



12-31-2013

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Recommended Citation

Beard, Karen H.; Faulhaber, Craig A.; Howe, Frank P.; and Edwards, Thomas C. Jr. (2013) "Rodent-mediated interactions among seed species of differing quality in a shrubsteppe ecosystem," *Western North American Naturalist*. Vol. 73 : No. 4 , Article 4.

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RODENT-MEDIATED INTERACTIONS AMONG SEED SPECIES OF DIFFERING QUALITY IN A SHRUBSTEPPE ECOSYSTEM

Karen H. Beard¹, Craig A. Faulhaber², Frank P. Howe^{3,4}, and Thomas C. Edwards Jr.⁵

ABSTRACT.—Interactions among seeds, mediated by granivorous rodents, are likely to play a strong role in shrubsteppe ecosystem restoration. Past studies typically consider only pairwise interactions between preferred and less preferred seed species, whereas rangeland seedings are likely to contain more than 2 seed species, potentially leading to complex interactions. We examined how the relative proportion of seeds in a 3-species polyculture changes rodent seed selectivity (i.e., removal) and indirect interactions among seeds. We presented 2 rodent species, *Peromyscus maniculatus* (deer mice) and *Perognathus parvus* (pocket mice), in arenas with 3-species seed mixtures that varied in the proportion of a highly preferred, moderately preferred, and least preferred seed species, based on preferences determined in this study. We then conducted a field experiment in a pocket mouse-dominated ecosystem with the same 3-species seed mixtures in both “treated” (reduced shrub and increased forb cover) and “untreated” shrubsteppe. In the arena experiment, we found that rodents removed more of the highly preferred seed when the proportions of all 3 seeds were equal. Moderately preferred seeds experienced increased removal when the least preferred seed was in highest proportion. Removal of the least preferred seed increased when the highly preferred seed was in highest proportion. In the field experiment, results were similar to those from the arena experiment and did not differ between treated and untreated shrubsteppe areas. Though our results suggest that 3-species mixtures induce complex interactions among seeds, managers applying these results to restoration efforts should carefully consider the rodent community present and the potential fate of removed seeds.

RESUMEN.—Las interacciones entre las semillas mediadas por roedores granívoros, podrían tener una gran influencia en la restauración del ecosistema de las estepas de arbustos. Estudios anteriores sólo consideran las interacciones en pares entre las especies de semillas preferidas y las especies de semillas menos preferidas, mientras que las siembras de pastizales pueden contener más de dos especies de semillas, lo cual generaría interacciones más complejas. Examinamos de qué manera la proporción relativa de semillas, en un policultivo de tres especies, modifica la selectividad de semillas de los roedores (lo cual equivale a eliminación) y las interacciones indirectas entre semillas. Presentamos dos especies de roedores, *Peromyscus maniculatus* (ratón ciervo) y *Perognathus parvus* (ratón de abazones), en áreas con mezclas de tres especies de semillas que variaban en la proporción de una especie de máxima, moderada o baja preferencia, según las preferencias que se determinaron en este estudio. Luego realizamos un experimento de campo en un ecosistema con predominancia de ratones de abazones con las mismas mezclas de semillas de tres especies, en estepas de arbustos “modificadas” (cantidad reducida de arbustos y mayor cantidad de cobertura de hierba de grandes hojas) y en estepas de arbustos “no modificadas.” En la arena experimental, encontramos que los roedores eliminaron más semillas de alto grado de preferencia, cuando la proporción de los tres tipos de semillas era igual. Las semillas de preferencia moderada se eliminaron en mayor cantidad, y hubo una proporción mayor de semillas de baja calidad. La eliminación de las semillas de menor grado de preferencia se incrementó, y se registró una mayor proporción de semillas de alta calidad. Los resultados del experimento de campo fueron similares a los de la arena experimental y no se registraron diferencias entre las estepas de arbustos modificadas y las estepas de arbustos no modificadas. Los resultados indican que las mezclas de tres especies de semillas generan interacciones complejas entre las semillas, cuando se aplican estos resultados a los intentos de restauración, se deben tomar precauciones al considerar la comunidad de roedores existente y el destino posible de las semillas eliminadas.

Shrubsteppe ecosystems consist of mosaics of shrubs (primarily sagebrush *Artemisia* spp.), perennial grasses, and forbs and cover approximately 60 million hectares in the western United States (West 1983, West and Young 2000). For decades, rangeland managers have used chemical, mechanical, and fire treatments

to reduce shrub density and increase forage for livestock in these ecosystems (Braun et al. 1976, McAdoo et al. 2004, McDaniel 2005). More recently, managers have implemented these treatments to create a mosaic of different-age stands of shrubs that benefit shrub-associated species (McGee 1982, McAdoo et

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al. 2004), often with a conservation emphasis on Greater Sage-Grouse (*Centrocercus urophasianus* Aldrich) (Connelly et al. 2000). As part of the treatments, conservation and management agencies often seed-treated areas with seed mixtures of palatable plant species to encourage a plant community that simultaneously favors livestock and wildlife.

When applying these treatments, it is important to consider how native wildlife may alter the trajectory of plant communities. Small mammals, for example, through herbivory and seed predation (Brown et al. 1979, Howe and Brown 2001, Howe and Lane 2004), have been implicated in the failure of past sagebrush ecosystem restoration activities (Howard 1950, Nelson et al. 1970). However, the role of small mammals is complicated, as some small mammals, such as heteromyid rodents (i.e., pocket mice and kangaroo rats), cache a considerable number of seeds (Vander Wall 1998), which behavior often benefits plant dispersal and recruitment (Longland et al. 2001). Furthermore, rodents are selective foragers that exhibit clear preferences for seed species in cafeteria trials (Everett et al. 1978, Kelrick et al. 1986, Henderson 1990, Kerley and Erasmus 1991). Thus, it is very possible that selective foraging by rodents alters the trajectory of posttreatment plant communities.

Results of cafeteria trials, however, are unlikely to provide a complete depiction of rodent-seed interactions. For example, studies demonstrate that association with neighboring prey items can change foraging behavior and alter the susceptibility of focal prey (Tahvanainen and Root 1972, Pfister and Hay 1988, Bergvall et al. 2006, Miller et al. 2007). From the perspective of a focal prey (i.e., seed) species, these predator-mediated indirect interactions (Wootton 1994, Abrams 1995) can take 2 forms: (1) “associational resistance” occurs when neighboring species decrease a focal species’ susceptibility to removal, and (2) “associational susceptibility” occurs when neighboring species increase a focal species’ susceptibility to removal (Atsatt and O’Dowd 1976, Wahl and Hay 1995, White and Whitham 2000, Barbosa et al. 2009).

Studies have examined associational resistance and susceptibility in the context of rodent-seed interactions. In forested ecosystems, researchers have found associational susceptibility (Caccia et al. 2006, Emerson et al.

