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Abstract. Seed predation by rodents had major direct and indirect impacts on experimental plantings of 16 species of herbaceous dicots of the prairie/savanna interface in southwestern Wisconsin. We broadcast seeds in the autumn of 1997 on 18 2 × 2 m plots surrounded by rodent-proof fencing. Experimental treatments included: (1) continuous rodent exclusion, (2) rodent access from December to April, and (3) rodent access from May to November. Highly selective seed predation by meadow voles (*Microtus pennsylvanicus*) during the winter directly reduced densities of the aggressive, large-seeded composite *Silphium integrifolium* by 59%. Indirectly, this suppression of *Silphium* resulted in 24–132% compensatory increases in the abundance of small-seeded species not eaten by voles, and a 33% increase in diversity of plant species as estimated by Simpson's *D*. Vole herbivory and granivory during the spring and summer had no influence on overall plant abundance or species richness. As these synthetic communities mature, initial winter suppression of *Silphium integrifolium* and the compensatory response of small-seeded composites and legumes not eaten by voles may foretell a divergence of community succession.

Key words: foraging theory; forbs; granivory; meadow vole; Microtus pennsylvanicus; *path analysis; prairie restoration; rodents; seed predation;* Silphium integrifolium; *tallgrass prairie.*

Introduction

Tallgrass prairie and the prairie/forest interface are among the two most endangered plant communities in North America (Noss et al. 1995, Sampson and Knopf 1996). Using methods adapted from regional restoration efforts (Rock 1981), we explored the potential effects of small-rodent granivory and herbivory on the reestablishment of dicot species commonly found in these habitats. We used replicated synthetic communities to determine whether optimal foraging theory can predict the direct effects of rodent granivory on these miniature restorations, and whether plausible inferences from such direct effects can predict the indirect responses from plants not eaten by rodents. The effort is part of a genre of studies (Howe and Brown 1999; H. F. Howe and J. S. Brown, *unpublished manuscripts*) intended to document and distinguish effects of small vertebrates on tallgrass communities.

The pervasive impacts of large mammals on grassland structure and diversity are increasingly well known (e.g., McNaughton 1984, Collins 1987, Milchunas et al. 1988, Huntly 1991, Howe 1994*a*, 1999*a*, Anderson and Briske 1995), but potentially comparable effects of small vertebrates are far less understood (Rose and Birney 1985, Reader 1991, 1992, Hulme 1996). Yet, ubiquitous small rodents almost certainly have widespread direct and indirect impacts on plant communities. At high densities, voles (*Microtus* spp.) devastate dicot communities (Batzli 1985), strongly alter community composition in native and planted California grasslands (Batzli and Pitelka 1970), and potentially alter the course of forest succession by eliminating or drastically reducing densities of seedlings of otherwise prominent eastern hardwood trees (Ostfeld and Canham 1993, Ostfeld et al. 1997). In tallgrass restorations in Illinois, seed-eating birds reduce overall seedling densities by >20% without affecting plant diversity, but selective herbivory by meadow voles (*Microtus pennsylvanicus*) reduces plant diversity during early succession without affecting overall plant density (Howe and Brown 1999). Foraging decisions of ubiquitous small birds and rodents appear likely to have widespread direct and indirect impacts on plant communities.

Here, we used exclosures to test for the direct and indirect consequences of rodent foraging on two general processes. First, we used controlled seedings of large- and small-seeded prairie and savanna dicots to determine whether rodents selectively deplete large-seeded species (Brown 1989). As a corollary, size-selective seed predation should indirectly promote the success of species with seeds too small to be preferred by rodents. Second, we tested for a vegetation response to herbivory by rodents. Voles should have selectively depleted relatively undefended or especially nutritious dicots (e.g., Batzli and Cole 1979, Cole and Batzli 1979, Lindroth and Batzli 1984, Howe and Brown 1999), and should promote the compensatory response of seedlings of species not eaten by rodents.

Unlike other experiments in this genre, which involved continuing exposure of some plots to granivores and herbivores, here we isolated the effects of seed selection from herbivory. Exclosures open to rodents

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TABLE 1. Species planted at 100/m² per species in 18 2 × 2 m exclosures in October 1997 in Wisconsin.

