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Original article

Effects of rodent species, seed species, and predator cues on seed fate

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ABSTRACT

Seed selection, removal and subsequent management by granivorous animals is thought to be a complex interaction of factors including qualities of the seeds themselves (e.g., seed size, nutritional quality) and features of the local habitat (e.g. perceived predator risk). At the same time, differential seed selection and dispersal is thought to have profound effects on seed fate and potentially vegetation dynamics. In a feeding arena, we tested whether rodent species, seed species, and indirect and direct predation cues influence seed selection and handling behaviors (e.g., scatter hoarding versus larder hoarding) of two heteromyid rodents, Ord's kangaroo rat (*Dipodomys ordii*) and the Great Basin pocket mouse (*Perognathus parvus*). The indirect cue was shrub cover, a feature of the environment. Direct cues, presented individually, were (1) control, (2) coyote (*Canis latrans*) vocalization, (3) coyote scent, (4) red fox (*Vulpes vulpes*) scent, or (5) short-eared owl (*Asio flammeus*) vocalization. We offered seeds of three sizes: two native grasses, Indian ricegrass (*Achnatherum hymenoides*) and bluebunch wheatgrass (*Pseudoroegneria spicata*), and the non-native cereal rye (*Secale cereale*), each in separate trays. Kangaroo rats preferentially harvested Indian ricegrass while pocket mice predominately harvested Indian ricegrass and cereal rye. Pocket mice were more likely to scatter hoard preferred seeds, whereas kangaroo rats mostly consumed and/or larder hoarded preferred seeds. No predator cue significantly affected seed preferences. However, both species altered seed handling behavior in response to direct predation cues by leaving more seeds available in the seed pool, though they responded to different predator cues. If these results translate to natural dynamics on the landscape, the two rodents are expected to have different impacts on seed survival and plant recruitment via their different seed selection and seed handling behaviors.

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1. Introduction

North American deserts are home to a diverse group of granivores that play a significant role in vegetation establishment via seed predation and dispersal (Kelt et al., 1996; Price and Jenkins, 1986). In the Great Basin, rodents from the family Heteromyidae, such as kangaroo rats (*Dipodomys* spp.) and pocket mice (*Perognathus* spp.), are among the dominant genera (Brown et al., 1979). Both kangaroo rats and pocket mice are known to harvest large quantities of seeds (Vander Wall et al., 1998), which may be placed in surface caches across their home ranges (scatter hoarding) or within larders inside their burrows (larder hoarding) (Vander Wall, 1990). Because these processes can influence recruitment and survival of plants (Reichman, 1979; Inouye et al., 1980; Schupp and Fuentes, 1995), knowledge of how seed selection and handling by

granivores are shaped by characteristics such as seed type as well as factors such as predation risk is important for understanding patterns of seed fate in the Great Basin.

Predation risk is thought to be a key influence on when and where rodents forage, resulting in spatial partitioning of foraging habitat by co-occurring species (Kotler, 1984; Brown et al., 1988). Pocket mice mostly use understory microhabitat where protective cover is available, thus reducing the probability of predation (Longland and Price, 1991), whereas kangaroo rats frequently venture into open microhabitat to forage (Brown et al., 1986). To assess predation risk, rodents may rely on "predator cues." Indirect predator cues are conveyed by the environment and interfere with the visibility or accessibility of the prey, such as lunar phase or shrub-covered versus open microhabitat. Direct predator cues originate from a predator's presence, and include vocalizations, visual, and olfactory signs (e.g., scat, urine).

Indirect and direct predator cues are both documented to alter heteromyid feeding behavior and habitat use. For example, the presence of avian and reptilian predators has reduced harvesting time by rodents and shifted their microhabitat use from open to

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shrub-covered areas in both lab and field settings (Brown et al., 1988; Bouskila, 1995). Similarly, mammalian predator scent reduced foraging activity of kangaroo rats, demonstrating their use of olfaction to assess predation risk (Herman and Valone, 2000). Interestingly, indirect cues may exert a greater influence on rodent behavior than direct cues (Jonsson et al., 2000; Orrock et al., 2004), suggesting that seed selection by rodents is subject to the presence, duration, and type of perceived predator risk (Lima and Bednekoff, 1999; Sundell et al., 2004). Indeed, in micro-habitats devoid of protective cover, rodents have demonstrated increased selection of preferred seeds over less preferred seeds (Hay and Fuller, 1981; Bowers, 1988; Leaver and Daly, 2003).

While it is well established that risk of predation affects rodent microhabitat use, foraging duration, and seed selection, the degree to which perceived predation risk influences seed handling behaviors that contribute to seed fate is not well known (Brown et al., 1986). Nonetheless, it is reasonable to assume that predator cues could affect post-harvest seed fate as rodent species respond to varying levels of risk. Besides potentially altering the types or proportion of seed consumed versus cached, predator cues might also alter the proportion of cached seeds that are scatter hoarded versus larder hoarded. Because scatter hoarded seeds are more likely to survive and emerge as seedlings than are seeds placed in the larder (discussed in Vander Wall, 1990), a shift in caching behavior should have consequences for plant establishment in natural settings.

In addition, it is important to consider differences among both rodent species and seed species in the fate of encountered seeds. While it is generally acknowledged that kangaroo rats and pocket mice differ in the proportion of seeds scatter hoarded versus larder hoarded (Jenkins and Breck, 1998; Price et al., 2000), the extent to which seed fate varies among seed species is uncertain. For example, highly-preferred (i.e., larger, more nutritious, etc.) seeds might be handled differently (e.g., scatter hoarded, consumed, etc.) than less preferred seeds (i.e., smaller, less nutritious, etc.). Lastly, because of differences in preference, and presumably desirability, seed species may differ in how their fate is affected by predator cues.

