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EFFECTS OF BIRDS AND RODENTS ON SYNTHETIC TALLGRASS COMMUNITIES

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Abstract. We used a bird and mammal enclosure design on plowed ground to test for the effects of granivory and herbivory by small vertebrates on early stages of tallgrass prairie succession. Seed predation by birds and browsing by rodents had major and additive impacts. In high- and low-density plantings, respectively, seed-eating birds reduced plant densities by 20% and 23% and grass biomass by 24% and 34%. Meadow voles did not affect plant numbers but reduced forb biomass by 35% in high- and 57% in low-density plantings. In high- and low-density plots, respectively, birds reduced species richness by 3% and 17% without influencing diversity; selective browsing by voles on two legumes and one coneflower left species number unaffected but reduced diversity by 4% and 25% by accentuating dominance of already-prominent species. Bird effects were more pronounced in high-density plantings, while vole effects were most pronounced in low-density plantings.

Results suggest that opportunistic finches and doves that seek out high seed concentrations depress tallgrass plant densities on open ground, while voles, which selectively forage on emerging vegetation, alter community structure, especially when their home ranges include low-density plant assemblages. Both results are likely to be relevant to native prairies after burns or other disturbance, and to ecological restoration.

Key words: *birds, seed predation by; diversity; experimental restoration; field experiment; foraging theory; granivory; herbivory; rodent browsing; tallgrass community, revegetation; tallgrass plantings, small vertebrate effects on; tallgrass prairie, composition and diversity; vole herbivory.*

INTRODUCTION

Do small vertebrates influence composition and diversity of tallgrass prairies? The question is important because tallgrass remnants on fertile, well-watered soils represent North America's "most endangered" major ecosystem (Noss et al. 1995). Influences of large (>5 kg) browsing mammals on native vegetation are increasingly well understood (Collins 1987, Milchunas et al. 1988), but such mammals are absent from most remnant prairies or restorations east of the Mississippi River. Remnant and restored tallgrass landscapes do harbor abundant small (<200 g) birds and mammals that could have important but unknown impacts on plant dynamics (Rose and Birney 1985). Here we use community restoration as an experimental tool (*sensu* Jordan et al. 1987, Howe 1994) to explore the effects of granivory and herbivory by small vertebrates on tallgrass vegetation.

Wholesale conversion of forb and shrub desert to grassland by seed-eating rodents has proven that the individual foraging decisions of small animals can shift ecological succession (Brown and Heske 1990), a discovery that echoed an earlier report that plant-eating voles can fundamentally alter California grasslands (Batzli and Pitelka 1970). We erected an enclosure experiment to simultaneously test the influence of small

seed-eating birds and seed-eating and herbivorous rodents on replicated synthetic tallgrass communities. The first general objective was to determine if small birds and mammals had detectable effects on community characteristics in accordance with general expectations of optimal foraging theory. We predicted that size-selective seed predation would result in (1) bird suppression of plant species with seeds of intermediate (0.2–2.0 mg) size (Pulliam 1985), (2) rodent suppression of plant species with large seeds (>2.5 mg; Hulme 1994), and (3) no direct effects of vertebrate granivory on plants with minute seeds (<0.2 mg; Pulliam 1985, Hulme 1994). We further predicted (4) that herbivorous voles, by far the most common small vertebrate herbivores at our site, would suppress dicots (Lindroth and Batzli 1984). Ultimately the experiment will test whether animal effects early in community succession have a continued impact on later successional trajectories through direct effects of herbivory or granivory or through indirect effects mediated through interactions among plant species.

METHODS

This experiment was established in Ware Field at the Morton Arboretum, Lisle, Illinois, USA, using regional restoration methods (Rock 1981). This former hayfield (*Bromus inermis*) on mesic clay soils has been mowed annually by Arboretum staff for 20 yr. In November 1995

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TABLE 1. Species planted in high (350 seeds·m⁻²·species⁻¹) or low (35 seeds·m⁻²·species⁻¹) densities in exclosures in June 1997 at the Morton Arboretum, Lisle, Illinois, USA. Species names follow Gleason (1963).