2012), associational resistance (Garcia et al. 2007, Emerson et al. 2012), and no evidence for such interactions (Hulme and Hunt 1999). In shrubsteppe ecosystems, researchers have observed associational susceptibility (Veech 2001, Veech and Jenkins 2005, Ostoja 2007), whereas managers have tried to induce associational resistance through the use of highly preferred “sacrifice” seeds that do not germinate and establish in the environment (Longland and Bateman 1998, Monsen et al. 2004). Most of these past studies (except see Veech 2000) have considered pairwise comparisons between preferred and less preferred seed species, even though managers are likely to use more than 2 seed species when reseeding.

The objectives of this study were to examine how the relative proportion of seeds in a 3-species polyculture changes rodent seed selectivity (i.e., removal) and indirect interactions among the seeds. To address these objectives, we used 2 common, nocturnal shrubsteppe rodents (deer mice *Peromyscus maniculatus* Wagner and Great Basin pocket mice *Perognathus parvus* Peale). Firstly, we presented rodents with equal proportions of 10 seed species to determine the rank order of preference for seed species commonly used in rangeland treatments. Secondly, we presented rodents with 3-species seed mixtures that varied in the proportion of a highly preferred, a moderately preferred, and a least preferred seed species in fixed-time arena trials. Finally, we conducted field trials where we presented rodents with 3-species seed mixtures varying in the proportion of the highly preferred, moderately preferred, and least preferred seed species in 2 types of environments, “treated” (reduced shrub and increased forb cover) and “untreated” sagebrush.

METHODS

Study Area

We conducted this study on Bureau of Land Management and privately owned lands in a cold-desert, shrubsteppe ecosystem in the northern half of Rich County, Utah. Mean annual precipitation is 315 mm; mean annual temperature is 3.3 °C, with mean maximum temperatures in July of 28 °C and mean minimum temperatures in January of -17 °C (Western Regional Climate Center, Reno, NV). Trapping to obtain rodents for the arena

TABLE 1. Ten seed species included in fixed-time cafeteria trials to assess preference by deer mice (*Peromyscus maniculatus*) and Great Basin pocket mice (*Perognathus parvus*).

Scientific name	Common name	Code	Origin	Class
<i>Achnatherum hymenoides</i>	Indian ricegrass	ACHY	Native	Perennial grass
<i>Agropyron cristatum</i>	Crested wheatgrass	AGCR	Nonnative	Perennial grass
<i>Bromus tectorum</i>	Cheatgrass	BRTE	Nonnative	Annual grass
<i>Elymus elymoides</i>	Squirreltail	ELEL	Native	Perennial grass
<i>Hesperostipa comata</i>	Needle and thread grass	HECO	Native	Perennial grass
<i>Linum lewisii</i>	Blue or prairie flax	LILE	Native	Perennial forb
<i>Medicago sativa</i>	Alfalfa	MESA	Nonnative	Perennial forb
<i>Onobrychis viciifolia</i>	Sainfoin	ONVI	Nonnative	Perennial forb
<i>Pseudoroegneria spicata</i>	Bluebunch wheatgrass	PSSP	Native	Perennial grass
<i>Sanguisorba minor</i>	Small burnet	SAMI	Nonnative	Perennial forb

experiment occurred in Duck Creek and New Canyon grazing allotments (latitude 41°38'–41°51' N, longitude 111°5'–111°24' W; elevation 1950–2230 m). We conducted field trials within a pasture in the Duck Creek grazing allotment (treated: 41°50' N, 111°11' W, untreated: 41°50' N, 111°11' W; elevation 2075–2090 m). The treated area was mechanically treated using a Lawson Pasture Aerator in 2003 and was immediately seeded with the species listed in Stringham (2010; Table A1). Treated areas had ~25% less shrub cover and ~50% more forb cover than untreated areas (Stringham 2010). A complete list of plant species present in the study area is found in Ripplinger (2010). Common rodent species include deer mice, Great Basin pocket mice (hereafter “pocket mice”), Wyoming ground squirrels (*Spermophilus elegans* Kennicott), least chipmunks (*Tamias minimus* Bachman), sagebrush voles (*Lemmiscus curtatus* Cope), and northern pocket gophers (*Thomomys talpoides* Richardson).

Seed Preference

We determined seed preferences of 29 deer mice and 23 pocket mice from June to August 2007. Cafeteria trials involved placing wild-caught rodents in 1.2 × 1.1 × 0.8-m wooden arenas and offering them a choice of seeds. We captured rodents for the trials by using Sherman live traps (H.B. Sherman Inc., Tallahassee, Florida). Arenas contained 2–4 cm of sand and included a nest box with cotton nesting material. Each rodent had a choice of seeds from 9 species commonly used in rangeland rehabilitation and one invasive species, cheatgrass (Table 1). We placed 2 g of each seed into ten 8 cm diameter petri dishes. We arranged petri dishes in an arc equidistant to the nest box entrance and randomly assigned seed

species to each dish. Fixed-time cafeteria trials in the arenas lasted from 20:30 at night to 5:30 in the morning, after which rodents were released at the site of capture. We weighed seeds remaining in each dish and ranked preference using a modified form of Chesson's α index that accounts for food depletion during the course of a trial (Manly et al. 1972, Chesson 1978).

Based on results of the preference experiment, we identified a highly preferred seed, a moderately preferred seed, and a least preferred seed to make 3 different 3-species seed mixtures for each rodent species (hereafter “treatments”; Table 2). For deer mice, we used Indian ricegrass (*Achnatherum hymenoides* Roem. & Schult.; highly preferred), blue flax (*Linum lewisii* Pursh.; moderately preferred), and alfalfa (*Medicago sativa* L.; least preferred). For pocket mice, we used Indian ricegrass (highly preferred), alfalfa (moderately preferred), and blue flax (least preferred). For each rodent species, there were 3 treatments: a high-quality treatment (mostly the most preferred seed), equal proportions treatment (equal proportions of all 3 seeds), and low-quality treatment (mostly the least preferred seed) that were based on each species' preferences (Table 2).

Arena Experiments

In July–September 2007 and June–August 2008, we conducted an experiment to examine how changes in the proportion and relative preference of seeds in a seed mixture affect rodent selectivity. We conducted 46 trials for deer mice and 54 for pocket mice in 2007, and 63 trials for both deer mice and pocket mice in 2008. For each trial, rodents were offered seeds representing one of the 3 treatments described in Table 2. We used the same arenas

TABLE 2. Mass of seeds (highly preferred, moderately preferred and least preferred) for three 3-species treatments offered to rodents in the arena experiment. Mixture names reflect the most abundant seeds in the mixture. Field experiments offered five 3-species treatments, including treatment 1 and treatments 2 and 3 for each rodent species. ACHY = *Achnatherum hymenoides*, LILE = *Linum lewisii*, and MESA = *Medicago sativa*.

