COMPARING THE EFFECTS OF GRANIVOROUS RODENTS ON PERSISTENCE OF INDIAN RICEGRASS (*ORYZOPSIS HYMENOIDES*) SEEDS IN MIXED AND MONOSPECIFIC SEED PATCHES

Joseph A. Veech[1,3] and Stephen H. Jenkins[2]

ABSTRACT.—In desert environments seeds are often heterogeneously distributed in small patches that vary in number of seed species and in seed density. Because seed harvest by rodents is often density dependent (a larger proportion of seeds is removed from high-density seed patches than from low-density patches), the proportion of residual or post-harvest seeds should be greater in low-density patches. In addition, seed preference can affect harvest. We tested whether the residual proportion of a highly preferred seed (Indian ricegrass, *Oryzopsis hymenoides*) was less when in a seed patch with a 2nd species (mixed-species patch) than when in a monospecific seed patch. We predicted that the increased overall seed density due to the presence of 2 species in a patch would result in a lower residual proportion of ricegrass seeds in the mixed-species seed patches than in the monospecific patches. As predicted, the residual proportions of Indian ricegrass seeds were less each time ricegrass was paired with one of 6 other species in mixed-species patches. Similarly, the residual proportion of each of those 6 species was less when paired with ricegrass than when in a monospecific patch. We speculate on the potential implications of these results for the population dynamics of plant species and the physical structure of plant communities.

Key words: *heteromyid rodent, Indian ricegrass,* Oryzopsis hymenoides, *density-dependent foraging, seed-tray experiment.*

Indian ricegrass (*Oryzopsis hymenoides*) is a perennial bunchgrass found throughout western North America. It is often associated with loose substrates such as the sand typical of sand dunes and other arid habitats (Jones 1990). It shares this habitat affinity with heteromyid rodents (family Heteromyidae), such as kangaroo rats (*Dipodomys*) and pocket mice (*Chaetodipus* and *Perognathus*), also widespread and locally abundant in arid parts of western North America. Indian ricegrass usually produces seeds during the summer months. Heteromyid rodents are capable of harvesting a large portion of the seed crop of some plant species (Soholt 1973, Nelson and Chew 1977, McAdoo et al. 1983, Longland et al. 2001), which they either immediately consume or cache for later use (McAdoo et al. 1983, Longland et al. 2001, Veech 2001). Many rodent species prefer seeds of Indian ricegrass over seeds of other plant species (McAdoo et al. 1983, Kelrick et al. 1986, Henderson 1990, Jenkins and Ascanio 1993, Longland and Bateman 1998, Veech 2001). Thus, Indian ricegrass may be an important

component in sustaining populations of granivorous rodents and, in some years, the caching of seeds by rodents may serve as a source of recruitment for ricegrass populations (McAdoo et al. 1983, Young et al. 1983, Longland et al. 2001).

Regardless of whether rodents have an overall positive effect on Indian ricegrass populations by caching seeds that subsequently germinate, or a negative effect due to seed consumption, the 1st step in this interaction is the harvest of seeds from the immediate area around adult plants. This area may be no larger than a dinner plate as the seeds are heavy and not likely to be dispersed by wind. Furthermore, the spatial distribution of seeds in desert ecosystems is often heterogeneous (Reichman 1976, Nelson and Chew 1977, Price and Reichman 1987, Henderson et al. 1988, Price and Joyner 1997, Anderson and MacMahon 2001); relatively dense concentrations of seeds of different species occur in depressions in the soil surface or against objects (e.g., small rocks, shrubs) that block the wind. Thus, the seed resource

[1]Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523.
[2]Ecology, Evolution, and Conservation Biology Program, Department of Biology, University of Nevada–Reno, Reno, NV 89557.
[3]Present address: Department of Biological Sciences, University of Northern Colorado, Greeley, CO 80639.

of granivorous rodents can be viewed as existing within distinct small spatial patches. Rodents forage for seeds in and among these patches.