Species	Family	Common name	Seed mass (mg)
Large seeds (>2.5 mg/seed)			
<i>Echinacea pallida</i>	Asteraceae	Pale coneflower	5.38
<i>Echinacea purpurea</i>	Asteraceae	Purple coneflower	4.05
<i>Elymus canadensis</i>	Poaceae	Canadian wild rye	5.88
<i>Desmanthus illinoensis</i>	Mimosaceae	Illinois bundleflower	5.32
<i>Heliopsis helianthoides</i>	Asteraceae	Early sunflower	3.52
<i>Sorghastrum nutans</i>	Poaceae	Indiangrass	2.60
Small seeds (0.20–1.5 mg/seed)			
<i>Koeleria cristata</i>	Poaceae	Junegrass	0.29
<i>Panicum virgatum</i>	Poaceae	Switchgrass	0.57
<i>Petalostemum purpureum</i>	Fabaceae	Purple prairie clover	1.54
<i>Phalaris arundinacea</i>	Poaceae	Canary reed grass	0.62
<i>Rudbeckia hirta</i>	Asteraceae	Black-eyed Susan	0.51
<i>Solidago rigida</i>	Asteraceae	Rigid goldenrod	0.72
Minute seeds (<0.20 mg/seed)			
<i>Achillea millefolium</i> var. <i>lanulosa</i>	Asteraceae	Native yarrow	0.06
<i>Gentiana flavida</i>	Gentianaceae	Cream gentian	0.11
<i>Heucheria richardsonii</i>	Saxifragaceae	Prairie alumroot	0.03
<i>Penstemon digitalis</i>	Scrophulariaceae	Pale penstemon	0.19
<i>Pycnanthemum virginianum</i>	Labiatae	Mountain mint	0.06
<i>Sporobolus cryptandra</i>	Poaceae	Sand dropseed	0.11

a backhoe was used to break sod in 24 14 × 14 m plots (4 plot × 6 plot grid), 12 of which were planted in the experiment discussed here. Lanes of old-field vegetation 5 m wide were left between plots. Prepared plots were disced and herbicided as needed before 1997 plantings. In the fall of 1996, a trencher was used to dig 0.5-m-deep trenches around each of 12 plots, which were bisected on each axis by similar trenches. This resulted in 4 7 × 7 m subplots nested within each of 12 14 × 14 m plots prior to the June 1997 plantings. Hardware cloth 1.23 m high fenced these nested 7 × 7 m subplots.

Eighteen plant species were selected according to stature, flowering phenology, grass or forb habit, and availability in seed nurseries (Table 1). Seed mixes were weighed separately for 48 7 × 7 m subplots and broadcast in damp sand on 20 June 1997 at either low density (35 seeds·m⁻²·species⁻¹) or high density (350 seeds·m⁻²·species⁻¹), yielding overall seed densities of 630 or 6300 seeds/m². Within each 14 × 14 m plot, four 7 × 7 m exclosures were randomly assigned to (1) exclude all small vertebrates, (2) admit birds and small rodents, (3) exclude birds but admit rodents, or (4) admit birds but exclude rodents.

To avoid edge effects, plants were sampled ≥1 m from the fence of each 7 × 7 m subplot. Between 22 and 25 October 1997, seedlings of experimental plants were counted in 240 1-m² squares. Between 18 and 24 November, aboveground biomass was determined by clipping vegetation in two randomly selected (exclusive of permanent plots) 0.5 × 0.5 m squares within each 7 × 7 m subplot. Samples were later dried to constant mass at 100°C.

We used two measures of plant diversity (Magurran 1988): (1) species richness as the number of species in a sample and (2) Simpson's diversity index:

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

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, while D accentuates the effect of numerical evenness in the species abundance distribution. The inverse of D is Simpson's index of numerical concentration C , a measure of dominance.

