Effects of Direct and Indirect Predator Cues on Heteromyid Seed Selection and Seed Fate

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EFFECTS OF DIRECT AND INDIRECT PREDATOR CUES ON HETEROMYID SEED PREFERENCE AND SEED FATE

by

Kelly Jean Sivy

Thesis submitted in partial fulfillment of the requirements for the degree of DEPARTMENTAL HONORS in Conservation and Restoration Ecology in the Department of Wildland Resources

Approved:

Thesis/Project Advisor
Dr. Eugene Schupp

Departmental Honors Advisor
Dr. Eugene Schupp

Director of Honors Program
Dr. Christie Fox

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Spring 2009
Many factors affect foraging behavior of rodents, including predation risk, which is thought to influence seed selection and seed handling by desert rodents in patchy environments. Understanding forces that drive seed selection and seed fate can aid understanding of rodents’ impacts on vegetation structure and dynamics. In a feeding arena study, we tested how indirect and direct predation cues influence seed selection and handling behaviors (e.g., scatterhoarding and larderhoarding) of two heteromyid rodents, *Dipodomys ordii* (Ord’s kangaroo rat) and *Perognathus parvus* (Great Basin pocket mouse), foraging on three seed species. The indirect cue was shrub cover: one half of the arena had sagebrush shrubs present while the other half was free of shrub cover. Direct cues, presented one per trial, were (1) control, (2) vocalization of *Canis latrans*, (3) scent of *C. latrans*, (4) scent of *Vulpes vulpes*, or (5) vocalization of *Asio flammeus*. We offered seeds of two native grasses, *Achnatherum hymenoides* (Indian ricegrass) and *Pseudoroegneria spicata* (bluebunch wheatgrass), and the non-native *Secale cereale* (cereal rye), each in separate plastic trays. *D. ordii* preferentially harvested *A. hymenoides* while *P. parvus* predominately harvested *A. hymenoides* and *S. cereale*. *P. parvus* was more likely to scatterhoard preferred seeds, whereas *D. ordii* mostly consumed and/or placed preferred seeds in a larder. Neither indirect nor direct cues significantly affected seed preferences. However, both species altered seed handling behavior in response to direct predation cues by leaving more seeds alive in the seed pool, though they responded to different predator cues. The two rodents are expected to have different impacts on plant recruitment in both natural and managed settings. Variation in preference, as revealed in this study, could be exploited as a component of reseeding strategies at sites where estimates of rodent community composition are available. To the extent that predator cues alter handling behavior, they provide a potential tool in developing restoration strategies that minimize seed loss.
ACKNOWLEDGEMENTS

We thank Michael White and the participants of the National Science Foundation supported Summer Science Camp project that were of great assistance in data collection and processing. We especially thank Tyler Logan for rodent trapping and transport and Ryan Barker for the construction of the arenas. John Shivik and Fred Knowlton provided advice on implementation of predator cues. We also extend thanks to the people and programs that made this project possible through funding or other support: Stephanie White, the Utah State University (USU) Ecology Center, the USU Undergraduate Research and Creative Opportunities Program (to KJS), the USU College of Natural Resources Undergraduate Independent Research Grants Program (to KJS), the USU Ecology Center research fellowship (to SMO), and a Utah State University School of Graduate Studies dissertation fellowship (to SMO), the Utah Agricultural Experiment Station, and the Sagebrush Steppe Treatment Evaluation Project, which is funded by the U.S. Joint Fire Science Program.
Table 1. Results from the ANOVAs for seed removal and seed fate. Dashes indicate terms not included in the statistical model.