Treatment	Mixture	Deer mice			Pocket mice		
		Highly	Moderately	Least	Highly	Moderately	Least
		ACHY (g)	LILE (g)	MESA (g)	ACHY (g)	MESA (g)	LILE (g)
1	Equal proportion	3	3	3	3	3	3
2	High quality	5.25	3	0.75	5.25	3	0.75
3	Low quality	0.75	3	5.25	0.75	3	5.25

and fixed-time trial structure as in the seed preference experiment. However, seeds were mixed and distributed evenly over a seed tray filled with sand rather than separated into petri dishes. Seed trays were made of a $50 \times 35 \times 4$ -cm wooden frame with a 20×20 -gauge mesh bottom that allowed sand to pass through but retained seeds. Trays were partially buried 2 cm into the sand at the start of each trial. After each trial, we collected, sorted, and weighed seeds remaining in the seed trays, nest jar, and sand.

Field Experiment

We exposed seeds to nocturnal rodents for one night 6 times in 2008 (2 Jun, 17 Jun, 1 Jul, 15 Jul, 31 Jul, and 13 Aug). Because nocturnal rodent behavior is influenced by the lunar cycle (Kelt et al. 2004), we conducted each experiment within 2 nights of the full or new moon to balance data collection over moon phases. Each experiment included 100 seed trays in the treated area and 100 trays in the untreated area. Trays were in transects that were 80 m apart and 40 m from and parallel to the treatment edge. Ten meters separated each tray along each transect.

Trays were of similar size to those used in the arena experiments ($51 \times 31 \times 4$ cm; Pactiv Shallow Full Size Aluminum Steam Table Pan, Lake Forest, IL). Trays were buried into the ground and filled with sand. In the untreated area, trays were placed so that half of each tray was under a shrub (primarily *Artemisia tridentata* Nutt., but under *Chrysothamnus viscidiflorus* Nutt. if *A. tridentata* was absent). In treated areas, trays were located at least 10 m from any shrub.

To determine deer and pocket mouse abundance near field trays, we established a 225-trap grid with 10-m spacing in both treated

and untreated areas. We trapped for three 5-night sessions between field experiment time periods 1 and 2, 3 and 4, and 5 and 6: 10–14 June, 7–11 July, and 4–8 August 2008, for a total of 1125 trap-nights per session in both areas. A robust design (Pollock 1982) was used to derive abundance estimates for each of the 3 sessions on the treated and untreated sites in Program MARK (White and Burnham 1999).

We randomly assigned one of 5 treatments (high and low quality for each species and equal proportions; Table 2) to each tray on each of the 6 dates. We had intended for these 5 treatments to represent equal, high-, and low-quality treatments for each rodent species. However, after analyzing trapping results, we assumed field trays were impacted primarily by pocket mice over the course of the study and, therefore, analyzed only the 3 pocket mouse treatments: high quality, equal proportions, and low quality, as described in Table 2.

Seeds were spread out as evenly as possible on top of the sand in each tray. Seeding was timed to be completed at dusk civil twilight to reduce the influence of diurnal rodent species. The following morning, seed collection started at dawn civil twilight. Seeds were sifted out of the trays by using a 20×20 -gauge mesh filter, sorted, and weighed to determine the amount of each seed species removed.

Statistical Analyses

To determine whether removal of seed species changed with treatments, we needed to account for variation in each trial in the amount of each seed available and in the amount of total seed removed by individual rodents. To do this, for each arena and field trial, we determined the difference (hereafter difference values) between the observed amount of seed

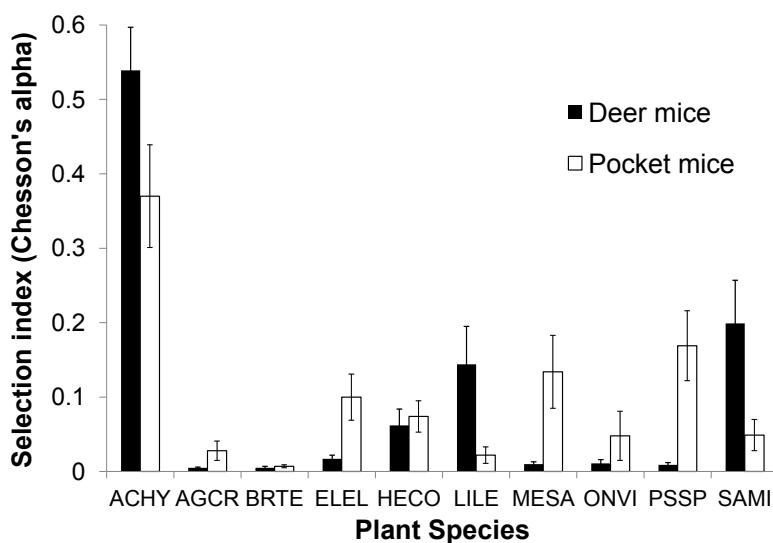


Fig. 1. Selection indices (Chesson's α ; error bars represent 1 SE) from cafeteria trials for deer mice (*Peromyscus maniculatus*) and pocket mice (*Perognathus parvus*). Greater values indicate greater preference. Plant species are abbreviated using genus and species names (see Table 1).

removed of each seed species and the expected amount of seed removed of each seed species. Thus, positive difference values indicated greater removal than expected, and negative difference values indicated less removal than expected. The observed amount of each seed species removed was measured directly. The expected amount of each seed species removed was determined by dividing the amount of that seed presented (0.75 g, 3 g, or 5.25 g) by the total amount of all seeds presented (9 g in all cases) and then multiplying by the total amount of seeds removed by the individual rodent. This adjustment standardized consumption and difference values to individual mice, each of which removed different amounts of the total seed available.

For the arena experiment, we assessed the effects of the 3 treatments (high-quality, equal, and low-quality mixtures) on difference values for each seed species separately using a one-way ANOVA. Treatment was the single fixed-effects factor in a completely randomized design. Separate analyses were conducted for each rodent species. Separate analyses were conducted for removal of total seeds. To determine pairwise differences among least-squares means, we used a Tukey–Kramer test.

For the field experiment, we used an ANOVA to assess the effects of treatment (3 levels: high-quality, equal, and low-quality mixtures),

date (6 levels), and site (2 levels: treated and untreated) on total seed removed and difference values for each seed removed. Treatment, date, site, and all 2- and 3-way interactions were included as fixed-effects factors. Separate analyses were conducted for removal of total seeds. To determine pairwise differences among least-squares means, we used a Tukey–Kramer test.