We used a feeding arena study to evaluate the simultaneous effects of indirect and direct cues on seed preference and seed fate by two heteromyid species foraging on three seed species. Based in part on previously published studies, we predicted: (1) Seed preference will be similar for both rodent species, with larger seeds removed in greater quantities compared to smaller seeds (Price, 1983). (2) Predator cues will increase the selection of preferred seeds over less preferred seeds (Hay and Fuller, 1981; Leaver and Daly, 2003). (3) Both rodent species will respond to treatments by (a) removing less seed under the influence of direct cues compared to the amount removed in control and (b) removing less seed under the influence of the indirect cues of open versus shrub portion of the arena (Orrock et al., 2004; Sundell et al., 2004). We further predict that (4) seeds removed in the absence of direct predator cues would be preferentially scatter hoarded or consumed whereas seeds removed when direct predator cues were present would be larder hoarded or neglected.

2. Methods

2.1. Animals

We used the two most common seed harvesting rodent species in the eastern Great Basin desert (Ostoja and Schupp, 2009), Ord's kangaroo rat (*Dipodomys ordii* Woodhouse) and the Great Basin pocket mouse (*Perognathus parvus* Peale). These species are thought to demonstrate spatial partitioning of microhabitat; large-bodied,

bipedal kangaroo rats travel in open patches between shrubs whereas the smaller pocket mice use regions under and adjacent to shrub canopies (Brown et al., 1986).

Our study took place from 19 June to 11 August 2006, when both rodent species are highly active (Ostoja and Schupp, 2009). Sherman live traps were used to capture individual rodents as needed at pre-established trapping grids located near Vernon Hills (UTM Zone 12, 384335 East, 4438482 North) and Simpson Springs (UTM Zone 12, 350537 East, 4437129 North) in Tooele County, Utah, USA, approximately 155 and 172 km southwest of Salt Lake City, Utah, respectively. Juveniles and reproductive adults were released upon capture. Non-reproductive adult animals were transported to the Green Canyon Ecology Center Research Facility in North Logan, Utah, where they were housed in individual cages (48 cm × 35.5 cm × 20 cm) in ventilated rooms with a 12 h light/12 h dark photoperiod. Animals were fed mixed bird seed and lettuce *ad libitum* and held in captivity for a minimum of 24 h habituation period prior to experimental trials. Each rodent individual was exposed to a single trial and returned to a marked cage indicating it had been used. Animals were then returned to their place of capture and released. All procedures were performed according to Utah State University Institutional Animal Care and Use Committee guidelines, approved protocol #1259.

2.2. Feeding arenas

We constructed three plywood feeding arenas (2.5 m × 2.5 m × 1.25 m) in buildings separate from where captive rodents were housed. To accommodate rodent burrowing behaviors, arenas were elevated 0.5 m on concrete blocks and a two-level wooden nest box (60 cm × 20 cm × 15 cm) was placed below the arena floor. The nest box was connected to the arena by two rubber hose corridors (7 cm diameter, maximum 1 m length) that were inserted into holes in the arena wall (Fig. 1). Arenas were filled to a depth of 10 cm with quarried sand, free of organic material such as seeds or other debris. To prevent rodent escape, the upper 10 cm of arena walls were lined with aluminum flashing and a removable wire screen covered the top of the arena while trials were in session.

To test the indirect cue of microhabitat, we created 50% cover of Wyoming big sagebrush (*Artemisia tridentata* (Nuttall) ssp. *wyomingensis* Beetle & Young) in one diagonal half of each arena (Fig. 1); 50% mean shrub cover is typical at the place of rodent

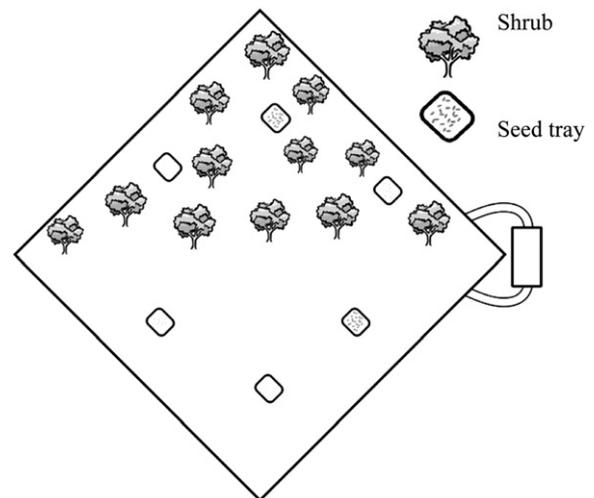


Fig. 1. Overhead view of a feeding arena with shrub and open micro-habitats and adjoining nest box. One tray of each of three seed species was present in each microhabitat.

capture and in other Wyoming big sagebrush communities throughout the region (NRCS, 1990). We secured sagebrush branches to wooden platforms and placed them uniformly throughout one half of the arena by burying the platforms in the sand. We replaced branches with fresh specimens weekly.

We offered seed from three grass species simultaneously. The three seed species vary in seed size; from smallest to largest, we used two important native grass species, Indian ricegrass (*Achnatherum hymenoides* (Roemer & Schultes) Barkworth) and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), and a non-native cereal rye (*Secale cereale* L.). Six plastic Tupperware® trays (12 cm × 12 cm × 5 cm) filled with sand were buried flush with the sand level in the arena, three in the sagebrush half and three in the open half (micro-habitats). Trays were placed in a circle with a minimum distance of 30 cm from arena edge and each other (Fig. 1). Each tray contained 3 g of a single seed species, with one replicate of each species in each microhabitat. Seed was gently incorporated into the sand in the plastic trays at the start of each trial. Assignment of individual seed species to seed trays within a microhabitat was randomly alternated throughout the study. After each trial, we recovered seeds from feeding arenas and assessed the proportions of seed placed in scatter hoards, larder hoards, consumed, and left unharvested.