Species†	Family	Common name	Seed mass (mg)
Large seeds (>3.0 mg/seed)			
Cassia marilandica	Fabaceae	Maryland senna	23.1
Desmanthus illinoensis	Mimosaceae	Illinois bundleflower	5.3
Desmodium glutinosum	Fabaceae	Hairy tick treefoil	32.1
Echinacea pallida	Asteraceae	Pale coneflower	5.4
Echinacea purpurea	Asteraceae	Purple coneflower	4.1
Heliopsis helianthoides	Asteraceae	Early sunflower	3.5
Lupinus perennis	Fabaceae	Lupine	23.2
Silphium integrifolium	Asteraceae	Rosenweed	15.2
Small seeds (<3.0 mg/seed)			
Achillea lanulosa	Asteraceae	Native yarrow	0.1
Aster laevis	Asteraceae	Smooth aster	0.2
Astragalus canadensis	Fabaceae	Canadian milk vetch	1.7
Dalea candida	Fabaceae	White prairie clover	1.4
Dalea purpurea	Fabaceae	Purple prairie clover	1.5
Lespedeza virginica	Fabaceae	Slender bush clover	2.8
Ratibida pinnata	Asteraceae	Yellow coneflower	0.6
Solidago rigida	Asteraceae	Rigid goldenrod	0.7

† Species names follow Fernald (1950). Habitat use was determined with the help of Deam (1940), Fernald (1950), Gleason (1963), Curtis (1959), Mohlenbrock (1986), and Swink and Wilhelm (1994).

in winter were closed in spring, whereas those open to herbivory in summer were closed in autumn. Of interest were echoes of effects of initial granivory (winter access) as compared with effects of initial herbivory (summer access) by the end of the first growing season.

METHODS

Site and preparation.—Our experiment was established at the edge of a 6-ha field occupied by a larger 1990 grassland restoration near Viola, Vernon County, Wisconsin, USA (43°32′ N, 90°20′ W; Howe 1994*b*, 1995, 1999*b*). Plots were positioned to simulate a grassland/ forest border in mesic to dry-mesic conditions. In 1995, ground for the exclosure experiment was plowed and disced. Eighteen 2 × 2 m plots were delineated by 0.6 m deep trenches dug with a trencher, and 1.2 m hardware clothe fences were erected. Two rows of 9 plots (a 2 × 9 grid) paralleled each other and a north–south forest border; the western line of nine plots was 4 m from an *Acer/Quercus/Carya* woodland border, the eastern line 2 m away was contiguous with the older restoration experiment. Lanes 2 m wide planted with Kentucky bluegrass (*Poa pratensis* L.) separated the plots. To minimize contamination by rhizomatous perennial weeds, the ground to be planted with prairie/savanna seeds was covered with black plastic from June 1995 until October 1997.

Exclosures.—At planting, three exclosures within each row were assigned as "winter access," three as "summer access," and three as "no access." For winter access plots, 2 5 × 5 cm gates were cut in each of four walls at ground level on 19 October 1997; these gates were closed on 24 April 1998. For summer access plots, similar gates were cut on 20 May 1998; these gates were closed on 4 November 1998. Plots to which rodents were denied access received no gates. All exclosures from which rodents were excluded for any given period of time were crowned with aluminum flashing borders, which overlapped the outside wall by 25–35 cm. All exclosures were fitted with 1.5 cm mesh plastic bird netting to exclude birds from 19 October 1997 to 20 May 1998. Large binder clamps prevented access by birds or slippage; heavy snow bowed the edges of the exclosures, but did not rip or loosen the nets. Nets were removed in May 1998 to limit insect herbivory by allowing bird access (Fowler et al. 1991, Marquis and Whelan 1994). Assignments within a row were random.

Plants.—To test seed-size selection, 16 dicot species and an interstitial cover of *Poa pratensis* (seed mass <0.2 mg at planting) were broadcast-seeded on 19 October 1997 (Table 1). To minimize wide differences in phylogenetic characteristics, eight composites and eight legumes were used (Table 1). Following Rock (1981), one bag of seeds mixed with damp sand was broadcast on slightly frozen ground on all 4 m² of each plot at a density of 100 seeds/m² per species. To minimize variance among plots and treatments, weeds were clipped or pulled by hand every two weeks from May through August.