<table>
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<tr>
<th>Experimental Factors</th>
<th>Seed Preference</th>
<th>Seed Fate</th>
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<td></td>
<td>df F P</td>
<td>df F P F P</td>
</tr>
<tr>
<td>Rodent</td>
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<td>1,10 48.72 &lt;0.01 0.02 0.90 8.53 0.02</td>
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<td>Seed Species</td>
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<td>2,94 50.09 &lt;0.01 5.39 0.01 21.48 &lt;0.01</td>
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<td>Rodent×Seed Species</td>
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Covariance Parameter Estimates

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Figure 1. Overhead view of a feeding arena with shrub and open microhabitats and adjoining nest box. One tray of each of three seed species was present in each microhabitat.
Figure 2. Mean proportion of seed removed (± 1 S.E.) by rodent species and seed species.

- A. hymenoides
- P. spicata
- S. cereale
Figure 3. Mean PC1 scores (± 1 S.E.) for seed fate by rodent species and seed species. Larger positive values indicate more seed scatterhoarded; larger negative values indicate more seed neglected (i.e., left in seed trays).
Figure 4. Mean PC2 scores (± 1 S.E.) for seed fate by rodent species and seed species. Larger positive values indicate more seed lardered and/or consumed (presumed to be removed from the seed pool); larger negative values indicate more seed scatterhoarded and/or neglected (presumed to remain viable in the seed pool).
Figure 5. Mean PC2 scores (± 1 S.E.) for seed fate by rodent species and direct predator cue. Larger positive values indicate more seed lardered and/or consumed (presumed to be removed from the seed pool); larger negative values indicate more seed scatterhoarded and/or neglected (presumed to remain viable in the seed pool).
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, Longland et al. 2001). In the Great Basin, rodents from the family Heteromyidae, namely *Dipodomys* spp. (kangaroo rats) and *Perognathus* spp. (pocket mice), are among the dominant genera (Brown, Reichmann & Davidson 1979). Both are known to harvest large quantities of seeds (Vander Wall et al. 1998), which may be cached across home ranges (scatterhoarding) or within larders inside their burrows (larderhoarding) (Vander Wall 1990). Because these processes can influence recruitment and survival of plants (Davidson 1977; Reichman 1979; Inouye, Byers & Brown 1980; Price and Jenkins 1986, Schupp and Fuentes 1995, Howe and Brown 2001), understanding the factors affecting seed selection and handling behaviors is important for understanding seed dispersal and plant dynamics.

Of the many factors that influence rodent feeding behavior, predation risk is thought to be a key influence on when and where rodents forage while mediating interspecific rodent competition. Because ecologically similar species often share limited resources, much research has focused on elucidating the various mechanisms allowing sympatric species to co-exist (Kotler & Brown 1988; Brown 1989; Reichman 1991). Specifically, predation risk is thought to influence spatial partitioning of foraging habitat by co-occurring species (Kotler 1984; Kotler 1985; Brown et al. 1988). Pocket mice are small, quadrupedal rodents that mostly use understory habitat where protective cover is available, reducing the probability of predation (Longland & Price 1991). Conversely, kangaroo rats are relatively larger bipedal rodents with enlarged auditory bullae (Webster & Webster 1971); although they frequently venture into open habitat, they are better equipped to detect and escape avian predators in open microhabitats (Brown et al. 1986).
Kotler (1984) suggested that understanding seed exploitation patterns is best achieved in the context of predator cues. Predator cues can be categorized as either "indirect" or "direct." Indirect cues, which are conveyed by the environment, ultimately affect predation risk by interfering with the visibility or accessibility of prey. Examples include lunar phase and microhabitat structure (i.e., open or shrub-covered habitat). Direct cues, which originate from a predator and indicate its presence, include vocalizations, visual cues, and olfactory signs (e.g., predator scat and/or urine). Indirect and direct cues are both documented to alter feeding behavior. Experimental manipulations have led to altered habitat use and foraging by heteromyids (Kotler 1984; Brown et al. 1988; Longland and Price 1991; Longland 1994). For example, during full moon periods *D. merriami* removed less seed than during a new moon and less seed from open interspaces than from shrub-covered microhabitats (Bowers 1988). The presence of avian and reptilian predators reduced harvesting time by rodents and shifted microhabitat use in both lab and field studies (Brown et al. 1988; Bouskila 1995). Similarly, mammalian predator scent reduced foraging activity of kangaroo rats, demonstrating that heteromyids rely on olfaction to assess predation risk (Herman & Valone 2000).