2.3. Experimental treatments

We tested direct cues in the form of scent and/or vocalization from the coyote (*Canis latrans* Say) and short-eared owl (*Asio flammeus* Pontoppidan), native predators frequently sighted throughout the eastern Great Basin (Steven Ostoja and Eugene Schupp, pers. obs.), and red fox (*Vulpes vulpes* L.), a non-native predator. Because scent from native fox spp. such as the kit fox (*V. macrotis*) and swift fox (*V. velox*) was not commercially available, we substituted scent from the red fox.

Direct cues, introduced one per trial per feeding arena, were one of the following: 1) control with no cue, 2) coyote vocalization, 3) coyote scent, 4) red fox scent or 5) short-eared owl vocalization. Each direct cue was tested one at a time with the indirect cue of vegetation cover. Vocalizations were simulated via playback of compact disc recordings of either coyote or short-eared owl calls; vocalizations were interspersed with intervals of silence ranging from 1 to 15 min with each rodent exposed to the same mix of calls and silent intervals. For scent cues, urine obtained from meat-fed animals (Wildlife Control Supplies, East Granby, CT) was dispensed via eyedropper in 1 mL quantities to each seed tray immediately prior to releasing a rodent into the arena. Two feeding arenas and associated equipment were respectively designated for coyote and fox scent cues throughout the study and housed separately to avoid scent contamination. Upon completion of each scent cue trial, contaminated sand was replaced with fresh sand to prevent odor intensification throughout the duration of the experiment.

2.4. Experimental trials

At dusk (approx. 20:00–21:00 h), we released one randomly selected rodent of one species into the nest box adjoining an arena; after 12 h the rodent was retrieved and returned to a marked cage indicating its use. The remaining contents of plastic seed trays were collected and recorded by rodent and seed species, direct cue, and tray location (indirect cue of open or shrub microhabitat). Contents of the nest box (larder) were also collected. We then methodically sieved all of the sand in the arena using mesh sieves fine enough to entrap the three seed species used in the study. All recovered seeds were later weighed and counted in the lab. Groups of three or more seeds found during sieving were recorded as a scatter hoarded

cache. Out of 180 recovered caches containing 28,510 seeds, we documented a total of 10 groups containing fewer than three seeds. Because of the difficulty in determining whether these 10 groups were active scatter hoards, they were considered incidental and this small number of seeds was not included in the final analysis.

Trials were grouped into sessions of three consecutive nights during which all five of the direct cues were tested. An individual rodent was used in only a single trial with a single direct cue. In the first arena, we alternated the direct cue on nights 1–3 among the control, short-eared owl, and coyote auditory cues. In the second and third arenas (housed individually to avoid scent contamination), we simultaneously conducted the coyote and red fox olfactory cues on one of the three nights. Trial sessions alternated between pocket mice and kangaroo rats. We conducted six sessions for each rodent species, resulting in six replicates per direct cue treatment per rodent species.

Three trials were omitted from the statistical analyses: two trials due to irreconcilable numerical errors in weighing, and one trial lost during experimentation. These were: kangaroo rat–red fox scent, pocket mice– control, and kangaroo rat–coyote vocalization.

2.5. Statistical analysis: Seed preference

Here, we consider preference as a metric not only for relative desirability, but also quantity harvested (because availability is constant). For each tray in each trial, the quantity of seed harvested was calculated as the difference between the weight of seed placed in the tray minus the weight of seed remaining in the tray. The proportion removed was the amount removed divided by the initial weight (3 g). The effects of rodent species, direct cues, microhabitat (indirect cue), and seed species on the proportion of seed removed were assessed using an analysis of variance of a four-way factorial in a split–split–split plot design. The “units” are random effects; the “factors” are fixed effects. The whole plot unit was a session; the whole plot factor was rodent species. The subplot unit was a trial; the subplot factor was direct cue. The sub–subplot unit was an arena half; the sub–subplot factor was microhabitat. The sub–sub–subplot unit was a seed tray; the sub–sub–subplot factor was seed species. To better meet assumptions of normality, data were arcsine-square root transformed prior to analysis. Mean comparisons were made as needed, using a stepdown Bonferroni adjustment to control family-wise Type I error rate. Analyses were performed with the MIXED and MULTTEST procedures in SAS/STAT software, Version 9.1.3 of the SAS System for Windows®.

2.6. Statistical analysis: Seed fate

Seeds were recovered by species after each trial and assigned to one of four fates: scatter hoarded (seed recovered from sieving sand in the arena), larder hoarded (seed recovered from nest box), neglected (seed remaining in seed tray), or consumed (seed otherwise unaccounted for). These groupings are based on the assumptions that the seeds have either been “removed” from the seed pool and are therefore unlikely to germinate (larder hoarded and presumed consumed), or will “persist” and potentially survive and germinate (neglected and scatter hoarded). The proportion of initial weight (6 g, 3 g in each microhabitat) was computed for each fate class. As compositional data (i.e., the sum of the proportions over the four fate classes is equal to one), fate proportions are strongly interrelated. To look at fates jointly, rather than separately, we characterized the variability among proportional fates using a principal component analysis (PCA) of the covariance matrix, following the methodology for compositional data described by [Khattree and Naik \(2000\)](#). The PCA generated three uncorrelated principal components (PC) (Table 1) that we used in subsequent

Table 1
Eigenvectors for principal components produced by the PCA.

| Seed fate outcomes | PC1 | PC2 | PC3 |
|--------------------|--------|--------|--------|
| Neglected | -0.695 | -0.514 | -0.053 |
| Larderred | -0.071 | 0.641 | -0.578 |
| Scatter hoarded | 0.714 | -0.461 | -0.167 |
| Consumed | 0.052 | 0.334 | 0.797 |

analyses; the fourth PC explained zero variability because of the compositional data constraint. Analysis was performed using the PRINCOMP procedure in SAS/STAT software, Version 9.1.3 of the SAS System for Windows®.