Data analyses were generated using the GLIMMIX procedure in SAS/STAT software, v. 9.2 for Windows (SAS Institute, Inc., Cary, NC). All tests were considered significant at the $\alpha = 0.05$ level.

RESULTS

Seed Preference

Individuals of both rodent species readily acclimated to the arenas, remaining in the nest boxes during the day and emerging at night to forage. Indian ricegrass was selected most often by both species, and both species had low preference for cheatgrass and crested wheatgrass (*Agropyron cristatum* Gaertn.; Fig. 1). The rank order of the selection index values for the other species, however, varied considerably between deer mice and pocket mice.

Arena Experiments

Deer mice in the arena experiment validated preferences found in the cafeteria trials

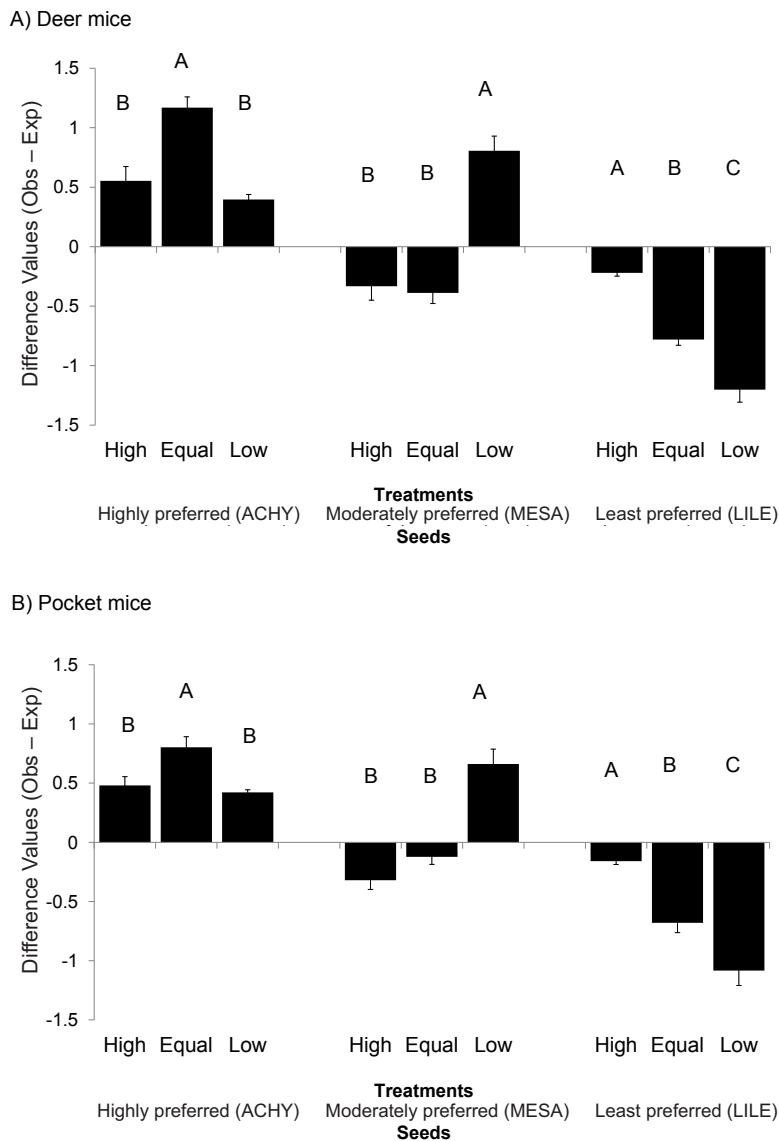


Fig. 2. Difference values (observed – expected; error bars represent 1 SE) of seeds removed of the highly, moderately, and least preferred seed in the high-quality, equal proportions, and low-quality mixtures: A, deer mice (*Peromyscus maniculatus*); B, pocket mice (*Perognathus parvus*) in an arena experiment. Mixtures are defined in Table 2. Different letters show significant differences for seed species among treatments ($P < 0.05$).

(Fig. 2A). This is best illustrated with the equal proportions treatment. For the highly preferred seed, difference values were greatest when the proportions of all seeds were equal (equal proportions mixture), rather than when the highly preferred seed was in highest proportion (high-quality mixture) or when the least preferred seed was in the highest proportion (low-quality mixture) (Fig. 2A). For the

moderately preferred seed, difference values were greatest when the least preferred seed was in the highest proportion (low-quality mixture) and not different between the high-quality and equal proportions mixtures. For the least preferred seed, difference values were greatest in the high-quality mixture compared to the equal proportions and the low-quality mixtures.

Pocket mice in the arena experiment also validated preferences found in the cafeteria trials in the equal proportions mixture (Fig. 2B). The results for pocket mice were very similar to those for deer mice. For the highly preferred seed, difference values were greater in the equal proportions mixture than in the high-quality or low-quality mixture (Fig. 2B). For the moderately preferred seed, difference values were greatest in the low-quality mixture and not different between the high-quality and equal proportions mixtures. For the least preferred seed, difference values were greatest in the high-quality mixture, rather than in the equal proportions or low-quality mixture.

There was no difference in total seeds removed among treatments for either deer mice or pocket mice (Supplementary Table 1). Deer mice moved negligible amounts of seeds into the nest jar or sand. Pocket mice, on the other hand, moved 17% into the nest jar and 28% into the sand of the total amount they removed.

Field Experiment

During the 3 trapping sessions, estimated pocket mouse abundance was 8 (SE 2), 18 (2), and 33 (2) individuals per trap area in the treated area and 35 (SE 3), 46 (3), and 36 (3) individuals per trap area (140 × 140 m) in the untreated areas (Supplementary Tables 2, 3). We were unable to estimate deer mouse abundance because of small sample sizes and low recapture rates, but we captured 0, 0, and 2 individuals per trap area in the treated area and 1, 6, and 2 individuals per trap area in the untreated area during the 3 trapping sessions, respectively. To provide comparable numbers for the pocket mice, we captured 7, 15, and 31 individuals in the treated area and 30, 39, and 31 individuals in the untreated areas during the 3 trapping sessions, respectively.

Across all treatments and time periods, greater proportions of Indian ricegrass seeds were removed (48.8%, SE 1.8) than alfalfa (47.0%, SE 1.8) and blue flax (41.4%, SE 1.6), which was consistent with pocket mouse but not deer mouse preferences. This pattern of pocket mouse preference is also well illustrated in the equal proportions treatment (Fig. 3).

For all 3 seeds, there was a significant effect of treatment on difference values (Table

3). For the highly preferred seed, difference values were greater in the equal proportions mixture than in the high-quality or low-quality mixture (Fig. 3). For the moderately preferred seed, difference values were greatest in the low-quality mixture, followed by the equal proportions and then the high-quality mixture. For the least preferred seed, difference values were greatest in the equal proportions mixture, rather than in the low-quality or the high-quality mixture. For the moderately and least preferred seeds, results revealed complex treatment × site × date interactions (Table 3; Supplementary Fig. 1).