Interestingly, studies quantifying the relative impacts of predator cues have generally found that indirect cues have a greater influence on rodent behavior than do direct cues, implying that seed harvesting may be reduced more by the introduction of an indirect than a direct predator cue (Kotler 1984; Jonsson, Koskela & Mappes 2000; Orrock, Danielson & Brinkerhoff 2004; Powell & Banks 2004). Indirect cues may be more influential by signaling a more permanent threat, as opposed to a direct cue that may be perceived as indicating only the momentary presence of a predator. This suggests that seed selection by rodents is likely subject to the presence, duration, and type of perceived predator risk (Lima & Bednekoff 1999; Orrock et al. 2004; Sundell et al. 2004).
Consequently, the preference of some seed species over others can be seen as the result of a trade-off between desirability and risk of predator attack (O’Dowd & Hay 1980). Indeed, in microhabitats devoid of protective cover, rodents have increased selection of preferred seeds over less preferred seeds (Hay & Fuller 1981; Bowers 1988; Leaver & Daly 2003).

While it is established that risk of predation affects differential patch use, foraging duration, and seed selection of quadrupedal and bipedal rodents, the degree to which perceived predation risk influences seed handling behaviors is not well known (Brown et al. 1986). Nonetheless, it is reasonable to assume that the presence, duration, and type of predation cues could affect post-harvest seed fate – i.e, the proportion of seeds consumed versus cached – as different rodent species respond to varying levels of risk. Because granivorous rodents contribute to plant establishment through seed predation and seed caching (Price & Jenkins 1986; Longland et al. 2001), forces that drive seed selection can have large impacts on vegetation structure and dynamics.

Besides potentially altering the proportion of seeds consumed versus cached, predator cues might alter the proportion of cached seeds that are scatterhoarded versus larderhoarded. Since scatterhoarded 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, there are potential applications for restoration strategies as well; if seed preferences and caching behavior can be altered by manipulating perceived predation risk, we may be able to implement more effective practices for seeding of desirable species. However, we are aware of no studies comparing seed fate in response to cues of predation risk. The simultaneous evaluation of the effect of indirect and direct cues on seed selection and seed handling (fate) by competing granivores can provide important insights as to how interactions among predators, granivores, and seeds affect plant establishment.
In a feeding arena study, we evaluated the effects of indirect and direct predation cues on seed preference, microhabitat selection, and seed fate by two heteromyid rodents abundant in the Great Basin, *Dipodomys ordii* (Ord's kangaroo rat) and *Perognathus parvus* (Great Basin pocket mouse). First, we assessed seed preference and associated seed handling behaviors by the two rodents for two important native grass species, *Achnatherum hymenoides* (Indian ricegrass) and *Pseudoroegneria spicata* (bluebunch wheatgrass), and a non-native cereal rye, *Secale cereale*, increasingly used in temporary restoration seeding. Second, we determined whether seed preference and handling behaviors were affected by the indirect cue of shrub cover and/or the direct cues of scent and/or vocalizations of *Canis latrans* (coyote) and *Asio flammeus* (short-eared owl), native predators frequently sighted throughout the western Great Basin (Steven Ostoja and Eugene Schupp, pers. obs.), and *Vulpes vulpes* (red fox), a non-native predator. Third, we recovered seeds from feeding arenas to assess how indirect and direct predation cues influence the proportion of cached seed placed in scatterhoards versus larderhoards.
METHODS

Animals

Our study took place from 19 June to 11 August 2006, when both rodent species are highly active (Steven Ostoja, unpub. data). Sherman live traps were used to capture *D. ordii* and *P. parvus* 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. Adult animals were transported to the Green Canyon Ecology Center Research Facility in North Logan, Utah, where they were housed in standard shoe box cages in ventilated rooms with a 12 hour light/12 hour dark photoperiod. Animals were fed mixed bird seed and lettuce *ad libitum* and held in captivity for a minimum of 24 hours prior to experimental trials. Each animal was used in one trial, after which it was returned to its place of capture and released. All procedures were performed according to Institutional Animal Care and Use Committee guidelines.