As noted above, we interpreted the first three principal components as metrics of seed handling behavior with consequences for seed fate and seed pool availability. For each principal component, the effects of rodent species, direct cue, and seed species on the principal component score were assessed using an analysis of variance of a three-way factorial in a split-split plot design. Because we could not determine the microhabitat origin of recovered seeds, these analyses cannot address the impact of indirect cue. The whole plot unit was a session; the whole plot factor was rodent species. The subplot unit was a trial; the subplot factor was direct cue. The sub-subplot unit was a seed tray; the sub-subplot factor was seed species. The “units” are random effects; the “factors” are fixed effects. Mean comparisons were made as needed using a stepdown Bonferroni adjustment to control family-wise Type I error rate. Analyses were performed with the MIXED and MULTTEST procedures in SAS/STAT software, Version 9.1.3 of the SAS System for Windows®.

3. Results

3.1. Seed preference

Seed preferences varied between rodent species (Table 2, rodent × seed species interaction; Fig. 2). Kangaroo rats showed

a strong preference for Indian ricegrass, with cereal rye being least preferred. In contrast, pocket mice removed similar proportions of Indian ricegrass and cereal rye, with bluebunch wheatgrass being least preferred. In general, pocket mice removed higher proportions of seeds than did kangaroo rats (Table 2, rodent main effect). Analysis of seed preference failed to reveal a significant effect of direct cues or the indirect cue of microhabitat, or any interactions involving cues (Table 2).

3.2. Seed fate

The first principal component (PC1) explained 50% of the total variance between seed fates and contrasted scatter hoarded and neglected seeds; both of these fate categories represent seeds still available in the seed pool. PC1 scores increased as the proportion of scatter hoarded seeds increased and as the proportion of neglected seeds decreased. The fates of seed species as expressed by PC1 varied between rodent species (Table 2, PC1 rodent by seed species interaction; Fig. 3). Pocket mice were more likely to scatter hoard its preferred seeds, especially Indian ricegrass, than to neglect seeds. In contrast, kangaroo rats were more likely to neglect than to scatter hoard all three seed species, particularly the least preferred cereal rye.

The second principal component (PC2) accounted for 36% of the total variance and contrasted seeds either larder hoarded or consumed (i.e., seeds removed from the seed pool) with seeds either scatter hoarded or neglected (i.e., seeds remaining in the seed pool). PC2 scores increased as the proportion of larder hoarded or consumed seeds increased and as the proportion of scatter hoarded or neglected seeds decreased. Seed fate as depicted by PC2 was influenced differently by the two rodent species (Table 2, PC2 rodent by seed species interaction; Fig. 4). Kangaroo rats were more likely to remove Indian ricegrass, its most preferred seed, from the seed pool by consumption or larder hoarding, and more likely to leave cereal rye, its least preferred seed, in the seed pool through scatter hoarding or neglect. In contrast, the behavior of pocket mice did not vary greatly across different seed species, as all seed species

Table 2
Results from the ANOVAs for seed preference and seed fate.^a

| Experimental Factors | Seed Preference | | | Seed Fate | | | | | | | |
|---|-----------------|-------|-----------------|-----------|-------|-----------------|-------|-----------------|-------|-----------------|--|
| | df | F | P | df | PC1 F | PC1 P | PC2 F | PC2 P | PC3 F | PC3 P | |
| Rodent | 1.10 | 22.20 | <0.01 | 1.10 | 48.72 | <0.01 | 0.02 | 0.90 | 8.53 | 0.02 | |
| Direct Cue | 4.39 | 1.31 | 0.28 | 4.38 | 1.43 | 0.24 | 0.53 | 0.71 | 1.78 | 0.15 | |
| Rodent × Direct Cue | 4.39 | 1.08 | 0.38 | 4.38 | 0.70 | 0.59 | 3.11 | 0.03 | 0.45 | 0.77 | |
| Microhabitat | 1.49 | 0.12 | 0.73 | — | — | — | — | — | — | — | |
| Rodent × Microhabitat | 1.49 | 0.54 | 0.47 | — | — | — | — | — | — | — | |
| Direct Cue × Microhabitat | 4.49 | 0.37 | 0.83 | — | — | — | — | — | — | — | |
| Rodent × Direct Cue × Microhabitat | 4.49 | 0.32 | 0.86 | — | — | — | — | — | — | — | |
| Seed Species | 2.192 | 59.43 | <0.01 | 2.94 | 50.09 | <0.01 | 5.39 | 0.01 | 21.48 | <0.01 | |
| Rodent × Seed Species | 2.192 | 27.90 | <0.01 | 2.94 | 13.88 | <0.01 | 14.62 | <0.01 | 0.90 | 0.41 | |
| Direct Cue × Seed Species | 8.192 | 1.80 | 0.08 | 8.94 | 0.94 | 0.49 | 1.01 | 0.43 | 0.60 | 0.77 | |
| Rodent × Direct Cue × Seed Species | 8.192 | 1.00 | 0.43 | 8.94 | 1.05 | 0.41 | 0.72 | 0.67 | 0.67 | 0.72 | |
| Microhabitat × Seed Species | 2.192 | 0.65 | 0.52 | — | — | — | — | — | — | — | |
| Rodent × Microhabitat × Seed Species | 2.192 | 0.15 | 0.86 | — | — | — | — | — | — | — | |
| Direct Cue × Microhabitat × Seed Species | 8.192 | 0.33 | 0.95 | — | — | — | — | — | — | — | |
| Rodent × Direct Cue × Microhabitat × Seed Species | 8.192 | 1.05 | 0.40 | — | — | — | — | — | — | — | |
| Covariance Parameter Estimates | Seed Preference | | | PC1 | | PC2 | | PC3 | | | |
| Session (Rodent) | 0.0012 | | | 0 | | 0 | | 0.0070 | | | |
| Direct Cue × Session (Rodent) | 0.0700 | | | 1.60 | | 1.62 | | 0.127 | | | |
| Direct Cue × Microhabitat × Session (Rodent) | 0 | | | — | | — | | — | | | |
| Residual | 0.1393 | | | 2.43 | | 3.21 | | 1.41 | | | |

Significant *P* values are in bold type.