To test for effects of diet selection, we included plant genera that are known to be eaten by the most common rodent herbivore in this field, *Microtus pennsylvanicus* (Howe and Brown 1999). Species included *Desmanthus illinoensis, Echinacea pallida, E. purpurea, Dalea candida,* and *D. purpurea.*

Seeds visible on the soil surface were counted in a central, permanently marked square meter in each exclosure on 29 March 1998. Early in the summer, seedlings of several experimental and weed species could not be distinguished. After plants matured enough to be readily recognized, reliable counts were made on 19 August and again on 11 October 1998. In each quarter of the 1-m² sample, the height of the tallest experimental dicot was recorded.

Estimates of plant density were augmented by two measures of plant biodiversity (Magurran 1988): species richness as the number of species in a sample, and Simpson's diversity index:

$$D = 1/\Sigma p_i^2$$

where p is the frequency of individuals of species i among all individuals from a given sample. Species richness accentuates the effect of rare species, whereas D accentuates the effect of numerical evenness in the species abundance distribution. The inverse of D is Simpson's index of numerical concentration, a measure of dominance.

Rodents.—Small mammals were live-trapped to determine the likely granivores and herbivores in the immediate vicinity of the plots. In each case, one Sherman live trap was placed outside the southeast corner of each of exclosure. These 18 traps served as a template for trap positions along the adjacent forest border and grassland restoration; 18 traps were placed 4 m and 8 m west in the forest border (1 m and 5 m inside the border), and 18 traps were placed 4 m and 8 m east of the exclosures in *Andropogon-*, *Panicum-*, and *Phalaris*-dominated restorations. Overall, the trapping area was 1500 m², of which 1000 m² was in grassy vegetation and 500 m² was in forest understory. Traps were baited with mixed cracked corn and sunflower seeds and were checked morning and evening for three days and three nights. Captured mammals were weighed, sexed, temporarily marked with individually unique fur clippings on the body, and released.

Censuses with 54 traps were conducted 18–21 October 1996, 14–18 August 1997, 17–19 October 1997, 18–22 May 1998, 17–22 August 1998, and 4–9 November 1998. In August and November 1998, an additional trap was placed within each exclosure.

Results

Emergence.—Fourteen of the 16 dicot species planted in the autumn of 1997 emerged during the 1998 growing season; only the legumes *Lespedeza virginica* and *Dalea candida* did not appear. Plots closed to rodents yielded 302 ± 30 seedlings/m², mean ± 1 SE (experimental dicots plus *Poa pratensis*) in July, 339 ± 19 seedlings/m² in August, and 302 ± 12 in October. Of these, experimental dicots (composites plus legumes) averaged 249 ± 25 seedlings/m² in July, 297 ± 19 in August, and 255 ± 16 in October, respectively. Seedling establishment continued into August, after which competition among plants increased mortality.

Once established, some species did not prosper. In plots continuously protected from rodents, the legumes *Desmodium glutinosum* and *Lupinus perennis* averaged 18.7 ± 4.4 plants/m² and 12.8 ± 2.6/m² in July, but only 2.2 ± 0.9/m² and 1.7 ± 0.8/m² by October, respectively. Most surviving individuals of these two species appeared to be unhealthy by October. Others were slow to appear: 1.5 ± 0.7 plants/m² *Aster laevis* were counted in protected plots in July, but 17.7 ± 3.2/m² were evident in the same plots in October. In general, legumes did not fare well, although some surviving individuals of *Astragalus canadensis*, *Cassia marilandica*, and *Desmanthus illinoensis* (and a few *Lupinus perennis*) appeared vigorous.

Surface seed counts.—Large seeds that could easily be counted on the soil surface in late March, 5 mo after sowing, included *Desmodium glutinosum*, a category termed "other legumes," and *Silphium integrifolium*. No seeds with mass <5 mg could be reliably counted.

Large seeds on the soil surface were dramatically depleted in the six exclosures exposed to rodents over the winter, as compared with the 12 inaccessible plots. Of 100 seeds/m² per species, *Desmodium glutinosum* averaged 43.0 ± 11.0 visible seeds/m² in inaccessible plots, but only 3.3 ± 1.8 in those open to rodents (t = 12.139, df = 12.1, $P < 0.001$; fractional degrees of freedom indicate that a t statistic was calculated with separate rather than pooled variances). Similarly, other legumes averaged 37.9 ± 18.6 seeds/m² in closed plots, but 14.2 ± 4.6 in plots with gates (t = 4.177, df = 13.4, P = 0.001). *Silphium integrifolium* averaged 41.6 ± 9.2 seeds/m² on the surface in inaccessible plots, but 12.2 ± 5.7 where rodents could enter freely (t = 8.297, df = 15, $P < 0.001$). These were not comprehensive censuses because seeds hidden in the soil could not be tallied, but they do show that large seeds were sharply depleted by rodents.