The harvesting of seeds by heteromyid rodents is sometimes density dependent (Price and Heinz 1984, Brown 1988, Bowers 1990, Mitchell and Brown 1990, Veech 2000, 2001). In the present study we define *density-dependent foraging* as the harvest (i.e., removal) of a larger proportion of seeds (of a given species) from patches with high overall seed densities than from patches with low densities. *Overall* seed density is defined as the combined density of seeds of all species. If the proportion of seeds harvested is density dependent, then the proportion of seeds that are not harvested is also density dependent. We refer to this latter proportion as residual seeds. We tested for differences in the residual number of Indian ricegrass seeds in patches consisting solely of ricegrass (monospecific patches) and patches consisting of ricegrass and seeds of 1 of 6 other species (mixed-species patches). The initial number of ricegrass seeds was the same in both types of patches; thus, the mixed-species patches represented a higher initial seed density than the monospecific patches.

We were primarily interested in testing whether the presence of a 2nd seed species could, by increasing overall seed density, affect the residual number of Indian ricegrass seeds. Previously, it was demonstrated that density-dependent harvest occurs when rodents forage in monospecific patches with substantially different initial seed densities (Brown 1988, Mitchell and Brown 1990, Veech 2000). Indeed, this type of density-dependent foraging is somewhat easy to demonstrate. However, density-dependent harvest may also occur under a different (and perhaps more realistic) scenario where differences in seed densities among patches are due to the presence of additional seed species, not merely to differences in the density of a single seed species. That is, the actual type of patch (monospecific seed patches versus patches with seeds of multiple species) might influence harvest rates and residual seed densities. The residual seeds not harvested from a patch may, in some cases, act as a channel of recruitment for a plant population. Thus, we also present our study as an example of the potential need to consider density-dependent foraging in studies and models of the population dynamics of plants producing seeds that are foraged by rodents.

We predicted that the residual number of Indian ricegrass seeds would be greater in monospecific patches than in mixed-species seed patches. We also compared the residual seed numbers of the other 6 species when paired with Indian ricegrass and when in a monospecific seed patch. Again, we predicted a greater number of residual seeds in monospecific seed patches because their lower total seed density induces less foraging.

METHODS

Description of Study Site

We measured rodent harvesting of seeds of *Oryzopsis* and 6 other plant species at a study site about 80 km northeast of Reno, Nevada, USA. These species were *Astragalus cicer*, *Panicum miliaceum*, *Sphaeralcea coccinea*, *Stanleya pinnata*, an unidentified species of *Lupinus*, and an unidentified species of *Penstemon*. All of the species were found at or near the study site except for *Panicum* and *Astragalus*, although a congener of *A. cicer* (*A. lentigenosus*) was found at the study site. We used *Panicum* (millet) as a proxy for a seed type that is highly preferred by rodents; *Panicum* is often used to trap rodents and to study their foraging behavior. We collected seeds of *Lupinus*, *Penstemon*, *Sphaeralcea*, and *Stanleya* at the study site while seeds of the other 3 species were obtained from a commercial supplier.

The heteromyid rodent community at the study site was diverse. Extensive trapping by other researchers has revealed the existence of 8 species: *Chaetodipus formosus, Dipodomys deserti, D. merriami, D. microps, D. ordii, Microdipodops pallidus, Perognathus longimembris,* and *P. parvus* (Breck and Jenkins 1997, Jones and Longland 1999). We live-trapped rodents on 21 June 1998 to confirm the existence of rodents on our study blocks (see next section). We caught 38 individuals representing 5 species in a total of 200 traps. The relative abundances of each species in terms of percentage of total individuals captured were *D. merriami* (71.1), *D. microps* (10.5), *M. pallidus* (2.6), *P. longimembris* (7.9), and *P. parvus* (7.9). Although there were also granivorous ants and birds at the study site, most of the seed harvesting that

occurred during the seed-tray experiment (see below) could be attributed to rodents because the seeds were covered with sand and not accessible to birds and ants (Longland et al. 2001).

Seed-tray Experiment

We measured harvesting of seeds of *Oryzopsis* and the other plant species by determining the number of seeds removed from trays containing a known number of seeds. Seed-tray experiments have been widely used for more than a decade to measure seed harvest by heteromyid rodents. Rodents readily enter seed trays to forage, particularly if the trays are filled with a natural substrate (e.g., sand). On several occasions we visually observed rodents foraging in our seed trays. Seed-tray experiments will overestimate absolute rates of seed harvest if rodents "learn" to use the trays as cues for foraging. However, our primary interest was in comparing harvest in monospecific seed patches (*Oryzopsis* only) with mixed-species seed patches (*Oryzopsis* and a 2nd species) and not in measuring absolute rates of harvest.