Feeding Arenas

We constructed three plywood feeding arenas (2.5 x 2.5 x 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-tiered wooden nest box (60 x 20 x 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.

Experimental Treatments
To test the indirect cue of microhabitat, we created 50% *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) cover in one diagonal half of each arena (Fig. 1); 50% mean shrub cover is typical at the place of rodent capture and in other Wyoming big sagebrush communities throughout the region (NRCS 1990). We screwed sagebrush branches to wooden platforms for stability, and placed them uniformly throughout one half of the arena by burying the platforms in the sand. We replaced branches with fresh specimens weekly.

Direct cues, introduced one per trial per feeding arena, were one of the following: 1) control with no cue, 2) vocalization of *C. latrans*, 3) scent of *C. latrans*, 4) scent of *V. vulpes* or 5) vocalization of *A. flammeus*. Each direct cue was tested one at a time with the indirect cue of vegetation cover. Vocalizations were simulated via continuous playback from compact discs with tracks of either *C. latrans* or *A. flammeus* calls. 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. Because scent from native *Vulpes* spp. such as *V. macrotis* (kit fox) and *V. velox* (swift fox) is not commercially available, we substituted scent from *V. vulpes*. 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.

**Experimental Trials**

We evaluated rodent preference among three grass seed species: *A. hymenoides*, *P. spicata*, and *S. cereale*. Six plastic Tupperware® trays (12 x 12 x 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 (microhabitats). Trays were placed in a circle with a minimum distance of 30 cm from arena edge.
and each other (Fig. 1). Each tray contained 3g of a single seed species, with one replicate of each species in each microhabitat. Assignment of individual seed species to seed trays within a microhabitat randomly alternated throughout the study. Seed was gently incorporated into the sand in the plastic trays at the start of each trial.

At dusk (approx. 20:00-21:00 hours), we released one randomly selected rodent of one species into the nest box adjoining an arena; after 12 hours the rodent was retrieved and returned to its cage. 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 sieved the sand in the arena using mesh sieves and recorded any seeds found during sieving as a scatterhoarded cache. All recovered seeds were later weighed and counted in the lab.

Direct cue trials were grouped into sessions of three consecutive nights during which all five of the direct cues were tested using unique rodent individuals. In the first arena, we alternated the direct cue on nights 1-3 among the control, owl, and coyote vocalization treatments. In the second and third arenas (housed individually to avoid scent contamination), we simultaneously conducted the coyote and fox olfactory cues on one of the three nights. Trial sessions alternated between *P. parvus* and *D. ordii*. We conducted six sessions for each rodent species, resulting in six replicates per direct cue treatment per rodent species.

**Statistical Analysis: Seed Preference**

For each tray in each trial, the amount of seed removed 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 (3g). The effects of
rodent species, direct cue, 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 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®.

Statistical Analysis: Seed Fate

For each seed species, seeds recovered after each trial were assigned to one of the following four fates: scatterhoarded (seed recovered from sieving sand in the arena), lardered (seed recovered from nest box), neglected (seed remaining in seed tray), or consumed (seed otherwise unaccounted for). Proportion of initial weight 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) that we used in subsequent analyses; the fourth PC explains 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.
We interpreted the first three principal components as metrics of seed handling behavior with consequences for 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. Otherwise, the design units and their corresponding factors were the same as described above for the seed removal analysis. Three trials were omitted from the analysis: two trials due to irreconcilable numerical errors in weighing, and one trial lost during experimentation. 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. 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®.
RESULTS

Seed Preference

Seed preferences varied between rodent species (Table 1, rodent × seed species interaction; Fig. 2). *D. ordii* showed a strong preference for *A. hymenoides*, with *S. cereale* being least preferred. In contrast, *P. parvus* removed similar proportions of *A. hymenoides* and *S. cereale*, with *P. spicata* being least preferred. In general *P. parvus* removed higher proportions of each seed species than did *D. ordii* (Table 1, 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 1).

