seed type was removed more in spring rapidly than non-local seeds ($\chi^2 = 15.50$, $df = 1$, $P < 0.0001$), and the percentage of local Utah juniper seeds left was actually lower (Table 5) than that of non-local western juniper seeds at the end of the 17 day trial (Figure 2). Removal of local and non-local cones also differed significantly ($\chi^2 = 643.84$, $df = 1$, $P < 0.0001$) with more local Utah juniper cones being removed than non-local western juniper cones.

In fall 2015, removal again differed significantly among the four seed and cone types at Shinn Peak ($\chi^2 = 1773.96$, $df = 3$, $P < 0.0001$). Seeds had higher removal rates than cones (Figure 3) with local western juniper seeds having the most seeds removed followed by non-local Utah
juniper seeds (Table 5). Removal varied between local and non-local seeds ($\chi^2 = 3.98, df = 1, P = 0.046$), as local western juniper seeds were removed more rapidly throughout most of the trial (Figure 3). Removal also differed significantly between local and non-local cones ($\chi^2 = 48.46, df = 1, P < 0.0001$) with non-local Utah juniper cones having higher removal than local western juniper cones (Table 5).

At my Pine Nut Mountains site in the fall, removal of the four types differed significantly ($\chi^2 = 270.90, df = 3, P < 0.0001$). Removal of the two seed types differed ($\chi^2 = 88.35, df = 1, P < 0.0001$) with non-local western juniper seeds having higher overall removal than local Utah juniper seeds (Table 5), but Utah juniper seeds were removed more rapidly until day 10. Cone removal rates were significantly different between the two types ($\chi^2 = 191.54, df = 1, P < 0.0001$), as local Utah juniper cones were removed more quickly but fewer western juniper cones were left after 17 days (Table 5).

Potential dispersers removing 4 seed and cone types

Trail cameras captured videos of various animal species removing four seed/cone types from all ten stations at both sites during spring and fall of 2015 (Table 6). Videos revealed that piñon mice removed local and non-local seeds and cones from the most stations for spring and fall combined at both Shinn Peak and the Pine Nut Mountains.

At Shinn Peak, piñon mice were recorded in spring removing at least one of the four seed/cone types at every station, and at 9 out of 10 stations during fall. California kangaroo rats (Dipodomys californicus) were recorded at Shinn Peak removing seeds at 4 stations in spring and 7 in fall. California kangaroo rats were also recorded removing non-local Utah juniper cones at 2 stations, although one of these cases did not represent true cone removal since the individual only removed seeds and left the husks (fruit) behind (Figure 4b). Local western juniper cones
were never taken by California kangaroo rats. Desert cottontails were only recorded in the fall, when they removed local and non-local cones. Dusky-footed woodrats (*Neotoma fuscipes*) were recorded removing both local and non-local cones in the spring and fall at Shinn Peak. They removed both local and non-local seeds from 1 station in the fall but were not recorded removing seeds in the spring. At one station in the fall, a desert woodrat (*Neotoma lepida*) removed all 4 types at Shinn Peak. In the spring, yellow-pine chipmunks (*Tamias amoenus*) removed local western juniper seeds, and in the fall they were recorded eating the husk of local cones and removing local seeds. Juniper titmice removed both local and non-local seeds from 1 station in the spring at Shinn Peak, and non-local Utah juniper seeds in the fall. In the spring, Townsend’s solitaires were recorded removing local western juniper cones only.

Piñon mice were also the most frequently recorded species at my Pine Nut Mountains site (Table 6). In the fall, piñon mice removed both local and non-local seeds from all 10 stations and also removed both cone types. Desert cottontails removed mostly cones of both types but were also recorded consuming seeds. Black-tailed jackrabbits (*Lepus californicus*) were recorded consuming local Utah juniper cones and non-local western juniper cones in spring and fall, but were only recorded eating local seeds in the spring. White-tailed antelope squirrels (*Ammospermophilus leucurus*) were only recorded in the spring removing local cones and non-local cones. Seeds had already been removed from the stations they visited, so it is unknown if they take juniper seeds. Another species only recorded in the spring was the California ground squirrel (*Otospermophilus beecheyi*) which removed local and non-local cones.