We established 3 blocks at the study site; blocks were separated by about 300 m. Each block consisted of 4 rows of 12 stations spaced 20 m apart. The spacing between adjacent rows was 80 m. At each station we placed 3 seed trays spaced 1 m apart. These trays were small aluminum pans (diameter 22.5 cm, depth 5.5 cm) containing seeds and sand. Together the 3 trays represented the following treatments: (1) 100 seeds of *Oryzopsis* without species X, (2) 100 seeds of species X without *Oryzopsis*, (3) 100 seeds of *Oryzopsis* with species X, and (4) 100 seeds of species X with *Oryzopsis*, where X refers to one of the 6 species previously listed. The first 2 treatments are represented by monospecific seed trays. We refer to the 3rd and 4th treatments as the mixed-species seed tray; that is, the mixed-species tray represents 2 treatments. Within each row, each pairing of *Oryzopsis* with another species was represented twice at randomly chosen stations and so each pairing was represented 8 times in each block. A total of 3 blocks yielded a sample size of 24 for each pairing. Note that with this experimental design we were not attempting to distinguish the effects of seed density from the effects of number of seed species (1 or 2) on harvest rates. That is, the treatment with a higher overall seed density also always contained 2 seed species.

In each seed tray we placed a 1-cm layer of sand that had been cleaned of all debris. We then sprinkled the seeds on this sand layer and covered the seeds with another 1-cm layer of sand to prevent harvesting by birds and ants. Trays were left out in the field for approximately 30 nights, allowing ample time for rodents to find and forage in all trays. We then collected the trays and counted the number of seeds remaining in each tray. This seed-tray experiment was conducted from 16 July 1998 to 13 August 1998 (run 1) and again from 17 August 1998 to 19 September 1998 (run 2). The experiment was conducted twice in the same summer because it was suspected that the depletion of naturally occurring seeds might affect the intensity of seed removal from the trays.

For each station we recorded 4 variables: the number of *Oryzopsis* seeds remaining in their monospecific tray ($NORY_{mono}$), the number of species X seeds remaining in their monospecific tray (NX_{mono}), and the number of *Oryzopsis* and species X seeds remaining in the mixed-species tray ($NORY_{mix}$ and NX_{mix}, respectively). We added 0.5 to the raw data to make zero values non-zero (<1% of the values in the entire data set were zero) and then log-transformed the data to achieve normality (Sokal and Rohlf 1995). The transformation succeeded in producing a more normal distribution although it was still slightly left-skewed because about 25% of the values represented ≤20 surviving seeds and 50% of the values represented ≥75 surviving seeds.

We were primarily interested in testing whether the proportions of residual seeds of *Oryzopsis* (and the other species) were different in the monospecific and mixed-species seed trays. However, we also tested for differences between the 2 runs of the seed-tray experiment and between the plant species. We conducted a split-plot ANOVA, in which Run and Species X were treated as categorical variables, with 2 and 6 levels respectively. Each station contained only 1 level of each variable; thus we had a split-plot design with Run and Species X as between-plot factors. A separate preliminary ANOVA did not reveal a block effect; thus it was not included. The within-plot factor was Type of Seed Patch with the following treatments: monospecific patch of

TABLE 1. Results of the ANOVA testing for an effect of Type of Seed Patch, Run, and Species X on the number of residual seeds of *Oryzopsis* and Species X.

Source	SS	DF	MS	*F*	*P*
Type of Seed Patch	37.6	3	12.5	42.2	< 0.001
Type of Seed Patch · Run	3.5	3	1.2	4.0	0.008
Type of Seed Patch · Species X	73.9	15	4.9	16.6	< 0.001
Type of Seed Patch · Run · Species X	26.4	15	1.8	5.9	< 0.001
Error	245.6	828	0.3	—	—