Seed Fate

The first principal component (PC1) explained 50% of the total variance among seed fates and contrasted scatterhoarded and neglected seeds; both of these fate categories represent seeds still available in the seed pool. PC1 scores increased as the proportion of scatterhoarded seeds increased and as the proportion of neglected seeds decreased. The fates of seed species varied between rodent species (Table 1, PC1 rodent by seed species interaction; Fig. 3). *P. parvus* was more likely to scatterhoard its preferred seeds, especially *A. hymenoides*, than to neglect seeds. In contrast, *D. ordii* was more likely to neglect than to scatterhoard all three seed species, particularly its less preferred seeds.

The second principal component (PC2) accounted for 36% of the total variance and contrasted seeds either lardered or consumed (i.e., seeds removed from the seed pool) with seeds either scatterhoarded or neglected (i.e., seeds remaining in the seed pool). PC2 scores increased as the proportion of lardered or consumed seeds increased and as the proportion of neglected or scatterhoarded seeds decreased. The two rodent species exerted different influences on seed fate, as depicted by PC2, among seed species (Table 1, PC2 rodent by seed species interaction; Fig. 4). *D. ordii*
ordii was more likely to remove A. hymenoides, its most preferred seed, from the seed pool by consumption and/or larding; and more likely to leave S. cereale, its least preferred seed, in the seed pool through scatterhoarding and/or neglect. In contrast, the behavior of P. parvus did not vary greatly across different seed species, as all seed species appeared equally likely to be larded and/or consumed versus scatterhoarded 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 1, PC2 rodent by direct cue interaction; Fig. 5). However, with adjusted pairwise comparisons (25 comparisons) no differences were significant. Nonetheless, trends are suggestive considering rodent species responded to different predator cues, and invite further work. For example, in the absence of a direct predator cue, D. ordii mostly consumed and/or larded seeds, whereas in the presence of coyote and fox scent the seed fate balance appeared to shift towards neglect. In contrast, P. parvus appeared to increase scatterhoarding and/or neglecting seeds in the presence of owl calls.

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 larded (presumably removed from the seed pool). PC3 scores increased as the proportion of consumed seeds increased and as the proportion of larded seeds decreased. The relative balance between consumption and larding tilted toward consumption for D. ordii and toward larding for P. parvus (Table 1, PC3 rodent main effect). The balance between consumption and larding differed among seed species (Table 1, PC3, seed species main effect): for A. hymenoides, the balance tilted toward consumption, for S. cereale, toward larding, with P. spicata being intermediate.
DISCUSSION

Seed Preference and the Quantity of Seed Harvested

This study demonstrated differing seed preference between *D. ordii* and *P. parvus*, although both species showed a strong preference for *A. hymenoides*. Interspecific differences in seed preference among rodent species have been documented before (Bowers 1982; Kelrick et al. 1986). Although early seed selection models sought to attribute these differences to a positive correlation between body size and seed size (Brown & Lieberman 1973), it is now well understood that seed preference is much more complex (Smigel 1974; Price 1983), being a function of multiple seed attributes such as caloric content, anatomy, water, nutritional content, and especially soluble carbohydrate content (as discussed in Kelrick et al. 1986). Variation in preference, as revealed in this study, could be exploited as a component of reseeding strategies at sites where estimates of rodent community composition are available.