*Small mammal trapping*

Before fall seed and cone removal trials, small mammals were trapped in order to identify scatter-hoarding rodent species that could act as potential dispersers of juniper seeds (Table 7).
At the Pine Nut Mountains, I captured a total of 25 individuals of six different rodent species known to scatter-hoard seeds of other plants. Deer mice (*Peromyscus maniculatus*) accounted for the greatest number of individuals followed by piñon mice and Panamint kangaroo rats. White-tailed antelope squirrels, Great Basin pocket mice (*Perognathus parvus*), and least chipmunks (*Tamias minimus*) were also captured. At Shinn Peak, I trapped 54 individual rodents of 7 species. Deer mice were again the most common followed by California kangaroo rats, piñon mice, yellow-pine chipmunks, golden-mantled ground squirrels (*Spermophilus lateralis*), Great Basin pocket mice and western harvest mice (*Reithrodontomys megalotis*).

**DISCUSSION**

Granivorous rodents were responsible for more removal overall than frugivores and herbivorous lagomorphs in my experiments. Even in my first experiment where cones were removed more rapidly than seeds, piñon mice removed more cones than frugivores at both sites. In experiment 2, which looked at removal of local and non-local western and Utah juniper seeds and cones, piñon mice removed both seeds and cones from the most stations at both sites (Tables 4 & 6). In all but the fall trial at the Pine Nut Mountains, piñon mice again removed more cones than frugivores. In the Pine Nut Mountains, Panamint kangaroo rats removed both seeds and cones in experiment 1 and in the spring trial of experiment 2. During the fall trial they removed only seeds from 3 stations. California kangaroo rats at Shinn Peak were not recorded in experiment 1, but were recorded removing local and non-local seeds in the spring and fall and non-local cones in the fall (but see Figure 4b).

The rapid removal of seeds by scatter-hoarding rodents across stations at both sites (Figures 2 & 3) illustrates that western and Utah juniper dispersal is likely more complex than previously thought, including rodents as well as frugivores. Piñon mice are known scatter-
hoarders that are effective dispersers of piñon pine seeds and have been found to make many caches with few seeds (Hollander & Vander Wall 2004). I have also found that they disperse and cache both western and Utah juniper seeds (see Chapter 1). Deer mice are known scatter-hoarders (Vander Wall et al. 2001) that were trapped at both sites, and although they were not recorded removing seeds during this study, they have been recorded removing (Longland & Dimitri in press) and caching western juniper seeds (Chapter 1). Other scatter-hoarders recorded removing seeds and cones included white-tailed antelope squirrels in the Pine Nut Mountains and yellow-pine chipmunks at Shinn Peak. White-tailed antelope squirrels have been found to be effective dispersers of several plants (Hollander & Vander Wall 2004; Beck et al. 2010; Waitman et al. 2012) and could play an important role in the dispersal of Utah juniper seeds. Yellow-pine chipmunks are important dispersal agents of shrubs and trees (Vander Wall 1992; Vander Wall 1994; Vander Wall 2003; Roth & Vander Wall 2005) and could potentially disperse western juniper seeds. Panamint kangaroo rats removed Utah and western juniper seeds and Utah juniper cones in both experiments in the Pine Nut Mountains. Previous studies have shown that although they larder-hoard many seeds, they also scatter-hoard seeds as well (Hollander & Vander Wall 2004; Beck & Vander Wall 2010). At Shinn Peak, California kangaroo rats removed local and non-local seeds. There are no published studies looking at the caching behavior of this species, but I have observed some caching of western juniper seeds (Chapter 1).

Utah juniper seeds were significantly larger and heavier than western juniper seeds containing more edible seed. Increasing seed size is potentially a sign of coadaptation between plants and scatter-hoarding rodents (Vander Wall 2001; Vander Wall 2003; Vander Wall 2010). Jansen et al. (2002) found that larger seeds were more likely to be cached and dispersed farther than smaller seeds of the same species. The seed coats of Utah juniper had more mass than those
of western juniper and were very difficult to open during seed extraction (Personal observation). Vander Wall (2010) suggests that a hard seed coat, which increases handling costs, is an adaptation by plants that can increase the scatter-hoarding behavior of rodents.