^a Dashes indicate terms not included in the statistical model.

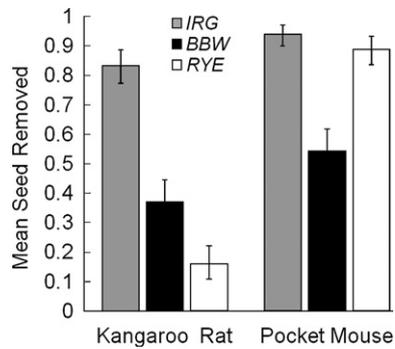


Fig. 2. Mean proportion of seed removed (± 1 S.E.) by rodent species and seed species. IRG = Indian ricegrass, BBW = bluebunch wheatgrass, RYE = cereal rye.

appeared equally likely to be larder hoarded and/or consumed versus scatter hoarded and/or neglected.

The two rodent species exhibited different responses to direct cues, as expressed by the balance between seed fates portrayed by PC2 (Table 2, PC2 rodent by direct cue interaction; Fig. 5), with kangaroo rats appearing to leave the most seeds in the seed pool in the presence of coyote scent and pocket mice appearing to leave the most seeds in the seed pool in the presence of owl vocalizations. However, with the large number of adjusted pairwise comparisons (25) no differences among rodent responses to individual cues (scent, vocalization, etc.) were significant.

The third principal component (PC3) explained the remaining 14% of total variance and represented a contrast between seeds consumed (definitely removed from the seed pool) versus larder hoarded (presumably removed from the seed pool). PC3 scores increased as the proportion of consumed seeds increased and as the proportion of larder hoarded seeds decreased. The relative balance between consumption and larder hoarding tilted toward consumption for kangaroo rats and toward larder hoarding for pocket mice (Table 2, PC3 rodent main effect). The balance between consumption and larder hoarding differed among seed species (Table 2, PC3, seed species main effect): for Indian ricegrass the balance tilted toward consumption, for cereal rye toward larder hoarding, with bluebunch wheatgrass being intermediate.

4. Discussion

4.1. Seed preference and the quantity of seed harvested

As predicted, the three seed species were not equally preferred. Seed preference differed between rodent species, which was inconsistent

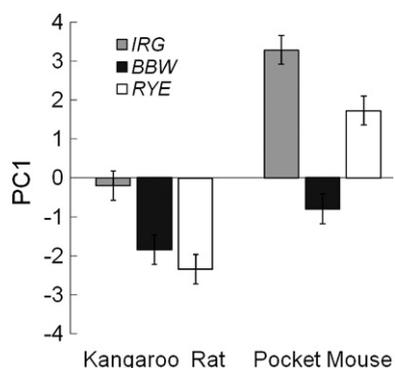


Fig. 3. Mean PC1 scores (± 1 S.E.) for seed fate by rodent species and seed species. Larger positive values indicate more seed scatter hoarded; larger negative values indicate more seed neglected (i.e., left in seed trays). IRG = Indian ricegrass, BBW = bluebunch wheatgrass, RYE = cereal rye.

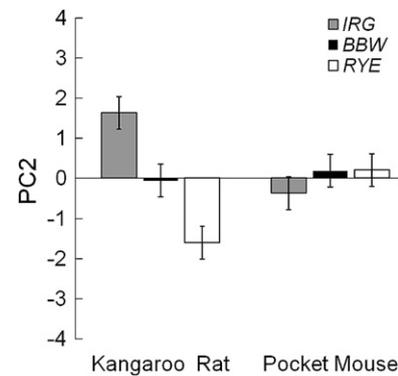


Fig. 4. Mean PC2 scores (± 1 S.E.) for seed fate by rodent species and seed species. Larger positive values indicate more seed larder and/or consumed (presumed to be removed from the seed pool); larger negative values indicate more seed scatter hoarded and/or neglected (presumed to remain viable in the seed pool). IRG = Indian ricegrass, BBW = bluebunch wheatgrass, RYE = cereal rye.

with our prediction. While both rodents showed a strong preference for Indian ricegrass, the smallest seed available in our study, the two rodents exhibited different preferences for bluebunch wheatgrass and cereal rye. Seed preference is a complex function of caloric content, anatomy, water, nutritional content, soluble carbohydrate content, seed size, seed availability, seed neighborhood composition, and more (Smigel and Rosenzweig, 1974; Price, 1983; Kelrick et al., 1986; Veech, 2001). Interspecific differences in seed preference among rodent species may relate to energetic needs stemming from different foraging movements (Bowers, 1982) or degree of physiological stress (Jenkins and Ascanio, 1993). Spatial and temporal patterns of seed availability may also influence seed selection by granivores (Ostojka, 2008), suggesting that seed size alone is an insufficient predictor for which seed will be selectively harvested.