For total seeds removed, there was no difference by treatment (Table 3). There was an interaction between treatment (high, equal, low) and date (Fig. 4). There was also an interaction between site (treated, untreated) and date, because more seeds were removed from untreated areas earlier in the season and from treated areas later in the season (Table 3; Fig. 5).

DISCUSSION

Seed Preference

Deer mice and pocket mice both preferred Indian ricegrass and exhibited low preference for cheatgrass and crested wheatgrass, but these rodents otherwise differed in their relative preferences. Previous studies on rodent-seed interactions across multiple sagebrush ecosystems also have noted a strong preference of rodents for Indian ricegrass (Everett et al. 1978, Kelrick et al. 1986, Henderson 1990, Veech 2001, Sivy et al. 2011) and low preference for cheatgrass seeds (Everett et al. 1978, Kelrick et al. 1986, but see Veech 2001). Deer mouse rank-preferences in this study corresponded well to those described in Everett et al. (1978).

Indirect Interactions

Our results demonstrated that the relative amount and identity of neighboring seeds can influence a focal seed's susceptibility to rodent removal. In general, our results with 3-species seed mixtures were consistent with previous 2-species and 3-species comparisons that had more evidence for associational susceptibility than associational resistance (Veech 2000, 2001, Veech and Jenkins 2005, Caccia et al. 2006, Ostojka 2007). We found associational susceptibility largely for the least preferred

TABLE 3. ANOVA results on the difference values (observed – expected) of seeds removed from seed trays from the field experiment conducted in Rich County, Utah. Seed species abbreviations are defined in Table 1. Bolded probability values are statistically significant.

Highly preferred seed (ACHY)				
Effect	Num df	Den df	<i>F</i> value	Pr > <i>F</i>
Treatment	2	672	11.13	<0.0001
Date	5	672	1.81	0.1077
Treatment × Date	10	672	0.90	0.5310
Site	1	672	0.14	0.7049
Treatment × Site	2	672	0.53	0.5917
Site × Date	5	672	0.87	0.4984
Treatment × Site × Date	10	672	1.43	0.1636
Moderately preferred seed (MESA)				
Effect	Num df	Den df	<i>F</i> value	Pr > <i>F</i>
Treatment	2	672	11.25	<0.0001
Date	5	672	3.53	0.0037
Treatment × Date	10	672	0.51	0.8846
Site	1	672	0.26	0.6116
Treatment × Site	2	672	2.55	0.0790
Site × Date	5	672	1.03	0.4006
Treatment × Site × Date	10	672	1.89	0.0441
Least preferred seed (LILE)				
Effect	Num df	Den df	<i>F</i> value	Pr > <i>F</i>
Treatment	2	672	5.34	0.0050
Date	5	672	2.55	0.0269
Treatment × Date	10	672	0.75	0.6743
Site	1	672	0.31	0.5769
Treatment × Site	2	672	0.56	0.5701
Site × Date	5	672	0.95	0.4483
Treatment × Site × Date	10	672	2.11	0.0220
Total seed removed				
Effect	Num df	Den df	<i>F</i> value	Pr > <i>F</i>
Treatment	2	672	1.00	0.3680
Date	5	672	32.87	<0.0001
Treatment × Date	10	672	2.58	0.0048
Site	1	672	19.24	<0.0001
Treatment × Site	2	672	1.00	0.3703
Site × Date	5	672	11.29	<0.0001
Treatment × Site × Date	10	672	1.34	0.2056

and moderately preferred seed, similar to other studies, which primarily found this result for the least preferred seed (see Veech 2001, Caccia et al. 2006). In general, the results from the arena experiments for the 2 rodent species were very similar, even though the seed mixtures for the 2 rodent species were made up of different seed species. This similarity suggests that the types of indirect interactions are consistent across the dominant rodents in this ecosystem.

More specifically, we found that in the high-quality mixture, where the proportion of the highly preferred seed was high, the least

preferred seeds were more likely to be removed by rodents and the highly preferred seeds were less likely to be removed. This suggests that least preferred seeds do not escape removal by association with high-quality seeds, even when the less preferred seed is in low abundance, and that the seed will, in fact, have a greater chance of removal.

Furthermore, we found that in the low-quality mixture, where the proportion of least preferred seed is high, moderately preferred seeds were more likely to be removed and the least and highly preferred seeds were less likely to be removed. More specifically, the

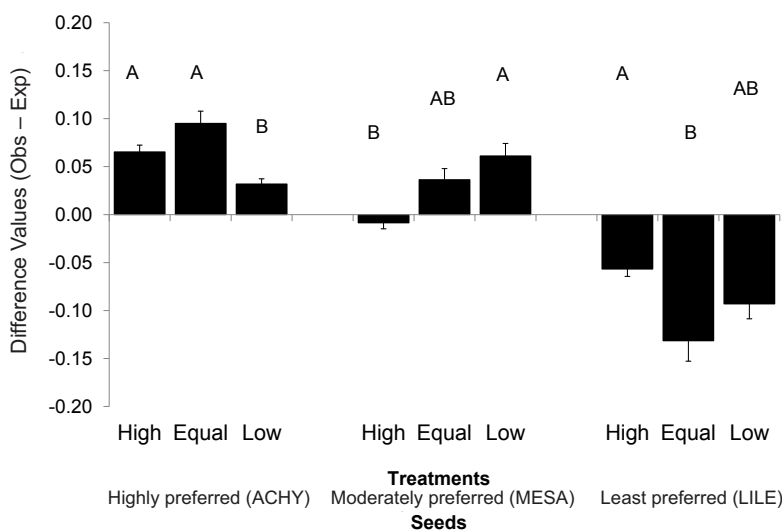


Fig. 3. Difference values (observed - expected; error bars represent 1 SE) of seeds removed of the highly, moderately, and least preferred seed in the high-quality, equal proportions, and low-quality mixtures during a field experiment in Rich County, Utah. Mixtures are those defined for pocket mice (*Perognathus parvus*) in Table 2. Different letters show significant differences for seed species among treatments ($P < 0.05$).