Seedling counts by species.—Seedling counts in August generally mirrored those in October (Table 2), with two exceptions. Sufficient numbers of *Desmodium glutinosum* and *Lupinus perennis* were present in August to test for the effects of rodent access, whereas by October, most of both species had disappeared in all plots. *Desmodium glutinosum* was significantly reduced in winter-access plots (2.0 ± 0.5 plants/m²) as compared with summer-access and no-access plots (15.2 ± 5.8 plants/m² and 16.5 ± 2.6/m²; $F_{2,15}$ = 4.268, $P < 0.05$). This result accords with the seed depletion of this species noted on the soil surface, but too few individuals survived the growing season to preserve the effect. Rodents had no apparent effect on *L. perennis*.

October seedling counts showed the direct reduction of one species from size-selective seed predation, and strong, indirect, positive responses of three species with seeds too small to be of interest to rodents (Table 2). *Silphium integrifolium*, a large-seeded and physically large prairie plant, experienced a 59% depletion on winter-access plots. Other statistically significant responses included increases in seedling numbers of *Aster laevis* (78%), *Ratibida pinnata* (56%), and *Astragalus canadensis* (132%) in winter-accessible plots as compared with summer-access and no-access plots.

TABLE 2. Seedling densities (no./m²) of eight composites and eight legumes, planted in a frost-seeding in October 1997 in 18 2 × 2 m exclosures and censused in October 1998. Also shown are results of univariate ANOVAs for each species.

Species binomial	Rodent access (no./m²)			$F_{2,15}$
	Winter	Summer	No access	
Large-seeded composites				
Echinacea pallida	20.3 ± 1.6	20.3 ± 3.4	21.5 ± 2.5	0.067
			37.3 ± 5.4	
Echinacea purpurea	38.5 ± 3.9	31.2 ± 7.6		0.335
Heliopsis helianthoides	28.2 ± 5.8	22.5 ± 4.8	21.2 ± 5.3	0.260
Silphium integrifolium	32.5 ± 3.2	74.0 ± 4.4	81.2 ± 3.7	55.617****
Small-seeded composites				
Achillea lanulosa	10.0 ± 2.7	5.0 ± 1.1	8.8 ± 1.5	1.828
Aster laevis	31.7 ± 4.6	17.7 ± 4.8	17.7 ± 3.2	3.594*
Ratibida pinnata	27.8 ± 3.2	17.3 ± 1.5	17.8 ± 1.0	7.608***
Solidago rigida	42.8 ± 5.4	34.5 ± 3.6	32.2 ± 3.1	1.813
Large-seeded legumes				
Cassia marilandica	2.5 ± 1.0	2.8 ± 1.0	2.2 ± 0.9	0.115
Desmanthus illinoensis	4.3 ± 1.7	3.2 ± 1.2	2.5 ± 1.4	0.409
Desmodium glutinosum	0.2 ± 0.2	2.3 ± 1.1	2.2 ± 0.9	2.077
Lupinus perennis	1.8 ± 0.7	2.6 ± 1.5	1.7 ± 0.8	0.260
Small-seeded legumes				
Astragalus canadensis	6.5 ± 1.3	2.2 ± 0.6	2.8 ± 0.7	6.519**
Dalea candida	0	0	0	
Dalea purpurea	0	0.2 ± 0.2	0.7 ± 0.3	2.600
Lespedeza virginica	0	0	0	

Notes: Numbers of seedlings per square meter (mean ± 1 SE) are indicated for six plots in each treatment level. Because each species was planted at 100 seeds/m², counts and their means are percentages.

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.005$, **** $P \leq 0.001$.