Oryzopsis, monospecific patch of species X, and mixed-species patch containing *Oryzopsis* and species X. The ANOVA provided a test of the effect of Type of Seed Patch on the number of residual seeds (df = 4 – 1). This was essentially a test of whether log-transformed values of $NORY_{mono}$, $NORY_{mix}$, NX_{mono}, and NX_{mix} differed, but with no distinction made among the 6 species represented by X. The ANOVA also tested for an interaction between Type of Seed Patch and Run [df = (4 – 1) · (2 – 1) = 3]. In addition, the interaction between Type of Seed Patch and Species X was tested by the ANOVA [df = (4 – 1) · (6 – 1) = 15]. This was essentially a test of whether the number of residual seeds of the 7 species (*Oryzopsis* and the 6 species X) differed and whether the differences were related to being in a monospecific versus mixed-species patch. Finally, the ANOVA also tested the interaction of Type of Seed Patch · Run · Species X [df = (4 – 1) · (2 – 1) · (6 – 1) = 15].

The relative effect of rodents on *Oryzopsis* seeds in monospecific and mixed-species seed patches was measured as the ratio of $NORY_{mono}$ to $NORY_{mix}$. Similarly, the effect of rodents on seeds of species X (without regard to the exact identity of X) in monospecific and mixed-species seed patches was measured as the ratio of NX_{mono} to NX_{mix}. A ratio significantly different from 1.0 indicates that proportions of residual seeds in monospecific and mixed-species patches were different. We also tested for differences between $ln(NX_{mono})$ and $ln(NX_{mix})$, separately for each species X, using paired *t* tests. The monospecific and mixed-species seed trays at each station formed a pair.

RESULTS

The type of seed patch clearly had a significant effect on residual seed numbers ($F_{3,828}$ = 42.2, P < 0.001) as revealed by the ANOVA (Table 1). Because NX_{mono}, NX_{mix}, $NORY_{mono}$, and $NORY_{mix}$ were significantly different, further tests to elucidate the differences were warranted. Combining data for both runs, the ratio of $ln(NX_{mono}):ln(NX_{mix})$ was significantly >1.0 (ratio = 1.048, $F_{12,276}$ = 4.5, P < 0.001) as was the ratio of $ln(NORY_{mono}):ln(NORY_{mix})$ (ratio = 1.073, $F_{12,276}$ = 4.3, P < 0.001). However, the ANOVA also revealed a significant interaction between Type of Seed Patch and the 2 runs of the seed-tray experiment as well as an interaction between type of patch and the 6 species represented by X (Table 1). Because of these interactions, we did not combine data from the 2 runs or any of the seed species in subsequent analyses. The proportion of residual seeds was lower during run 2 than run 1 for all species (Fig. 1). In addition, some species (e.g., *Penstemon* and *Stanleya*) tended to have greater residual seed numbers than the other species (Fig. 1).

Paired *t* tests were conducted to further elucidate these differences between species, type of patch, and the 2 runs of the seed-tray experiment. For each run and each species, we tested H_0: $ln(NX_{mono})$ – $ln(NX_{mix})$ = 0 against the alternative hypothesis H_1: $ln(NX_{mono})$ – $ln(NX_{mix})$ > 0. For all species, the proportion of residual seeds was significantly greater in the monospecific seed trays than in the mixed-species seed trays for at least 1 run of the seed-tray experiment, typically for both runs (Table 2). We also tested for a difference in the residual number of *Oryzopsis* seeds in the monospecific seed trays and when paired with each of the other 6 species in the mixed-species seed trays. We found only 2 instances of significant differences. After run 2 of the seed-tray experiment, the residual number of *Oryzopsis* seeds was greater in monospecific seed trays than in trays also containing *Astragalus* (mean difference = 0.533, $s_{\bar{x}}$ = 0.162, N = 24, t = 3.28, P = 0.0016). The same result
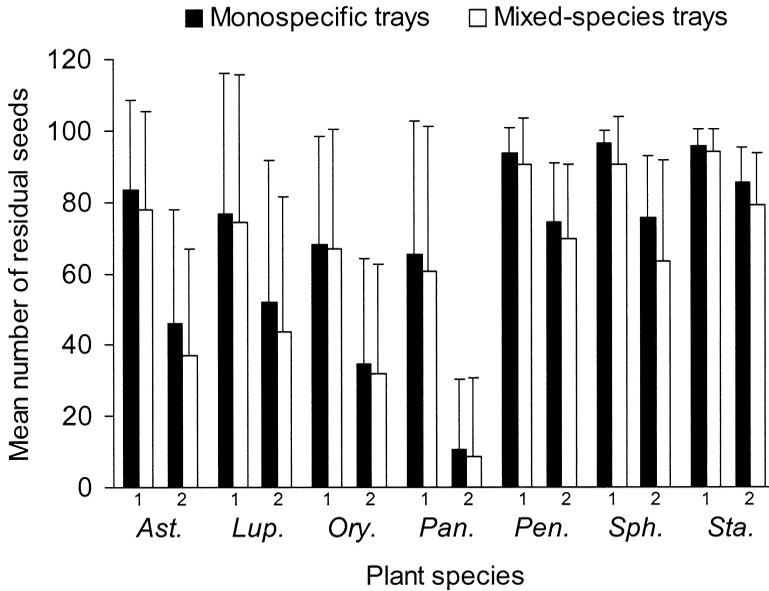
Fig. 1. Mean number of residual seeds in the monospecific and mixed-species seed trays for each of the 7 plant species used in this study. Names of plant species are abbreviated as the first 3 letters of the genus name. Numbers 1 and 2 along the x-axis refer to runs 1 and 2 of the seed-tray experiment. Note that the number of residual seeds was always greater during run 1 and always greater in the monospecific than in the mixed-species seed trays. Results for *Oryzopsis* are for its pairings with all other species ($N = 144$ for each bar). Error bars represent +1 s.