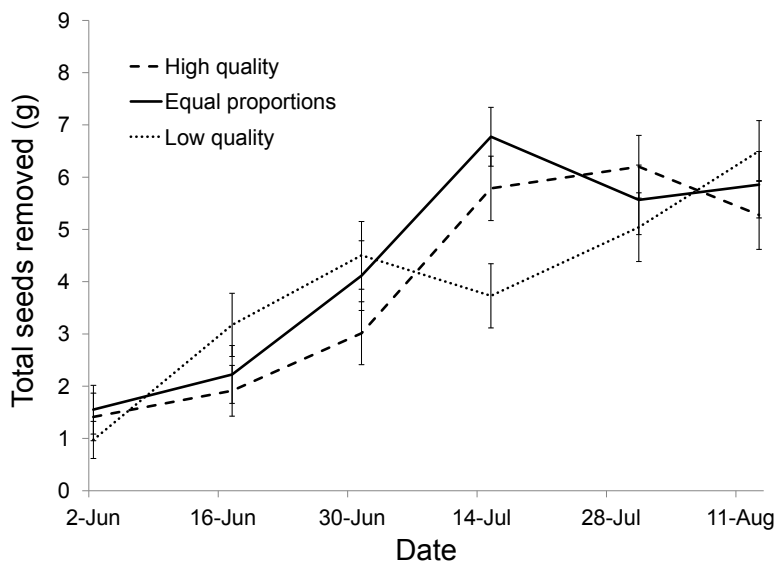


Fig. 4. Total seeds removed from seed containing from the high-quality, equal proportions, and low-quality seed mixtures during a field experiment in Rich County, Utah.

moderately preferred seed was removed more when the least preferred seed was in high abundance and the highly preferred seed was in low abundance.

The result that the highly preferred seeds experienced less removal in low-quality mixtures is unlike some studies of rodent-seed

interactions, which did not find evidence of associational resistance for highly preferred seeds (Veech 2000, 2001, Veech and Jenkins 2005, Caccia et al. 2006, Ostojka 2007). However, similar to the results of this study, Emerson et al. (2012) detected associational resistance for untreated sunflower seeds mixed

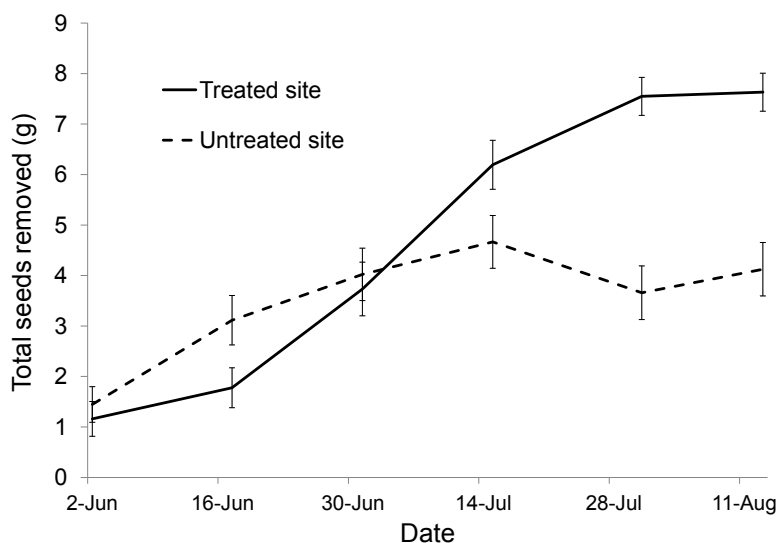


Fig. 5. Total seeds removed from seed trays in a treated area (shrubs removed) and untreated area during a field experiment in Rich County, Utah.

with higher proportions of sunflower seeds treated to be less palatable, and Garcia et al. (2007) found associational resistance for a preferred seed in mixtures with higher proportions of less preferred seeds. In our study, rodents removed more of the moderately preferred seed in a low-quality patch, possibly due to increased difficulty in locating the highly preferred seed. In summary, we found that we could “protect” a highly-preferred seed by increasing the proportion of the least preferred seed, but that this would in turn increase removal of the moderately preferred seed.

Results from the field experiment, which we assume primarily show the preferences of pocket mice, had trends similar to results from the arena experiments for pocket mice. The only real difference in trends between the arena and field experiments was that, in the field experiment, the least preferred seed had lower difference values in the equal proportions treatment than in the low-quality treatment. This difference implies that, in the low-quality mixtures in the field, rodents will forage more on the least preferred seed when it is abundant. In addition, though the same trends were typically observed in the 2 experiments, the difference values in the field were lower than those in the arena, suggesting that the effects were not as strong. It is difficult

to know what drove this weaker effect in the field. It may reflect differences in rodent density (i.e., rodent density may have been lower in the field) and that in the field there are other food sources that rodents could utilize. In addition, it is possible that multiple rodents visited the tray over time and that each rodent encountered a different patch quality based on what previous rodents left behind, thereby dampening the indirect interactions.

Though we found that the amount and identity of neighboring seeds influences a focal seed's susceptibility to removal, we did not find that differences in the structure or composition of the ecosystem influenced indirect interactions among seeds (but see Caccia et al. 2006, as in Nunez et al. 2008). More specifically, whether seeds were located in areas that had been treated (where seeds had reduced shrub cover and increased forb cover) or untreated (where seeds were placed underneath a shrub) did not influence the indirect interactions among seeds. We had hypothesized that treatments might influence the results because of perceived differences in predation risk. Perhaps the increase in herbaceous cover offset the reduction in shrub cover, in which case responses might differ in newly treated areas with less herbaceous cover. Alternatively, even though rodents are thought to be more selective under high predation

risk (Bowers 1988, Leaver and Daly 2003), it is possible that perception of risk for rodents has no effect on indirect interactions among seeds (Sivy et al. 2011).

The overall increase in total seed removal over the season is likely the result of the general shift in these rodents' diets from insects and green foliage to seeds as the availability of seeds increases over the course of the season. We did find that total seed removal in treated and untreated sites differed across the season, with rodents removing more seeds from untreated areas earlier in the season and more from treated areas later in the season. Greater seed removal early in the season in the untreated area could have occurred because of the higher rodent populations in the untreated area early in the season. Greater seed removal in the treated area later in the season might have occurred because of the increase in rodent abundance in the treated, but not the untreated, area over the season or because of an influx of pre-adults in the treated area. Trapping data indicated that pre-adults accounted for most of the rise in rodent abundance in the treated area in August, and it is possible that pre-adults remove more seeds than adults to fuel growth and development.

We were focused on how 3-seed interactions affected selectivity. It is important to note that our experiments did not follow the fate of individual seeds outside of the arena experiment and that not all removed seeds are consumed, especially those removed by pocket mice (Vander Wall et al. 2005). Pocket mice possess external cheek pouches that allow them to collect and cache a considerable number of seeds (Vander Wall 1998); in fact, in our arena experiment, we found that 45% of the removed seed was either brought back to the nest jar or scattered in the sand, and pocket mice did this for all 3 species that were removed. We found that deer mice in the arena, on the other hand, did this only for a negligible amount of seed (Vander Wall et al. 2001). In the field, it is very likely that the majority of seeds that pocket mice do not consume will be placed in burrows and shallow caches and that the seeds may germinate from the latter (Longland et al. 2001). Thus, in areas where heteromyid rodents dominate, seed species, especially those with large seeds that are unlikely to experience abiotic burial, may benefit from being removed from the surface

where desiccation, ultraviolet radiation, and predation by other animals is high, especially in arid environments (Longland et al. 2001). However, in areas where deer mice dominate, we hypothesize that seed caches do not play as large of a role in plant recruitment. Testing how the indirect interactions observed in this study translate into plant recruitment is an important area for future research.