Although indirect and direct predator cues affect heteromyid foraging (Kotler and Brown, 1988; Longland, 1994; Orrock et al., 2004), contrary to our prediction we failed to detect a seed preference response to indirect or direct cues. It is possible that seed preferences are so strong that they do not change in response to predator threat. Alternatively, facets of risk perception by rodents may explain the lack of predator cue effects on seed preference. Lima and Dill (1990) suggested that prey may assume there is high risk in novel situations until experience provides a more detailed assessment of threats. Thus, rodents may not have perceived our “no-risk” environment (control treatment and shrub microhabitat)

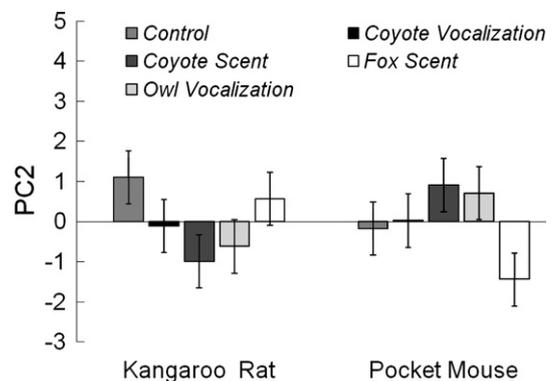


Fig. 5. Mean PC2 scores (± 1 S.E.) for seed fate by rodent species and direct predator cue. Larger positive values indicate more seed larder and/or consumed (presumed to be removed from the seed pool); larger negative values indicate more seed scatter hoarded and/or neglected (presumed to remain viable in the seed pool).

as truly risk-free, and therefore opted for constant vigilance. Further, our feeding arenas may have been too small to accurately represent micro-habitats segregated by risk.

Lastly, the lack of a direct cue response may also be explained by the season of our study, which took place in summer. Low responsiveness to predator cues from related rodent species has been documented during summer when compared with fall and winter (Bouskila, 1995; Herman and Valone, 2000). That said, we opted to conduct our research during summer months when Great Basin perennials begin to drop their seed and rodent activity is high (Ostoja and Schupp, 2009). Moreover, a summer study was thought to better capture seed harvesting behavior prior to the onset of active resource management, when rodents, triggered by cooler temperatures, may shift from actively harvesting seed to managing their seed caches (Murray, 2003).

4.2. Seed fate

Seeds within a seed pool face several possible fates. They may remain where they are, neglected by granivores to eventually either germinate or die, or they may be harvested; once harvested, seeds may be consumed immediately, scatter hoarded, or larder hoarded (Vander Wall et al., 2005). Consumption by rodents results in seed death and a reduction in the seed pool. Scatter hoarding does not directly remove seeds from the seed pool and can result in germination or dispersal if the seeds are not recovered. Larder seeds, unless moved to a scatter hoard or discarded above ground, are removed from the seed pool given the likelihood of consumption and the depth of the larder which typically inhibits germination and emergence (Hulme, 1998). Thus, of our four categories of seed fate, neglected and scatter hoarded seeds remain alive in the seed pool while consumed and larder hoarded seeds are removed from the seed pool.

In this context, the principal components describing variability in our seed fate model are biologically significant with respect to seed pool dynamics primarily because they (1) contrast alternative seed fates that leave seed in the seed pool (scatter hoarded versus neglected), shown here to vary by rodent species, and (2) contrast seed fates that either leave seeds in the seed pool (scatter hoarded and neglected) or remove them from the seed pool (consumed and larder hoarded), also shown to vary by rodent species.

In our experiment, 50% of the variance between seed fates was explained by whether seeds were scatter hoarded or neglected. Rodent behavior depended strongly on the seed species present, as both rodent species were more likely to scatter hoard preferred seed species than non-preferred seed species. Although scatter hoarded and neglected seeds both remain in the seed pool temporarily, the ultimate fate of these two alternatives is not likely to be equivalent. Neglected seeds may remain vulnerable to desiccation or consumption by non-caching seed consumers such as insects and birds. Assuming incomplete seed recovery, scatter hoarded seeds may experience greater chances for survival. For example, scatter hoarding can result in improved hydration and germination and even facilitate directed dispersal of seeds to more suitable micro-habitats (Vander Wall, 1990).

Numerous enclosure experiments have yielded insight as to the influence of rodents on plant establishment (Heske et al., 1993; Howe and Brown, 2000; Howe et al., 2002). Seeds of some plant species, such as the Indian ricegrass used in our study, have even been shown to benefit from handling and/or caching by granivores (Vander Wall, 2010). Because Indian ricegrass seeds must be buried to germinate (Young et al., 1994), placement in a scatter hoard is an immediate advantage conferred by rodents. Indian ricegrass seeds cached by Merriam's kangaroo rats (*Dipodomys merriami*) were more 1.5 times more likely to germinate than unhandled seeds,

suggesting that the relationship may in fact be mutualistic rather than detrimental (Longland et al., 2001). Further, heteromyids may increase the germinability of Indian ricegrass via their differential selection of seed morphs and subsequent removal of parts that induce dormancy within the seed (McAdoo et al., 1983). Although germination from scatter hoarded caches is generally low, the amount of seed scatter hoarded by rodents can be large, suggesting that un-recovered seed caches may represent a meaningful contribution to plant establishment (McAdoo et al., 1983; Hulme, 1998).

The 36% of the variance in seed fates explained by whether seeds are left in the seed pool as opposed to being removed from the seed pool is also critical. Kangaroo rats tended to remove their most preferred species from the seed pool while leaving their least preferred species in the seed pool. In contrast, pocket mice did not strongly discriminate between removing and leaving seeds in the seed pool for any species. Thus, at this stage, seed preference strongly affected the initial fate of seeds encountered by kangaroo rats but not of seeds encountered by pocket mice.