Although sensitivity of heteromyids to indirect and direct predator cues is well documented (discussed herein), we failed to detect a clear seed preference response to any cues. It is possible that seed preferences are so strong that they do not change in response to predator threat, although the lack of a cue effect on the amount of seeds harvested argues against this. Alternatively, facets of risk perception by rodents may explain the lack of direct and indirect 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, prey may not perceive an artificial “no-risk” environment (in our study, the “control” treatment and shrub microhabitat) as truly risk-free. Instead the animal opts for constant vigilance, which may further explain why we failed to detect a significant direct cue effect on seed harvesting. Similarly, persistent vigilance may explain why we failed to detect a change in seed preference in response to indirect cues, contrary to evidence
from previous research that microhabitat cover affects heteromyid foraging (Kotler 1984; Kotler & Brown 1988; Longland 1994; Mandelik, Jones & Dayan 2003; Orrock et al. 2004). Additionally, the size of our feeding arenas may have been too small to accurately represent microhabitats segregated by risk, inducing animals to engage in anti-predator behavior by default.

The lack of direct cue responses in our seed preference trials may also be explained by the seasonal timing of our study, as this appears to be influential in determining the degree of rodent response. Our study took place in summer, when rodent activity is presumably high (Steven Ostoja, unpublished data), yet some studies indicate low responsiveness to predator cues for related rodent species during summer months: Herman and Valone (2000) found foraging kangaroo rats to be unresponsive to the scent of the mammalian predator *Urocyon cinereoargenteus* (Gray fox) during summer, whereas fox scent limited rodent foraging to shrubs in winter. Similar seasonal effects were found by Bouskila (1995) when investigating how interactions among illumination, microhabitat, and snake presence drove foraging behavior of kangaroo rats; rats were less responsive to all predator cues in summer than in fall.

A better understanding of how season influences rodent responsiveness to direct cues could be useful, as most reseeding operations in the Great Basin are done in the fall (Monsen & Stevens 2004). If rodents indeed show increased sensitivity to predator cues in the fall, the introduction of such cues, in the form of predator urine or recorded vocalizations, may have the potential to effectively minimize seed loss by rodents during fall reseedings.

**Seed Fate**

The results from our seed fate model yield interesting insights as to the potential impacts of rodent seed preferences and handling behaviors on patterns of plant establishment. Seeds within a
seed pool (the population of viable seeds within the soil) face several possible fates: they may remain where they are, neglected by granivores to eventually either germinate or die, or they may be harvested by granivores (Vander Wall et al. 2005). If harvested, seeds may be consumed immediately, scatterhoarded, or larderhoarded (Vander Wall et al. 2005; Gómez, Puerta-Piñero & Schupp 2008). Consumption by rodents presumably results in seed death, reducing availability of that seed in the seed pool. Scatterhoarding does not directly remove seed from the seed pool and can result in dispersal if the seed is not recovered. In contrast, lardered seed is assumed to be removed from the seed pool given the likelihood of consumption and the depth of the larder which typically inhibits germination and emergence (Smith & Reichmann 1984; Hulme 1998). Thus, of our four categories of seed fate, neglected and scatterhoarded seeds remain alive in the seed pool while consumed and larderhoarded 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 plant establishment primarily because they 1) contrast alternative seed fates that leave seed in the seed pool (neglected versus scatterhoarded), shown here to vary by rodent species, and 2) contrast seed fates that either leave seeds in the seed pool (neglected and scatterhoarded) or remove them from the seed pool (consumed and larderhoarded), also shown to vary by rodent species. In our experiment, 50% of the variance among seed fates was explained by whether seeds were scatterhoarded or neglected, suggesting that the major variation in seed fate lies in this distinction.