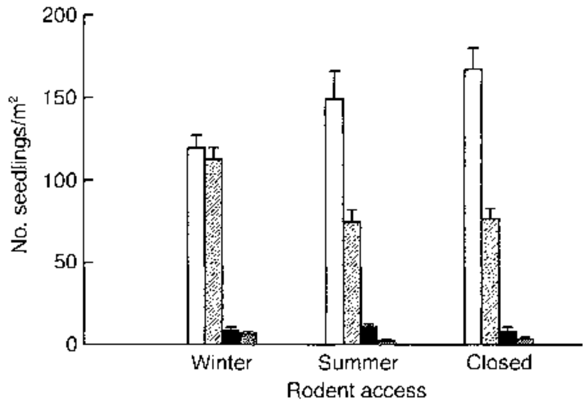

FIG. 1. Seedling density (mean + 1 SE) in October as a function of rodent access to seeds broadcast on the soil surface in the previous year. Large-seeded composites (open bars) were apparently depressed by vole access ($F_{2,15} = 3.340$, $P = 0.06$), an effect entirely due to severe depression of *Silphium integrifolium* ($F_{2,15} = 55.617$, $P < 0.001$), a prairie species with seeds of a size (15 mg) easily handled by voles and mice. As a group, composites with seeds too small to be preferred by rodents (diagonal hatching; seeds <0.1 mg) increased with rodent access ($F_{2,15} = 9.368$, $P < 0.002$). Large-seeded legumes (solid bars) did not differ appreciably across treatments ($F_{2,15} = 0.373$, $P > 0.9$), but small-seeded legumes (cross-hatched bars) increased with winter access ($F_{2,15} = 4.708$, $P < 0.05$). Responses of small-seeded composites and legumes are indirect effects in the path analysis (Fig. 2).

Two other small-seeded composites, *Achillea lanulosa* and *Solidago rigida,* showed positive, but not statistically significant, increases on winter-access plots in ANOVAs with three treatment levels (winter access, summer access, no access).

Mean seedling numbers are similar for closed and summer-access plots for virtually all species (Table 2). If these categories are pooled for contrast with winter-access plots from the October census, *F* statistics and significance levels predictably rise. The notable changes are that *Desmodium glutinosum* retains enough individuals to show the expected depression in winter-access plots ($F_{1,16} = 4.403$, $P = 0.05$) and the small-seeded composite, *Solidago rigida,* shows an expected positive response to rodent activity in the previous winter ($F_{1,16} = 3.661$, $P < 0.05$, one-tailed test).

Seedling counts by guild.—A design stratified by taxon and seed size in which seed-size categories within a taxon respond similarly to rodent access may also be profitably evaluated with a multivariate analysis of guild response (Fig. 1). Here, the large-seeded guild of composites is not coherent because *Silphium integrifolium* alone is responsible for the guild depression in winter-access plots ($F_{2,15} = 3.340$, $P = 0.063$). Other guilds are more natural; large-seeded legumes do not respond to rodent access ($F_{2,15} = 0.373$, $P > 0.9$), small-seeded composites increase with winter-access by rodents ($F_{2,15} = 9.368$, $P < 0.002$), as do small-seeded legumes ($F_{2,15} = 4.708$, $P < 0.05$, an indirect

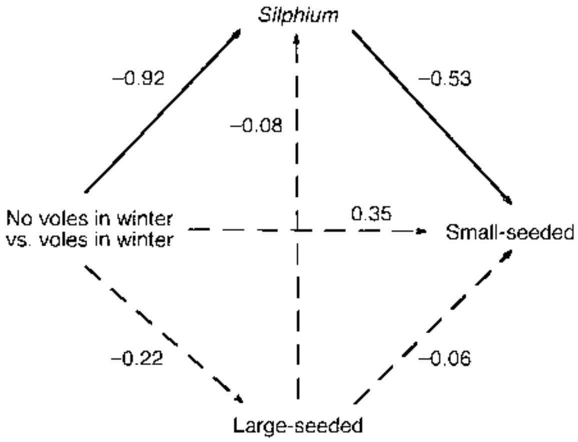

FIG. 2. Path coefficients for direct effects of winter access by voles (*Microtus pennsylvanicus*) to seeds broadcast on the soil surface. Voles strongly depress *Silphium integrifolium* ($F_{1,16}$ = 91.22, $P < 0.001$), and *Silphium integrifolium* depresses a guild of six small-seeded species ($F_{1,14}$ = 6.14, $P < 0.05$). Path analysis does not show a direct effect of voles on the small-seeded guild ($F_{1,14}$ = 2.79) but indicates a strong indirect effect of suppression of *Silphium integrifolium* in releasing the small-seeded plants (Fig. 1, Table 2). Other direct effects are as predicted by sign but are not statistically significant.

effect on small-seeded plants in the path analysis). The combined value for small-seeded composites pools numerical increases in four species, which were individually significant in two cases and not significant in two cases (Table 2). A multivariate analysis of variance with these four variables (large- and small-seeded composites, large- and small-seeded legumes) indicates that combined responses are general (Wilks' lambda = 0.160, $F_{8,24}$ = 4.501, $P < 0.001$).