The design permits simultaneous tests of effects of seeding density, seed eating by birds, seed eating or herbivory by rodents, and the interactions of these effects on replicated sets of multi-species tallgrass communities. We used a partially hierarchical ANOVA to test for the effects of birds, mammals, and planting density on the density, biomass, composition, and diversity of the emerging assemblages. Bird (presence/absence) and mammal (presence/absence) variables are fully crossed with each plot, and plot is a subgroup variable nested within density levels. Dependent variables were the mean values of plant numbers (5 samples/subplot) and plant biomass (2 samples/subplot) from samples within each 7 × 7 m subplot. In this way the data were compressed to 48 data points (1 mean per subplot × 4 subplots per plot × 12 plots = 48).

Birds were counted by J. S. Brown, H. F. Howe, and G. Turner-Erfort during site visits from June through August. In early October, small mammals were censused with three days and nights of live-trapping with 139 Sherman traps. Traps were placed in a 7 × 13 grid

TABLE 2. General characteristics of plots in October following broadcast seeding in June (1997). Means (± 1 SE) are shown for bird or vole access at high densities (6 plots at 350 seeds·m⁻²·species⁻¹) or low densities (6 plots at 35 seeds·m⁻²·species⁻¹).

	Density (seeds m ⁻²)			Biomass (g/0.25 m ²)		
	High (H)	Low (L)	Signif. H vs. L	High (H)	Low (L)	Signif. H vs. L
Birds						
Absent (A)	62.4 \pm 4.7	14.6 \pm 1.3	***	36.4 \pm 3.7	6.8 \pm 1.8	***
Present (P)	49.6 \pm 3.1	10.9 \pm 0.7	***	28.8 \pm 3.1	4.8 \pm 1.6	***
Significance, A vs. P	*(t)	NS		*(t)	NS	
Voies						
Absent (A)	56.7 \pm 3.9	12.7 \pm 1.1	***	34.1 \pm 4.1	7.6 \pm 1.6	***
Present (P)	55.3 \pm 4.9	12.8 \pm 1.2	***	27.2 \pm 3.2	4.0 \pm 1.6	***
Significance, A vs. P	NS	NS		*	*	

Notes: Values used are means of experimental species sampled in five samples of 1 m² per 7 \times 7 m subplot for plant number and means of two sets of clippings from samples of 0.25 m² for biomass. An asterisk indicates significance from ANOVA; an asterisk with a "(t)" indicates significance ($P < 0.05$) from post hoc Tukey tests where a density \times animal interaction occurs.

* $P < 0.05$, *** $P < 0.001$; NS = nonsignificant at $P < 0.05$.

surrounding the enclosure site, including vegetated aisles between 14 \times 14 m plots (~ 1.6 ha). In addition, two traps were placed within each of the 48 subplots. Traps were baited with oatmeal and checked morning and evening. All captured animals were weighed, sexed, ear-tagged, and released.

RESULTS

Of 18 species planted in June 1997, 12 emerged the first season and were easily documented in permanent sample plots. Emergence success (plants/seeds planted \times 100) ranged from $\lll 1\%$ for some species with minute seeds (< 0.2 mg/seed) to 15% for *Panicum virgatum* in low-density plots. Flowering and seeding were common in *P. virgatum*, and occurred at least occasionally in *Desmanthus illinoensis*, *Heliopsis helianthoides*, *Petalostemum purpureum*, *Rudbeckia hirta*, *Sorghastrum nutans*, and *Sporobolus cryptandrus*.

In six species common enough for statistical evaluation (*D. illinoensis*, *Echinacea purpurea*, *H. helianthoides*, *Panicum virgatum*, *Petalostemum purpureum*, *R. hirta*), high planting density increased October seedling number ($F_{1,10} \geq 28-46$, $P \ll 0.001$); for these species, save *P. purpureum*, high plant density increased November biomass ($F_{1,10} \geq 7-44$, $P < 0.05$).