emerged when *Oryzopsis* was paired with *Panicum* during run 2 (mean difference = 0.727, $s_{\bar{x}}$ = 0.188, $N = 24$, $t = 3.88$, $P = 0.0008$). However, when residual numbers of *Oryzopsis* seeds were pooled across all 6 other species, the larger sample size provided a more powerful test, and significant differences between monospecific and mixed-species patches were found for run 1 (mean difference = 0.078, $s_{\bar{x}}$ = 0.046, $N = 144$, $t = 1.71$, $P = 0.045$) and run 2 (mean difference = 0.221, $s_{\bar{x}}$ = 0.067, $N = 144$, $t = 3.32$, $P = 0.0006$).

DISCUSSION

As predicted, the type of seed patch (monospecific or mixed-species) influenced the number of residual seeds that remained after rodents foraged within the patches. For each plant species, the number of residual seeds was lower in the mixed-species seed patches than in the monospecific seed patches (Fig. 1). These differences are consistent with density-dependent foraging given that the monospecific and mixed-species seed patches differed

in initial overall seed density. Researchers often use seed trays to study foraging behavior (Brown 1988, Brown et al. 1988, 1992, Valone and Brown 1989, Mitchell and Brown 1990, Kotler et al. 1993, Hughes et al. 1995, Meyer and Valone 1999, Mohr et al. 2003). Our definition of density-dependent foraging and our use of the seed-tray experiment do not allow for any inferences about the behavior of individual rodents. Rather, density-dependent foraging is seen as a collective property of the community of granivorous rodents. The 2 types of seed patches also differed in composition (1 versus 2 seed species), and thus differences in residual seed proportions may also have emerged from foraging behavior (e.g., assessment of patch quality based on composition) not due to seed density.

We wish to direct attention to the potential effect of seed foraging by rodents on plant population dynamics. Thus, instead of deciphering the intricacies of foraging behavior, we were primarily interested in the way in which the initial species composition and seed density within a seed patch affect the final

TABLE 2. Results of the paired *t* tests for each plant species and each of the 2 runs of the seed-tray experiment.

Species	Run	Difference in no. residual seeds in monospecific and mixed seed trays[1]	$s_{\overline{x}}$	t	P
Astragalus	1	5.7	0.043	2.16	0.021
	2	9.1	0.110	2.51	0.010
Lupinus	1	2.6	0.149	1.91	0.034
	2	8.5	0.129	2.55	0.009
Panicum	1	4.8	0.126	2.54	0.009
	2	1.7	0.277	1.86	0.038
Penstemon	1	3.2	0.023	1.95	0.032
	2	5.0	0.057	1.62	0.059
Sphaeralcea	1	6.0	0.035	2.18	0.018
	2	12.2	0.091	3.11	0.003
Stanleya	1	1.3	0.018	0.84	0.205
	2	6.3	0.050	1.79	0.043