Path analysis.—The direct and indirect effects of the winter access of voles can be modeled with path analysis where rodent access (winter-access vs. pooled summer-access and no-access plots) may directly influence *Silphium integrifolium*, other large-seeded species, and small-seeded species. In addition, *Silphium integrifolium* may competitively suppress other large- and small-seeded species; and the other large-seeded species may directly suppress the small-seeded species. Most direct effects in this path model (Fig. 2) have the predicted signs: winter access has negative direct effects on *Silphium integrifolium* and other large-seeded species, *Silphium integrifolium* has negative direct effects on other large-seeded species and small-seeded species, and the other large-seeded species have a negative effect on the small seeded species. Two paths, the direct effect of winter access on *Silphium integrifolium* ($F_{1,16}$ = 91.22, $P < 0.001$) and the direct effect of *Silphium integrifolium* on small-seeded plants ($F_{1,14}$ = 6.14, $P < 0.05$) are statistically significant. In summary, rodents strongly suppressed one otherwise formidable competitor, and six of the small-seeded species benefitted from reduction of *Silphium integrifolium* to greater or lesser degrees (Fig. 2).

Diversity.—Rodent granivory during the winter dramatically increased dicot diversity, as measured by Simpson's *D*, with a mean value of 7.50 ± 0.32 in winter-access plots, a value of 5.68 ± 0.22 in summer-access plots, and value of 5.57 ± 0.31 in closed plots. The overall ANOVA was highly significant ($F_{2,15}$ = 13.95, $P < 0.001$). Retrospective analysis showed that diversities did not differ between exclosures kept closed or opened during the summer (Tukey test, $P >$ 0.95), but the mean diversity of plots opened to rodent granivory during the winter was much higher than the other two treatments (Tukey tests, $P < 0.001$).

The number of dicot species present was not affected by rodents. Richness of experimental dicots ranged from 11.5 ± 0.3 species in plots open to rodents in winter to 12.5 ± 0.6 species in those plots closed to rodents, but differences were not significant ($F_{2,15}$ = 1.069, $P > 0.35$).

Rodents.—Five species of rodents were trapped within the immediate vicinity of exclosures. Of these, meadow voles (*Microtus pennsylvanicus*) were by far the most abundant in grassy habitat, and were the only ones trapped adjacent to or in exclosures. Overall, abundances ranged from a low of 114 voles/ha known to be alive in August 1997 to a minimum of 387 voles/ha in August 1998. The other granivorous rodent trapped in grassy habitat was the meadow jumping mouse (*Zapus hudsonius*), which was abundant during the summer of 1997 in forest habitat (11 captures) and occurred in grassy habitat (two captures). This species was also caught in May (n = 1) and August (n = 4) 1998. *Zapus hudsonius* becomes torpid in early autumn and has not been caught in fall censuses. In each census, 3–11 white-footed mice (*Peromyscus leucopus*) and 0–3 deer mice (*P. maniculatus*) were trapped only in the forest, although they could forage in nearby grassy habitats. Four eastern chipmunks (*Tamias striatus*) were repeatedly caught in the forest border in August 1997, but only one was caught once in October. This species begins torpor in October. The two *Peromyscus* species remain active throughout the winter.

DISCUSSION

Either granivory or herbivory can alter composition of plant communities. Seed or seedling predators (sensu Janzen 1969) selectively remove individuals of some species more than others, thereby potentially giving a competitive edge to the less preferred species. Heavy seed predation by heteromyid rodents is almost certainly responsible for replacement of large-seeded forbs by small-seeded grasses in an Arizona desert (Brown and Heske 1990, Heske et al. 1993). Herbivory can also be a powerful influence on succession in mesic habitats. Seedling predation by meadow voles may eliminate maple (*Acer rubrum*, Aceraceae) and ash (*Fraxinus americana*, Oleaceae) recruitment, and may reduce abundance of several other tree species by 60–80% (Ostfeld and Canham 1993, Ostfeld et al. 1997). Vertebrate predation on either seeds or seedlings may stall or even redirect the course of succession, and can be expected to have implications for directed succession with restoration objectives (sensu Luken 1990). Remnant and restored plant communities may reflect what small vertebrates at any time and place fail to eat, as well as the indirect interactions that those diet choices precipitate.