While differences between western and Utah juniper seeds did not seem to deter granivores, the differences in cones did. In the Pine Nut Mountains, Panamint kangaroo rats removed Utah juniper cones and seeds in both spring trials but never removed non-local western juniper cones in the spring trial of experiment 2 (Table 2 & 3). Conversely, at Shinn Peak California kangaroo rats never removed local western juniper cones in all three of my trials. However, in the fall trial at one station, an individual husked all 100 non-local Utah juniper cones removing the seeds and leaving the husk behind (Figure 4b). This could indicate that Utah juniper cones with their dry husks that can easily be peeled or cracked off are more attractive to granivorous rodents, who are not interested in consuming the husks. The resinous western juniper cones might be less attractive for such rodents, as it is difficult to cleanly remove the seeds without releasing sticky resin. Endozoochory by frugivorous birds could make seeds more available to rodents by consuming the resinous husk and passing intact seeds in feces.

I recorded more frugivory for western juniper cones than Utah juniper cones in my experiments. Townsends’s solitaires and a gray fox consumed whole western juniper cones at Shinn Peak and dispersed them away from the trays as did herbivorous desert cottontails. Conversely, in the Pine Nut Mountains, there was no removal of cones by frugivorous birds or mammals. Herbivorous lagomorphs were recorded consuming Utah juniper cones but often left the seeds behind (Figure 4); however, they consumed western juniper cones whole in most cases. In the fall trial of experiment 2 at Shinn Peak, non-local Utah juniper cones were removed more rapidly than local western juniper. However, this was due to removal by scatter-hoarding rodents.
not frugivores. The slow removal of western juniper cones was likely in part due to a large cone crop at the Shinn Peak site where birds were regularly observed removing cones directly from tree canopies. Utah juniper cone production in the Pine Nut Mountains was lower and much more inconsistent with fewer scattered trees producing cones (Personal observation).

Nutritional analyses revealed that the husks of western juniper and Utah juniper cones had similar fat and crude protein content. Western juniper husks had a higher percentage of moisture and more total digestible nutrients (TDN), while Utah juniper husks had more starch and acid detergent fiber (ADF) which reduces digestibility. The lack of moisture and digestible nutrients and high fiber in Utah juniper husks could explain the apparent lack of documented frugivory of Utah juniper cones in the literature and during my study, where only herbivorous lagomorphs and rodents removed Utah juniper cones.

Although frugivores can be effective dispersers by moving many seeds away from the parent plant often over longer distances than scatter-hoarders, dispersal through endozoochory can result in the aggregation of seeds due to disperser behavior (Vander Wall & Beck 2012). Previous studies of juniper dispersal by frugivorous birds and carnivores have described the large accumulation of seeds at commonly used perching sites and along trails used by mammals (Chavez-Ramirez & Slack 1993; Chavez-Ramirez & Slack 1994; Garcia 2001). Lagomorphs such as, black-tailed jackrabbits and desert cottontails, have been reported dispersing Utah (Schupp et al. 1999) and western juniper seeds (Schupp et al. 1997) through endozoochory, but they do not appear to be effective dispersers (Schupp et al. 1997; Schupp et al. 2010).

Dispersal of many juniper species by endozoochory is well documented in the literature, and this is likely the ancestral mode of dispersal. However, as Chambers et al. (1999) suggested, juniper dispersal by frugivores might only represent one end of a spectrum where species with
more fleshy husks, such as western juniper, are largely dispersed by birds, and those with more fibrous husks are dispersed by scatter-hoarding rodents. Beck & Vander Wall (2010) hypothesize that desert peach (*Prunus andersonii*) has adapted to more xeric environments by relying on scatter-hoarding rodents to disperse seeds, producing drier fruits that require less water than those of its fleshy-fruited ancestors. This could be a potential explanation for the dry cones produced by Utah juniper which inhabits more xeric environments compared to western juniper.