[1]Values shown are the mean ($NX_{mono} - NX_{mix}$) paired at each station; *t* tests were applied to ln-transformed data (df = 24 for each test). Standard errors are for the transformed data.

proportion of residual seeds. Presumably, residual seeds may germinate in the spring if conditions are appropriate. Seed patches containing only 1 species tended to have a greater number of residual seeds than did patches containing seeds of 2 plant species. Thus, it is possible that germination of seedlings from the former type of patch is more probable than germination from mixed-species patches. If so, the 2 types of patches may differ in their potential as sources of recruitment for the plant population of a given species.

The composition of a seed patch might not only affect the absolute number (or probability) of recruits but also the spatial patterning of a plant community. The proportion of residual *Oryzopsis* seeds in the mixed-species patches varied depending upon which other species was present. For example, during late summer (after run 2 of the seed-tray experiment) there were fewer *Oryzopsis* seeds in patches with *Panicum* seeds than in patches with *Stanleya* seeds. Thus, differences between species might affect the physical structure of the plant community; we might expect to find adult *Oryzopsis* individuals paired with *Stanleya* more so than with a plant species whose seeds are preferred by the rodents. Indeed, of the 7 plant species in this study, heteromyid rodents have distinct and consistent preferences for some seeds and avoidance of others (Veech 2001). Seed preference may, in part, be due to seed size and the nutritional content of the seeds (Lockard and Lockard 1971, Reichman 1977, Kelrick et al. 1986, Henderson 1990, Podolsky and Price 1990, Jenkins and Ascanio

1993). *Oryzopsis* is a highly preferred seed with an average mass of 3.7–4.4 mg and high carbohydrate content, whereas the average mass of *Penstemon,* a highly avoided seed, is 0.9–1.1 mg. Seed size is widely thought to affect competition among seedlings (Harper 1977, Rees and Westoby 1997); perhaps, the effect of seed size on seed harvest is another basic feature of plant population biology.

In the specific case of *Oryzopsis* and other seeds preferred by rodents, the harvest of seeds may have either positive or negative effects on plant population dynamics. Heteromyid rodents are known to cache the seeds of many different species in shallow subsurface scatterhoards (Reynolds 1958, Smith and Reichman 1984, McAuliffe 1990, Longland 1995). Caching of Indian ricegrass seeds has been documented (McAdoo et al. 1983, Young et al. 1983, Breck and Jenkins 1997, Pyare and Longland 2000, Longland et al. 2001) and may actually have a net positive effect on Indian ricegrass populations when seedlings emerge and establish from the caches (Longland et al. 2001). Alternatively, harvest may also be followed by immediate or later consumption of seeds after recovery from caches.

Our study demonstrates that the harvest of Indian ricegrass seeds depends upon the density of seeds in the patch as well as the presence of seeds of other species. The presence of a 2nd seed species elevated overall seed density such that harvest of ricegrass seeds was increased, perhaps due to density-dependent foraging by heteromyid rodents. Such knowledge might be useful in attempts to

restore degraded rangeland. Indian ricegrass is valued as forage for livestock (Robertson 1976, Jones 1990, Orodho and Trlica 1990, Young et al. 1994, Bich et al. 1995) and is often used in rangeland restoration (Plummer and Frischknecht 1952, Jones 1990, Young et al. 1994, Grantz et al. 1998, Humphrey and Schupp 1999, 2002). Our results suggest that the success of efforts to restore Indian ricegrass may depend on which other species are present in the seed bank and the degree to which seeds are heterogeneously distributed in patches.

Finally, the results of our study could also be interpreted as another demonstration of short-term apparent competition (Holt and Kotler 1987) among seed species (Veech 2001), because seed "predation" was greater in the mixed-species seed patches. Recall that the residual numbers of seeds were less in such patches. Short-term apparent competition is the decreased survival of a prey species when in a patch with a 2nd prey species than when alone (Holt and Kotler 1987). It can occur if the 2 prey species share a predator species. Invoking the concept of apparent competition is not necessary to understand our results; however, the concept does reemphasize that the fate of seeds in a patch depends on whether seeds of other species are also present in the patch.

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