Implications of diet choice

Diets of free-living rodents may be both highly selective and highly variable. Diet emerges from a hierarchy of spatial scales and behavioral decisions that leads to consumption of some foods disproportionate to their availabilities (Brown and Morgan 1995). Factors influencing diet selectivity include the value of the food in reward per unit handling time (Pulliam 1974), encounter rate (Getty and Pulliam 1993), and the risk of feeding at one location as compared with another (Brown et al. 1988). The interplay of these factors determine seed or foliage selection and depletion, and therefore potential influence on plant communities.

This interplay may result in contingent effects for plants that are difficult to predict. For instance, it is axiomatic that, other things being equal, rodents prefer seeds that are easy to find and handle safely. Yet, other things are rarely equal. Large, energy-rich seeds are usually the best endowed with mechanical or chemical defenses (Janzen 1969), or apparently choice seeds may occur at a site too risky to encourage thorough foraging (Brown 1992). In either case a seed expected to be exploited exhaustively because of its high energy content may not be touched. Under other circumstances, it may be depleted if it happens to be the most nutritious seed available or if the perceived risk of predation is low.

Granivory.—Seed selection may have general or specific effects. In a study in Illinois, we have found that seed-eating birds reduce the overall plant abundance in high-density plantings by ~20%, but have no influence on plant diversity (Howe and Brown 1999). A general depression in numbers may have differential effects on growth and eventual dominance of the survivors, but any influences of bird granivory on plant species composition are too subtle to detect in early restorational succession. On the other hand, size-selective reduction of dicot seeds by heteromyid rodents does transform forb-dominated desert to grassland (Brown and Heske 1990), thereby indicating that foraging decisions of these obligate granivores are consistent with expectations from theory predicting size-selective seed predation and fundamental impacts on plant communities.

The rodent granivores on our experimental dicot communities had both expected and unexpected effects. All things being equal, we expected large seeds within each taxonomic group to be selectively depleted by rodents. Because legume seeds were generally larger than composite seeds, we expected generally greater depletion of legumes than of composites. Consistent with expectations from optimal foraging theory, eight small-seeded species escaped detectable depletion by rodents. Instead, rodents (primarily meadow voles, *Microtus pennsylvanicus*), selectively depleted one large-seeded composite, *Silphium integrifolium*, and one large-seeded legume, *Desmodium glutinosum*, but ignored six other large-seeded species. Moreover, *Desmodium glutinosum* depletion by rodents had little if any influence on dicot communities because the species fared poorly after germination and establishment.

Rodent disinterest in six of eight large seeds sowed in our plots may indicate that the rejected seeds are distasteful, toxic, mechanically protected, cryptic, or some combination of these four defenses. Meadow voles have consistently rejected *Desmanthus illinoensis* and *Lupinus perennis* seeds in seed selection trials in Illinois (G. Turner-Erfort, J. S. Brown, and H. F. Howe, *unpublished data*), suggesting chemical or mechanical defenses, and the massive seeds of *Cassia marilandica* similarly may be less preferable than alternatives to a rodent that is primarily herbivorous, even in winter (Lindroth and Batzli 1984). However, in feeding trials in Illinois, voles ate *Echinacea purpurea* seeds, which were apparently not eaten at all in rodent-accessible plots in Wisconsin. Either alternative foods were better or scattered seeds of this species were not as easily encountered and used as those in feeding trays.

There is greater potential for use of exclosures by several rodent species in a forest border or savanna simulation such as our Wisconsin study than in open grassland, but we suspect that meadow voles were by far the most important consumers in both cases. Of the five rodent species trapped near the Wisconsin exclosures, only voles and *Zapus hudsonius* were actually trapped in the grassy habitat, and *Zapus* hibernates well before sowing occurred (Hoffmeister 1989). Moreover, meadow voles effectively exclude *Peromyscus* when the former are at high densities (Grant 1972). Voles in our study maintained or even increased their population densities in excess of 120 voles/ha during the winter in which seed depletion occurred.