The distinction between consumed seed versus larder hoarded seed that described 14% of the variance in our seed fate model is probably of less direct importance to plants, considering the limited evidence that seed placed in the larder remains viable or that rodents may subsequently place larder hoarded seed in surface caches. Nonetheless, the behavioral differences between the rodent species depended on seed identity as well. While kangaroo rats tended to consume seeds and pocket mice tended to larder hoard seeds, Indian ricegrass, a species highly preferred by both rodents, was more likely to be consumed than larder hoarded. Cereal rye, heavily preferred by pocket mice and nearly ignored by kangaroo rats, was more likely to be larder hoarded than consumed. This is likely explained by the intense harvesting by pocket mice of cereal rye combined with its tendency to larder hoard seeds.

Seed fate appeared to be altered by predator cues. Interestingly, the two rodents appeared to respond to different predator cues, with kangaroo rats shifting towards leaving more seeds in the seed pool in the presence of canid scents, especially by neglecting seeds, while pocket mice appeared to shift towards leaving more seeds in the seed pool in response to owl vocalizations, by increasing scatter hoarding and/or neglect of seeds. Although no differences were significant due to the large number of comparisons, these patterns suggest how predation risk, as perceived via olfactory and auditory cues, may mediate interactions between sympatric granivores interacting in a risk-heterogeneous environment (Kotler, 1984). In addition to exploiting different micro-habitats, rodents may further partition their space by responding to different types of predators. Although the kangaroo rat's large body size, bipedal locomotion and enlarged auditory bullae render them well equipped to detect and escape avian predators (Kotler and Brown, 1988), they may be especially alert to signs of a mammalian predator against which they may be more vulnerable. Small-bodied, quadrupedal pocket mice accustomed to using shrub understory as protective cover may be especially alert to the perceived presence of avian predators that exploit prey in open micro-habitats. This interesting and to our knowledge novel interaction suggests how predator cues may influence the amount of seed in the seed pool based on rodent community composition and could serve as an area of future study.

4.3. Conclusion

Our results indicate that seed preference and handling behavior vary between kangaroo rats and pocket mice, which could have potential impacts on plant recruitment. While we did not detect an influence of microhabitat structure, this might have been an artifact of experimental design. Direct cues were not shown to impact seed

preferences and overall harvesting, although we suggest further investigation into the relative influence of specific direct cues and their differential effects on rodent species. We did find evidence that predator risk can alter seed fate and that different rodents respond to different predators. Finally, we found that variability in seed fates can be characterized by outcomes that are biologically relevant to seed pool dynamics and potentially plant establishment, and that these outcomes are dependent on seed species, rodent species, and to some extent on predator cues. The potential for both species to shift behavior towards leaving more seeds in the seed pool – whether through neglect or scatter hoarding – under risk of predation might minimize loss of seeds.

As to how well our results may extend to natural systems, admittedly there are limitations to the realism of an arena study. Using feeding arenas allowed us to effectively assess rodent response while controlling for numerous factors that are difficult to control in the field, such as illumination, wind, temperature, existing seed bank, unaccounted seed loss, predators, and presence of other granivores, rodent or otherwise. While we are unaware of any explicit comparisons of lab and field tests, species-specific patterns of microhabitat use and foraging under the influence of predation risk using captive animals (Kotler et al., 1991, 2010) are similar to results demonstrated in the field with wild rodent populations (Kotler, 1984; Longland and Price, 1991) indicating consistency between the lab and field for effects of habitat and predation risk. Therefore, we view our results as important preliminary insights to factors that may influence seed fate dynamics, thus providing groundwork for future investigation in an applied setting. As such, results from our lab study have potential to effectively translate to dynamics occurring across the landscape.