Some plants are able to take advantage of both frugivores and scatter-hoarders in a two-phased dispersal system, or diplochory (Vander Wall & Longland 2004; Vander Wall et al. 2005; Enders & Vander Wall 2012; Beck & Vander Wall 2012). Longland and Dimitri (in press) found that scatter-hoarding rodents removed western juniper seeds that had been collected and cleaned from bird feces. Rodents have also been recorded removing Ashe juniper seeds from carnivore scat (Chavez-Ramirez & Slack 1993), and deer mice have been shown to cache seeds after removing them from bear feces (Enders & Vander Wall 2012). Diplochory could be an important dispersal system for juniper species with fleshy cones, with scatter-hoarding rodents moving seeds away from aggregations left by frugivores under perches or along trails to more suitable microsites and burying them in superficial caches. Seed dispersal of *Juniperus* with dry cones, such as Utah juniper, are more likely accomplished only by scatter-hoarding rodents that are able to easily remove seeds from the leathery husks.

Removal of seeds and cones could not always be described as a choice among all 4 types throughout each trial in my experiments, as often times one animal removed all of one or two types before other potential dispersers discovered the station. For example, at many stations kangaroo rats removed all seeds in the first night. In the Pine Nut Mountains, white-tailed antelope squirrels removed cones of both types, but seeds had already been removed from the
stations. White-tailed antelope squirrels could be potential dispersers of Utah juniper seeds, as they have been found to be important dispersers of *Prunus andersonii* (Beck et al. 2010) which is found in low abundance at my site.

Rates of removal and the species removing seeds are likely underestimated in my study. Rodents, especially mice, often seemed very nervous and flighty around stations which could have been due to the presence of human scent, despite efforts to reduce it, or the presence of trail cameras. Despite my cameras having blackout flashes that are not supposed to disturb animals during video recording, many animals looked at the cameras and sometimes seemed to run off when videos started recording possibly deterring them from removing more seeds or cones. Scatter-hoarding species such as Great Basin pocket mice, white-tailed antelope squirrels, least chipmunks and yellow-pine chipmunks that were trapped at my sites (Table 5) but rarely or never seen during my experiments could be potential dispersal agents of juniper that were just missed in my experiments.

My research suggests that the dispersal of juniper seeds is not restricted to frugivory but can include additional pathways, specifically dispersal by scatter-hoarding rodents. I hypothesize that junipers with juicy resinous cones such as western juniper are likely dispersed directly by frugivores or by scatter hoarding rodents that remove seeds from cones and also through diplochory, where scatter hoarding rodents secondarily disperse seeds that have passed through the gut of a frugivore (Vander Wall and Longland 2004; Vander Wall et al 2005; Beck & Vander Wall 2011; Enders and Vander Wall 2012). Junipers with drier more fibrous fruit such as Utah juniper probably rely more on scatter-hoarding rodents to disperse seeds. This change in dispersal system has been documented in other lineages of plants (Hollander & Vander Wall
2009; Beck & Vander Wall 2010) and could be an adaptation by juniper to more xeric environments (Bronstein et al 2007).

My study only provides a small snapshot of processes that are occurring over much larger spatial and temporal scales. Across the ranges of western and Utah junipers, seed dispersal mutualisms likely vary as additional scatter hoarding species that are not found at my sites could be important in other parts of the range of these trees. Also, cone production by junipers is highly variable temporally providing an important resource in one year and being almost absent the next. Western and Utah juniper seem to provide an important food resource for a variety of species and this should be considered in future management decisions.
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Table 1. Means (± SD) of whole fresh cone morphometrics for western (N=25) and Utah juniper including whole cone mass (cones + seeds), husk mass (cones – seeds), and the percentage of whole cones that is husk (husk mass/whole cone mass) are given for cones collected at Shinn Peak on Nov. 2, 2012 and at the Pine Nut Mountains on Nov. 6, 2012. Cones were kept in a cooler and immediately placed in the freezer after returning from the field to reduce any water loss that might occur.