Finally, rodent granivory extensive enough to change plant communities may not always occur. Rodents strongly modify their foraging behavior when the perceived risk of predation is high; they leave foods at substantially higher residual densities under higher predation threat in the open than under cover (Brown et al. 1988). Meadow voles, in particular, eschew bare ground (Kaufman et al. 1990). No rodent granivory was detected in our Illinois experiment, probably because the most abundant rodents in the field, meadow voles, failed to forage effectively in much larger open plots (14 × 14 m) until late summer, when most seeds had germinated and the ground was covered by vegetation (Howe and Brown 1999). In Wisconsin, the plots were much smaller, were bordered by thick vegetation, were covered by snow most of the winter, and had much larger seeds in the large-seed category than in the Illinois experiment (neither *Silphium integrifolium* nor *Desmodium glutinosum* was used in Illinois).

Perhaps as a testament to the conditional nature of diet choice, effects of folivory also contrasted sharply in our Illinois and Wisconsin experiments. Meadow vole herbivory on two common subdominant species in the Illinois experiment, *Desmanthus illinoiensis* and *Echinacea purpurea,* sharply reduced plant diversity by accentuating the advantages of dominant grasses and less preferred forbs (Howe and Brown 1999). The same rodent did not show any signs of herbivory on the foliage of either of these plants, or others, in Wisconsin. The only apparent effects were the granivory on *Silphium integrifolium,* which increased plant diversity as previously reported.

Implications for plant diversity

Animal consumption of plants may increase, decrease, or have no effect on plant diversity (Huntly 1991). Suppression of dominant vegetation by large mammalian herbivores generally increases plant diversity by allowing those subdominant plant species to prosper that would otherwise be competitively excluded (e.g., Belsky 1986, Collins 1987, Vinton et al. 1993, Knapp et al. 1999). The effect is to transform competitively saturated communities to unsaturated assemblages that can admit additional species (Cornell and Lawton 1992). On the other hand, consumers that selectively remove subdominant species may decrease plant diversity by removing small populations already competitively suppressed by dominant vegetation. This will probably be the ultimate effect of tree seedling herbivory by microtine rodents (Ostfeld and Canham 1993), and is the effect of herbivory on legumes by microtines in our Illinois experiment (Howe and Brown 1999). Finally, general reduction of numbers may not have detectable effects on plant diversity, as is the case in avian granivory in our Illinois experiment, because birds neither remove species nor alter dominance. The critical issue in determining herbivore or granivore influence is the link between animal effects on plant dominance that affect plant diversity.

In depleting an otherwise aggressive dicot, *Silphium integrifolium,* the effects of granivory by meadow voles and possibly other rodents in our Wisconsin experiment resemble ungulate suppression of dominants more than their usual role of selectively suppressing subdominants. The initial effect that we observed was an increase in the number of three small-seeded species, *Aster laevis, Astragalus canadensis,* and *Ratibida pinnata.* Decreased dominance resulted in a change in the composition of these synthetic communities, as expressed by a sharp increase in Simpson's diversity (D).

How long will these effects last? These and another potentially impacted small-seeded species, *Solidago rigida,* are robust as adults and may be capable of persistence in the face of competition from *Silphium integrifolium* once they occupy the space. Moreover, large-seeded plants that did not respond to *Silphium integrifolium* suppression during the first season may respond during the second season. In adaptive terms, small-seeded species are likely to be more opportunistic than large-seeded species (Harper 1977), but their early success may or may not foretell competitive success with slower, but nonetheless formidable, *Cassia, Desmanthus, Echinacea,* or *Heliopsis* species. Highly significant reductions of large-seeded *Desmodium glutinosum* by seed-eating rodents had no obvious impact on these communities because the species did not prosper at this site in any treatments.

Implications for conservation and restoration

Small-rodent herbivory may also be a potent, but unnoticed, force in established and restored tallgrass communities (Howe and Brown 1999). Preference of both meadow voles and prairie voles (*Microtus ochrogaster*) for dicots is well established in both native grassland and agricultural habitats (Cole and Batzli 1979, Lindroth and Batzli 1984), and the net effect of foraging by these often superabundant rodents may be structural alteration of plant communities. Our study, in particular, suggests that selective seed depletion by microtine and other rodents of some large and charismatic prairie species such as *Silphium integrifolium* may be reflected in the scarcity of these plants and in the relative fortunes of their competitors. For tallgrass restorations, the success of some species and the character of the communities overall may well be influenced by the variations in ambient vole populations at the time of planting, or during subsequent stages of plant succession. The composition of many herbaceous communities may, in short, reflect the direct or indirect effects of what these rodents choose not to eat in any given place and time, considering their numbers and the foraging choices open to them.

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