Although scatterhoarded and neglected seeds both immediately remain in the seed pool, the ultimate fate of these two alternatives are likely not equivalent and therefore of major importance from the perspective of plants (see Longland et al. 2001). Neglected seeds may remain vulnerable to desiccation or consumption by non-caching seed consumers such as some insects and birds (Vander
Alternatively, scatterhoarded seeds may have greater chances for survival assuming incomplete seed recovery (Vander Wall 1990). Soil caching can result in improved hydration and germination, reduced density-dependent mortality, and even directed dispersal to more suitable microhabitats (Vander Wall 2001). Moreover, seeds of some plant species may benefit from handling by caching granivores. *A. hymenoides* seeds cached by *D. merriami* were more likely to germinate when compared to unhandled seeds and seeds harvested by non-caching granivores, suggesting that the relationship may in fact be mutualistic rather than detrimental (Longland et al. 2001). While germination from scatterhoarded caches is generally low, the amount of seed scatterhoarded by rodents can be large, and cached seeds that are un-recovered may be a meaningful contribution to plant establishment (McAdoo et al. 1983; Hulme 1998). Considering only seed left in the seed pool in our study, *D. ordii* tended overall to neglect more seeds while *P. parvus* tended to scatterhoard more seeds. However, rodent behavior depended strongly on the seed species present, as both rodent species were more likely to scatterhoard preferred seed species than non-preferred seed species.

Nonetheless, 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 still critical as it is an important distinction from the perspective of plants. *D. ordii* showed a tendency to remove its most preferred species from the seed pool while leaving its least preferred species in the seed pool. In contrast, *P. parvus* 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 fate of seeds encountered by *D. ordii* but not of seeds encountered by *P. parvus*.

The distinction between consumed seed versus larderhoarded seed is probably of less importance to plants. Nonetheless, there are important behavioral differences between the rodent
species, with *D. ordii* tending to consume seeds and *P. parvus* tending to larderhoard them, although the distinction between these fates depended on seed identity as well. *A. hymenoides*, a species highly preferred by both rodents, was more likely to be consumed than larderhoarded, while *S. cereale*, heavily preferred by *P. parvus* but nearly ignored by *D. ordii*, was more likely to be larderhoarded than consumed. This is likely explained by *P. parvus*’s large harvesting of *S. cereale* combined with its tendency to larderhoard seeds.

Combining all of the patterns, then, *D. ordii* tended to remove preferred seed species from the seed pool via consumption and leave less preferred species in the seed pool by neglecting them. Although *D. ordii* was more likely to neglect than scatterhoard seeds overall, this species did scatterhoard its preferred species more than the less preferred seed species. *P. parvus*, however, tended to leave its preferred seed species in the seed pool via scatterhoarding while leaving the least preferred seed species in the seed pool by neglecting it. Considering its high preference by both rodents, the harvesting and potential for subsequent scatterhoarding of *A. hymenoides* is likely beneficial relative to neglect and desiccation or possible predation by a non-caching consumer. A less preferred seed species, such as *P. spicata*, is less vulnerable to mortality by rodent consumption given its tendency to be neglected; however it also may be more vulnerable to desiccation or predation by a non-caching consumer.

*P. parvus* tended to larderhoard and, especially, scatterhoard harvested seeds, whereas *D. ordii* tended to consume, rather than larder or scatterhoard harvested seeds. Contrary to our results, Jenkins and Breck (1998) reported that large heteromyids such as kangaroo rats place more seeds in their larders than do smaller species; however, similar to our results, they also suggested that pocket mice tend to scatterhoard more seed than kangaroo rats. Because kangaroo rats are thought to be a dominant aggressor in foraging communities (Kotler 1984; Leaver & Daly 2001), their tendency to
amass large amounts of seed in their larders may relate to their ability to defend it (Jenkins & Breck 1998; Leaver & Daly 2001). These findings are consistent with our observation that when comparing scatterhoarding versus larderhoarding, *D. ordii* frequently larderhoarded, as opposed to scatterhoarded, its preferred seed species. The propensity to larder preferred seed has been previously documented in *D. merriami* (Merriam's kangaroo rat) (Leaver 2004), and may relate to the dominant behavior of kangaroo rats compared to smaller species such as *P. parvus*. If a resource is highly desirable, placing it in the larder would be preferable to scatterhoarding as it reduces the likelihood of cache pilferage by other individuals and may be worth the cost of defense.