Implications

Seeding with seed mixtures is a pervasive and costly management action that needs to be further investigated to enhance its effectiveness. The seed mixtures used in the present study are representative of those used in actual, ongoing restoration actions on sagebrush ecosystems. In our 3-seed mixtures, we found that for both common rodent species, preferred seeds "escape" removal with an increase in the proportion of less preferred seeds. Thus, managers may be able to reduce removal of a highly preferred seed by increasing the abundance of the least preferred seed, especially if a moderately preferred seed is present and more abundant than the highly preferred seed. We also found that seeding mixtures with a greater proportion of highly preferred seeds did not prevent removal of less preferred seeds. Thus, managers are not likely to protect an expensive, less preferred seed by increasing the proportion of inexpensive, more preferred seed. Furthermore, it is very important that managers view these results in light of the type of rodent community and the types of interactions that rodents have with seeds after they remove them. More specifically, in some ecosystems, removal is beneficial and may be the preferred response. Interactions among seeds in mixtures with more than 3 species are likely to show even more complex interactions, and much more research is needed in this area to understand how to seed effectively.

ACKNOWLEDGMENTS

Research was funded in part by the Utah Division of Wildlife Resources, the Utah Department of Natural Resources—Endangered Species Mitigation Fund, the Natural Resources Conservation Service, the Quinney Foundation, and the United States Geological Service. Funding also came through the Utah Division

of Wildlife Resources Great Basin Research Center via Pittman–Robertson Federal Aid to Wildlife Restoration Grant W-82-R. We thank the BLM, the USDA Forest Service, the Rich County Coordinated Resource Management Group, and local landowners for support; R. Norvell, J. Ripplinger, J.A. MacMahon, J. Martin, T.A. Monaco, and G. Oliver for technical and logistical support; S.M. Ostoja, S.K.M. Ernest, and R.J. Ryel for helpful advice; R. Choi and C. Olson for statistical analyses; J.H. Welch, S.N. Casebolt, E.A. Fuerst, D.S. Green, C.M.J. Hiher, and J.D. Wood for field assistance; and D.S. Green, J.T. Cheney, G.F. Diamond, J. Gibson, and M. Warren for lab assistance. Mention of any product by name does not constitute endorsement by the U.S. Geological Survey. Research was conducted under Utah State University IACUC Permit #1316.

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Received 14 November 2012

Accepted 4 June 2013

SUPPLEMENTARY TABLE 1. ANOVA results on the difference values (observed – expected) of seeds removed from seed trays in the arena experiment. Seed species abbreviations are defined in Table 1. Rodent species are deer mouse (*Peromyscus maniculatus*) and Great Basin pocket mouse (*Perognathus parvus*). Bolded probability values are statistically significant.

Rodent species	Variable	Num DF	Den DF	F value	Pr > F
Deer mouse	Total seed removed	2	59	0.22	0.8035
	Highly preferred seed (ACHY)	2	59	16.95	<0.0001
	Moderately preferred seed (LILE)	2	59	25.73	<0.0001
	Least preferred seed (MESA)	2	57	14.06	<0.0001
Pocket mouse	Total seed removed	2	60	2.66	0.0784
	Highly preferred seed (ACHY)	2	60	45.08	<0.0001
	Moderately preferred seed (MESA)	2	60	25.45	<0.0001
	Least preferred seed (LILE)	2	55	14.34	<0.0001

SUPPLEMENTARY TABLE 2. *Perognathus parvus* population modeling methods. We trapped for three 5-night sessions between field experiment time periods (10–14 June, 7–11 July, and 4–8 August 2008) for a total of 1125 trap-nights per session in both areas. A robust design was used to derive abundance estimates for each of 3 primary occasions on the treated and untreated sites, each consisting of 5 secondary occasions (Pollock 1982). Apparent survival (Φ), capture probability (p), recapture probability (c), and apparent abundance (N) were modeled as (i) constant, (ii) varying between treated and untreated sites, (iii) varying by time, and (iv) constrained over primary periods. Because temporary emigration was infrequent, γ' and γ'' were kept constant (see Kendall and Nichols [1995] for definitions). All over-parameterized models were removed from analysis, based on standard error estimates (Zwolak and Foresman 2008). We used model averaging to reduce model selection bias (White 1999).

Model	AIC _c	Δ AIC _c	AIC _c weights	Model likelihood	Number of parameters
$\Phi(\cdot)\gamma'(\cdot)\gamma''(\cdot)p1(\cdot)p2(\cdot)p3(\cdot)c1(\cdot)c2(\cdot)c3(\cdot)N1(g)=N2(g)=N3(g)$	308.4156	0	0.7601	1	11
$\Phi(\cdot)\gamma'(\cdot)\gamma''(\cdot)p1(\cdot)p2(\cdot)p3(\cdot)c1(\cdot)c2(\cdot)c3(\cdot)N1(\cdot)N2(\cdot)N3(\cdot)$	312.1242	3.7086	0.119	0.1566	12
$\Phi(\cdot)\gamma'(\cdot)\gamma''(\cdot)p1=c1p2=c2p3=c3N1(g)=N2(g)=N(g)$	313.4063	4.9907	0.06268	0.0825	8
$\Phi(\cdot)\gamma'(\cdot)\gamma''(\cdot)p1(\cdot)p2(\cdot)p3(\cdot)c1(\cdot)c2(\cdot)c3(\cdot)N1(g)N2(g)N3(g)$	314.1658	5.7502	0.04288	0.0564	15
$\Phi(\cdot)\gamma'(\cdot)\gamma''(\cdot)p1(g)p2(g)p3(g)c1(\cdot)c2(\cdot)c3(\cdot)N1(\cdot)N2(\cdot)N3(\cdot)$	317.1022	8.6866	0.00988	0.013	15
$\Phi(\cdot)\gamma'(\cdot)\gamma''(\cdot)p1=p2=p3, c1=c2=c3N1(\cdot)N2(\cdot)N3(\cdot)$	318.2942	9.8786	0.00544	0.0072	8