<table>
<thead>
<tr>
<th>Species</th>
<th>Whole Cone (mg)</th>
<th>Wet Husk (mg)</th>
<th>Husk/Cone %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western juniper</td>
<td>803.1 ± 82.32</td>
<td>650.96 ± 72.19</td>
<td>81 ± 2.1</td>
</tr>
<tr>
<td>Utah juniper</td>
<td>658.6 ± 71.38</td>
<td>517.68 ± 58.24</td>
<td>78 ± 3.4</td>
</tr>
</tbody>
</table>
Table 2. Summary of nutritional analysis for western and Utah juniper husks (50.0g/species) done by Ward Laboratories, Inc (Kearney, NE). The percentages are based on dry material for all but moisture.

<table>
<thead>
<tr>
<th>Site</th>
<th>Moisture %</th>
<th>Crude Protein %</th>
<th>Fat %</th>
<th>Starch %</th>
<th>Acid Detergent Fiber %</th>
<th>Total Digestible Nutrients %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western juniper</td>
<td>37.68</td>
<td>3.1</td>
<td>7.4</td>
<td>4.0</td>
<td>19.7</td>
<td>63.1</td>
</tr>
<tr>
<td>Utah juniper</td>
<td>12.58</td>
<td>3.2</td>
<td>8</td>
<td>5.1</td>
<td>40.2</td>
<td>55.9</td>
</tr>
</tbody>
</table>
Table 3. Summary of dry seed morphometrics for western and Utah juniper (N=25). Seeds were measured, cracked open to confirm that they were full and then oven dried (40°C, 48 h). The mean (± SD) length and diameter were measured before drying. The whole seed mass (mean ± SD) was measured after drying, then seeds were removed and seed coats were weighed. Seed weight was obtained through subtraction (whole seed – seed coat), as it was difficult to remove the edible portion of the seed intact once they had been dried.

<table>
<thead>
<tr>
<th>Species</th>
<th>Length (mm)</th>
<th>Diameter (mm)</th>
<th>Whole Seed (mg)</th>
<th>Seed Coat (mg)</th>
<th>Seed (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western juniper</td>
<td>5.49 ± 0.58</td>
<td>4.06 ± 0.45</td>
<td>35.92 ± 9.87</td>
<td>35.92 ± 9.87</td>
<td>6.56 ± 1.87</td>
</tr>
<tr>
<td>Utah juniper</td>
<td>7.20 ± 0.48</td>
<td>5.87 ± 0.52</td>
<td>121.2 ± 28.05</td>
<td>121.2 ± 28.05</td>
<td>10.36 ± 4.63</td>
</tr>
</tbody>
</table>
Table 4. Summary of potential dispersers observed in Experiment 1 using trail camera videos. The total number of stations a species was recorded by trail cameras removing seeds (N=10) and/or cones (N=10) are given for the Pine Nut Mountains and Shinn Peak.

<table>
<thead>
<tr>
<th>Pine Nut Mountains</th>
<th>Species</th>
<th>Cones</th>
<th>Seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Piñon Mouse</td>
<td>9</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Panamint kangaroo rat</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Desert cottontail</td>
<td>3</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Juniper titmouse</td>
<td>0</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Shinn Peak</th>
<th>Species</th>
<th>Cones</th>
<th>Seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Piñon Mouse</td>
<td>5</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Townsend's solitaire</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Gray fox</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>
Table 5. Summary of overall removal at Shinn Peak and the Pine Nut Mountains for experiment 2. Removal of 100 seeds and cones of each species (4 types) was monitored over 17 days in the spring and fall of 2015 at 10 stations. Values given are the percentage of seeds out of 1000 left on day 17.

<table>
<thead>
<tr>
<th>Season</th>
<th>Type</th>
<th>Shinn Peak (Western juniper)</th>
<th>Pine Nut Mts (Utah juniper)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>Western juniper seeds</td>
<td>99.8</td>
<td>97.1</td>
</tr>
<tr>
<td></td>
<td>Western juniper berries</td>
<td>92.5</td>
<td>18.6</td>
</tr>
<tr>
<td></td>
<td>Utah juniper seeds</td>
<td>99.9</td>
<td>91</td>
</tr>
<tr>
<td></td>
<td>Utah juniper berries</td>
<td>34</td>
<td>75.1</td>
</tr>
<tr>
<td>Fall</td>
<td>Western juniper seeds</td>
<td>92.2</td>
<td>99.7</td>
</tr>
<tr>
<td></td>
<td>Western juniper berries</td>
<td>43.7</td>
<td>99.2</td>
</tr>
<tr>
<td></td>
<td>Utah juniper seeds</td>
<td>90</td>
<td>97.7</td>
</tr>
<tr>
<td></td>
<td>Utah juniper berries</td>
<td>74.2</td>
<td>96.1</td>
</tr>
</tbody>
</table>
Table 6. A summary of species recorded on trail camera videos removing local and non-local cones and seeds from 10 stations at the Pine Nut Mountains and Shinn Peak. Local seeds and cones are shaded in gray for both sites. The total number of stations out of 10 a species is recorded by trail cameras removing each of the 4 types is listed for spring and fall trials.