On the contrary, other studies have found kangaroo rats to scatterhoard more seeds than smaller heteromyids (Price, Waser & Macdonald 2000; Leaver & Daly 2001). Differences in food hoarding behaviors may reflect a balance between resource domination by kangaroo rats and greater cache pilfering by pocket mice, leaving kangaroo rats to scatterhoard more seeds and pocket mice to larderhoard more seed (Leaver & Daly 2001). Refining our understanding of the differences between rodent species handling behaviors, and the circumstances under which they vary, may help minimize seed loss in a restoration context and reduce potential for impacting future plant population.

We found no evidence that the proportion of seed harvested varied with predator cue. However, predation risk did influence seed fate depending on the species of seed consumer and the type of predation risk cue. Coyote vocalizations did not alter seed fate for either rodent species. *D. ordii* appeared to respond mostly to canid scents; in the presence of these olfactory cues they tended to leave more seeds in the seed pool, especially by neglecting seeds. Alternatively, *P. parvus* responded mostly to owl vocalizations, but in a similar manner; with owl calls they tended to leave more seeds in the seed pool. Kotler (1984) found that foraging behavior of quadrupedal mice exhibited the most sensitivity to predation risk when compared to species with superior predator
avoidance. However, in our study the relative sensitivity of the two rodents to predation risk appeared to depend on the identity of the predator, which is an important finding. These results overall support the hypothesis that predation risk may mediate interactions between sympatric granivores interacting in a risk-heterogeneous environment (Kotler 1984), but it is important to consider that different predators likely will have different impacts on rodent species interactions.

The potential for both species to shift behavior towards leaving more seeds in the seed pool—whether through neglect or scatterhoarding—under risk of predation might minimize loss of seeds, which could translate into a potential strategy for mitigating impact on reseeded areas. For example, the early application of direct predator cues following restoration seeding might increase at least initial seed survival.

In conclusion, our results indicate that seed selection and handling behavior vary between *D. ordii* and *P. parvus*, 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 appear to have no impact on 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. Though minimal, we did find evidence that predator risk can alter seed fate and that different rodents respond to different predators; these results have implications for seedling recruitment. Finally, we found that variability in seed fates can be characterized by outcomes that are biologically relevant to plant establishment, and that these outcomes are dependent on seed species, rodent species, and to some extent on predator cues. To the extent that predator cues alter handling behavior, they provide a potential tool in developing restoration strategies that minimize seed loss.
LITERATURE CITED


Natural Resources Conservation Service. (1990) Tooele County (Tooele Area Soil Survey), Utah.


Kelly Sivy earned a Bachelor of Science degree in Conservation and Restoration Ecology with a wildlife emphasis and a minor in Biology. She graduated in spring of 2009 as valedictorian of the College of Natural Resources at Utah State University. Originally from Connecticut and Colorado, she has lived in Logan for the past 15 years. Sivy enjoys travel, food, and hiking and skiing in the beautiful canyons of Cache Valley. She is a Quinney scholar and a Seely-Hinckley scholar, and a Department of Wildland Resources honors student. Her undergraduate research studying the foraging behavior of kangaroo rats earned her the designation for College of Natural Resources Undergraduate Researcher of the year in 2007, later that year she presented her research at the Ecological Society of America/Society for Ecological Restoration joint conference in San Jose, California. Along with being actively involved with research, Sivy has participated in the undergraduate teaching fellows program at USU, acting as a teaching fellow for two undergraduate courses, earning the title of College of Natural Resources Undergraduate Teaching Fellow of the year for 2009. In the summer of 2008, Sivy traveled to Ethiopia as part of a USU study abroad program to study the social and environmental impacts of globalization on developing countries. She plans to attend graduate school to further explore her developing research interests in wildlife conservation and ecology.