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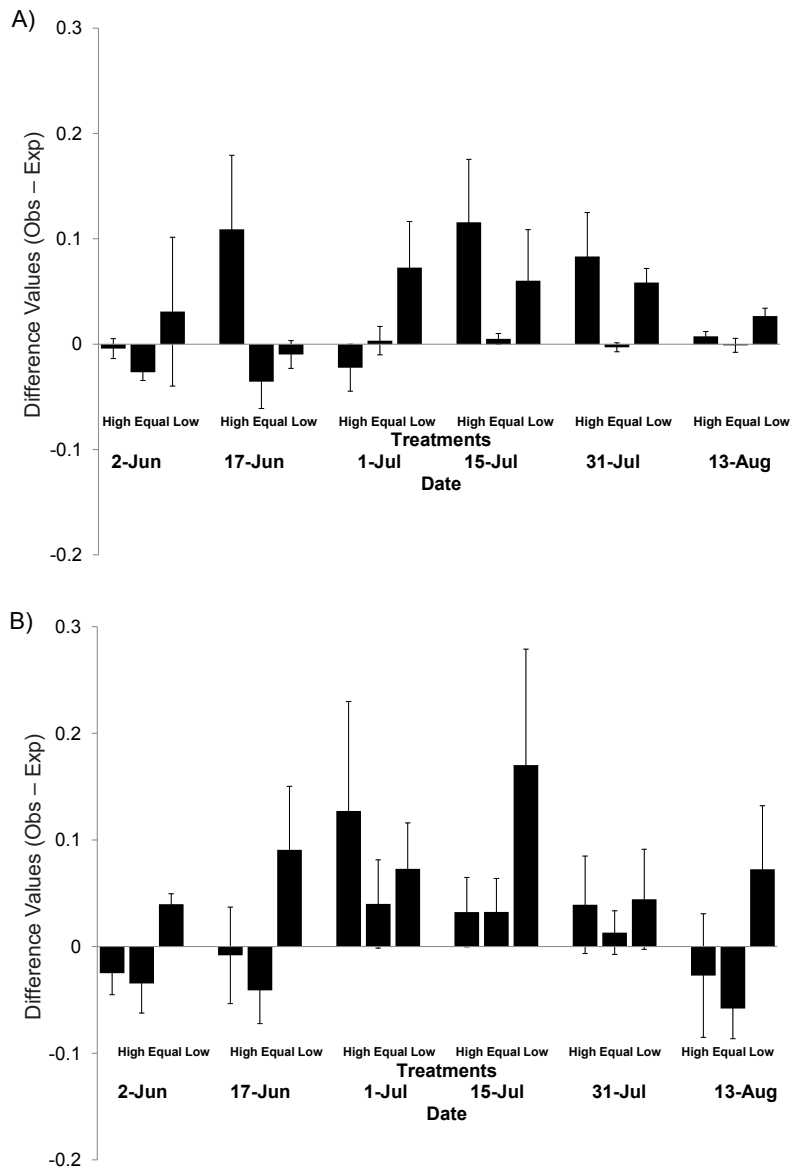
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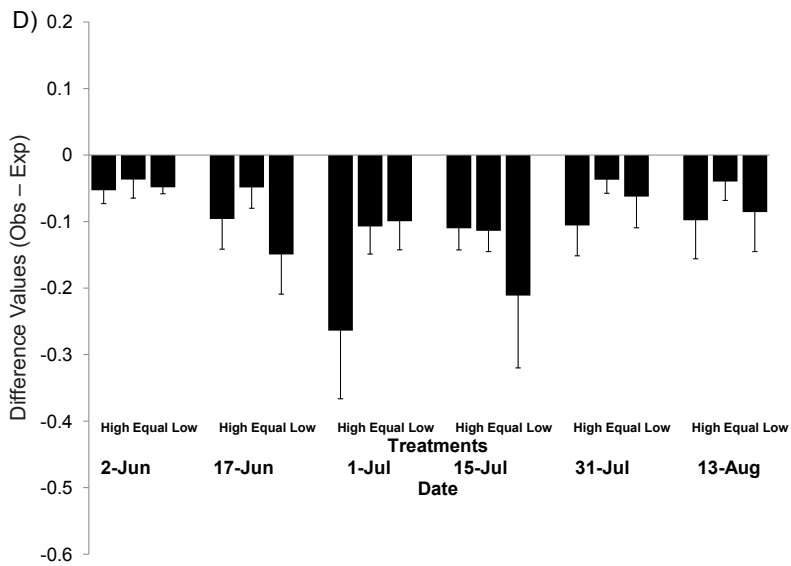
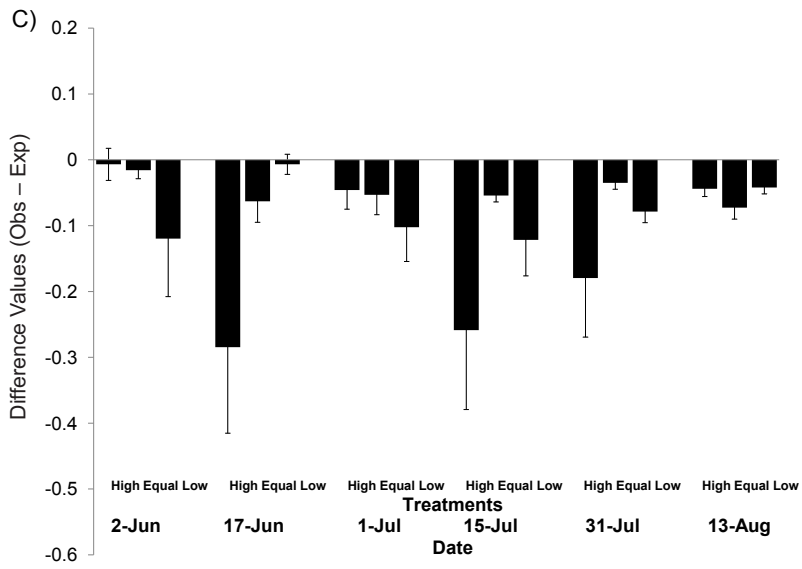
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SUPPLEMENTARY TABLE 3. *Perognathus parvus* abundance estimates over 3 sessions in treated and untreated areas during summer 2008. LCI and UCI show lower and upper 95% confidence interval estimates, respectively.

Session	Area	Abundance	SE	LCI	UCI
1	Treated	7.87	1.56	4.81	10.93
1	Untreated	34.79	3.08	28.75	40.84
2	Treated	17.54	2.30	13.02	22.05
2	Untreated	45.59	3.45	38.82	52.35
3	Treated	33.46	2.12	29.30	37.62
3	Untreated	36.21	2.88	30.56	41.85



Supplementary Fig. 1. Difference values (observed – expected; error bars represent 1 SE) in the high-quality, equal the least preferred seed in (C) treated and (D) untreated areas in Rich County, Utah. Mixtures are those defined for



proportions, and low-quality mixtures for the moderately preferred seed in (A) treated and (B) untreated areas, and for pocket mice (*Perognathus parvus*) in Table 2.