<table>
<thead>
<tr>
<th>Species</th>
<th>Pine Nut Mts</th>
<th>Spring</th>
<th></th>
<th>Fall</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Cones</td>
<td>Seeds</td>
<td>Cones</td>
<td>Seeds</td>
<td>Cones</td>
<td>Seeds</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Juos</td>
<td>Juoc</td>
<td>Juos</td>
<td>Juoc</td>
<td>Juos</td>
<td>Juoc</td>
<td></td>
</tr>
<tr>
<td>Panamint kangaroo rat</td>
<td></td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Piñon mouse</td>
<td></td>
<td>8</td>
<td>5</td>
<td>7</td>
<td>7</td>
<td>3</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>Desert cottontail</td>
<td></td>
<td>5</td>
<td>7</td>
<td>1</td>
<td>2</td>
<td>9</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>Black-tailed jackrabbit</td>
<td></td>
<td>8</td>
<td>4</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>White-tailed antelope squirrel</td>
<td></td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>California ground squirrel</td>
<td></td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species</th>
<th>Shinn Peak</th>
<th>Spring</th>
<th></th>
<th>Fall</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Cones</td>
<td>Seeds</td>
<td>Cones</td>
<td>Seeds</td>
<td>Cones</td>
<td>Seeds</td>
<td></td>
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<td>Juos</td>
<td>Juoc</td>
<td>Juos</td>
<td>Juoc</td>
<td>Juos</td>
<td>Juoc</td>
<td></td>
</tr>
<tr>
<td>California kangaroo rat</td>
<td></td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td>2</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Piñon mouse</td>
<td></td>
<td>9</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>4</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Desert cottontail</td>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Dusky-footed woodrat</td>
<td></td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Desert woodrat</td>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Yellow-pine chipmunk</td>
<td></td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Juniper titmouse</td>
<td></td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Townsend's solitaire</td>
<td></td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 7. Summary of fall 2015 small mammal trapping which occurred over three nights and three days using commercial bird seed. Trapping at the Pine Nut Mountains site began on October 6, 2015 and ended on October 8, 2015. At Shinn Peak, trapping began on October 21 and ended on October 23, 2015. Trapping grids consisted of 4 rows of 80 live Sherman traps placed 15 m apart.

<table>
<thead>
<tr>
<th>Pine Nut Mtns</th>
<th>Shinn Peak</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>No. Individuals</td>
</tr>
<tr>
<td>White-tailed antelope squirrel</td>
<td>3</td>
</tr>
<tr>
<td>Panamint kangaroo rat</td>
<td>5</td>
</tr>
<tr>
<td>Deer mouse</td>
<td>8</td>
</tr>
<tr>
<td>Piñon mouse</td>
<td>5</td>
</tr>
<tr>
<td>Great Basin pocket mouse</td>
<td>2</td>
</tr>
<tr>
<td>Least chipmunk</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>total</strong></td>
<td><strong>25</strong></td>
</tr>
</tbody>
</table>
Figure 1. Survival curves for Utah juniper cones and seeds at the Pine Nut Mountains and western juniper cones and seeds at Shinn Peak for experiment 1. Low survival indicates high rates of removal.
Figure 2. Survival curves for Shinn Peak and the Pine Nut Mountains for the spring trial of experiment 2.
Figure 3. Survival curves for Shinn Peak and the Pine Nut Mountains for the fall trial of experiment 2.