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References

- Bouskila, A., 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology* 76, 165–178.
- Bowers, M.A., 1982. Foraging behavior of heteromyid rodents: field evidence of resource partitioning. *J. Mammal.* 63, 361–367.
- Bowers, M.A., 1988. Seed removal experiments on desert rodents: the microhabitat by moonlight effect. *J. Mammal.* 69, 201–204.
- Brown, J.H., Davidson, D.W., Munger, J.C., Inouye, R.S., 1986. Experimental community ecology: the desert granivore system. In: Diamond, J., Case, T.J. (Eds.), *Community Ecology*. Harper and Row Publishing, New York, pp. 41–61.
- Brown, J.H., Reichman, O.J., Davidson, D.W., 1979. Granivory in desert ecosystems. *Annu. Rev. Ecol. Syst.* 10, 201–227.
- Brown, J.S., Kotler, B.P., Smith, R.J., Wirtz II, W.O., 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia* 76, 408–415.
- Hay, M.E., Fuller, P.J., 1981. Seed escape from heteromyid rodents: the importance of microhabitat and seed preference. *Ecology* 62, 1395–1399.
- Herman, C.S., Valone, T.J., 2000. The effect of mammalian predator scent on the foraging behavior of *Dipodomys merriami*. *Oikos* 91, 139–145.
- Heske, E.J., Brown, J.H., Guo, Q., 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia* 95, 520–524.
- Howe, H.F., Brown, J.S., 2000. Early effects of rodent granivory on experimental Forb communities. *Ecol. Appl.* 10, 917–924.
- Howe, H.F., Brown, J.S., ZornArnold, B., 2002. A rodent plague on prairie diversity. *Ecol. Lett.* 5, 30–36.
- Hulme, P.E., 1998. Post-dispersal seed predation: consequences for plant demography and evolution. *Persp. Plant Ecol. Evol. Syst.* 1, 32–46.
- Inouye, R.S., Byers, G.S., Brown, J.H., 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* 61, 1344–1351.
- Jenkins, S.H., Ascanio, R., 1993. A potential nutritional basis for resource partitioning by desert rodents. *Am. Mid. Nat.* 130, 164–172.
- Jenkins, S.H., Breck, S.W., 1998. Differences in food hoarding among six species of heteromyid rodents. *J. Mammal.* 79, 1221–1233.
- Jonsson, P., Koskela, E., Mappes, T., 2000. Does risk of predation by mammalian predators affect the spacing behavior of rodents? Two large scale experiments. *Oecologia* 122, 487–492.
- Kelrick, M.L., MacMahon, J.A., Parmenter, R.R., Sisson, D.V., 1986. Native seed preferences of shrub-steppe rodents, birds, and ants: the relationships of seed attributes and seed use. *Oecologia* 68, 327–337.
- Kelt, D.A., Brown, J.H., Heske, E.J., Marquet, P.A., Morton, S.R., Reid, J.R., Rogovin, K.A., Shenbrot, G., 1996. Community structure of desert small mammals: comparisons across four continents. *Ecology* 77, 746–761.
- Khattrjee, R., Naik, D.N., 2000. Multivariate Data Reduction and Discrimination with SAS Software. SAS Institute Inc, Cary, North Carolina.
- Kotler, B.P., 1984. Risk of predation and the structure of desert rodent communities. *Ecology* 65, 689–701.
- Kotler, B.P., Brown, J.S., 1988. Environmental heterogeneity and the co-existence of desert rodents. *Annu. Rev. Ecol. Syst.* 19, 281–307.
- Kotler, B.P., Brown, J.S., Hasson, O., 1991. Factors affecting Gerbil foraging behavior and rates of Owl predation. *Ecol. Lett.* 2, 2249–2260.
- Kotler, B.P., Brown, J., Mukherjee, S., Berger-Tal, O., Bouskila, A., 2010. Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. *Proc. Royal Soc. B-Biological Sci.* 277, 1469–1474.
- Leaver, L.A., Daly, M., 2003. Effect of predation risk on selectivity in heteromyid rodents. *Behav. Process* 64, 71–75.
- Lima, S.L., Bednekoff, P.A., 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* 153, 649–659.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640.
- Longland, W.S., 1994. Effects of artificial bush canopies and illumination on seed patch selection by heteromyid rodents. *Am. Mid. Nat.* 132, 82–90.
- Longland, W.S., Jenkins, S.H., Vander Wall, S.B., Veech, J.A., Pyare, S., 2001. Seedling recruitment in *Oryzopsis hymenoides*: are desert granivores mutualists or predators? *Ecology* 82, 3131–3148.
- Longland, W.S., Price, M.V., 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology* 72, 2261–2273.
- McAdoo, J.K., Evans, C.C., Roundy, B.A., Young, J.A., Evans, R.A., 1983. Influence of heteromyid rodents on *Oryzopsis hymenoides* germination. *J. Rangel. Manag.* 36, 61–64.
- Murray, A. L., 2003. Competitive environment and temperature affect food-hoarding behavior of Merriam's kangaroo rats (*Dipodomys merriami*). Masters thesis, University of Nevada, Reno. Natural Resources Conservation Service, 1990. Tooele County (Tooele Area Soil Survey), Utah.
- Orrock, J.L., Danielson, B.J., Brinkerhoff, R.J., 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behav. Ecol.* 3, 433–437.
- Ostojka, S.M., 2008. Granivores and restoration: implications of weed invasion and context-dependent seed removal. Doctoral dissertation, Utah State University, Logan.
- Ostojka, S.M., Schupp, E.W., 2009. Conversion of sagebrush shrublands to exotic annual grasslands negatively impacts small mammal communities. *Divers. Distrib.* 15, 863–870.
- Price, M.V., 1983. Laboratory studies of seed size and seed species selection by heteromyid rodents. *Oecologia* 60, 259–263.
- Price, M.V., Jenkins, S.H., 1986. Rodents as seed consumers and dispersers. In: Murray, D.R. (Ed.), *Seed Dispersal*. Academic Press, Sydney, Australia, pp. 191–235.
- Price, M.V., Waser, N.M., MacDonald, S., 2000. Seed caching by heteromyid rodents from two communities: implications for coexistence. *J. Mammal.* 81, 97–106.
- Reichman, O.J., 1979. Desert granivore foraging and its impact on seed densities and distributions. *Ecology* 60, 1085–1092.

- Schupp, E.W., Fuentes, M., 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2, 267–275.
- Smigel, B.W., Rosenzweig, M.L., 1974. Seed selection in *Dipodomys merriami* and *Perognathus penicillatus*. *Ecology* 55, 329–339.
- Sundell, J., Dudeck, D., Klemme, I., Koivisto, E., Pusenius, J., Ylonen, H., 2004. Variation in predator risk and vole feeding behavior: a field test of the risk allocation hypothesis. *Oecologia* 139, 157–162.
- Vander Wall, S.B., 1990. *Food Hoarding in Animals*. University of Chicago Press, Chicago, IL. 3–4.
- Vander Wall, S.B., Forget, P.M., Lambert, J.E., Hulme, P.E., 2005. Seed fate pathways: filling the gap between parent and offspring. In: Forget, P.M., Lambert, J.E., Hulme, P.E., Vander Wall, S.B. (Eds.), *Seed Fate: Predation, Dispersal and Seedling Establishment*. CABI Publishing, Cambridge, pp. 1–8.
- Vander Wall, S.B., Longland, W.S., Pyare, S., Veech, J.A., 1998. Cheek pouch capacities and loading rates of heteromyid rodents. *Oecologia* 113, 21–28.
- Vander Wall, S.B., 2010. How plants manipulate the scatter-hoarding behavior of seed-dispersing animals. *Philos.Trans. R. Soc. Biol. Sci.* 365, 989–997.
- Veech, J.A., 2001. The foraging behavior of granivorous rodents and short-term apparent competition among seeds. *Behav. Ecol.* 12, 467–474.
- Young, J.A., Blank, R.R., Longland, W.S., Palmquist, D.E., 1994. Seeding Indian ricegrass in an arid environment in the western Great Basin. *J. Rangel. Manag.* 47, 2–7.