Small granivorous birds commonly foraged for seeds in the plots. Records of birds from June through August indicated plot use by Song Sparrows (*Melospiza melodia*; 21 g), Savannah Sparrows (*Passerculus sandwichensis*; 20 g), Goldfinches (*Carduelis tristis*; 13 g), Brown-headed Cowbirds (*Molothrus ater*; 44 g), House Sparrows (*Passer domesticus*; 28 g), and Mourning Doves (*Zenaidura macroura*; 130 g). Between 25 June and 8 July, spot checks revealed 2-4 doves feeding in the plots on five of six occasions.

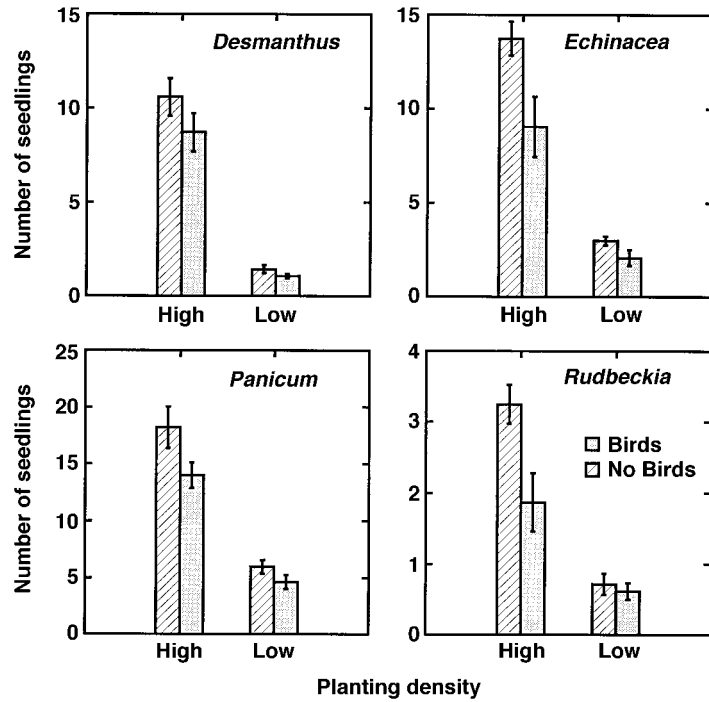
Three days and nights of live trapping yielded 85 individual meadow voles (*Microtus pennsylvanicus*; 38 g),

13 short-tailed shrews (*Blarina brevicauda*; 23 g), 1 white-footed mouse (*Peromyscus leucopus*; 24 g) at a nearby treeline, 1 small shrew (*Sorex* spp.; 10 g), and 1 thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*; 160 g). Voies accounted for almost all vertebrate herbivory.

Small vertebrates had dramatic effects on plant density, biomass, species richness, and diversity. Seed-eating birds strongly depressed the number and biomass of plants on the plots, with a far more potent effect in high-density (350 seeds·m⁻²·species⁻¹) than low-density (35 seeds·m⁻²·species⁻¹) plots (Table 2; Fig. 1). In high-density plots, birds caused a 23% drop in grass numbers and a 32% drop in grass biomass. Due to compensatory growth, a 20% drop in forb numbers in high-density plots accessible to birds was not reflected in a drop in biomass. Generalized suppression of plants by seed-eating birds had no influence on species richness in high-density plots (birds absent vs. present: 6.8 \pm 0.2 vs. 6.6 \pm 0.2 species/m² [means ± 1 SE]) but did result in a loss of one species/m² (17%) on low-density plots (5.0 \pm 0.3 vs. 4.2 \pm 0.3 species/m²; $F_{1,30} = 6.318$, $P < 0.05$), presumably by chance elimination of rare species. Birds did not influence structure of the communities, as estimated by diversity (*D*), because they did not amplify or diminish plant dominance.

Vole herbivory was highly selective, affecting primarily *Petalostemum purpureum* density (Fig. 2), *Desmanthus illinoensis* biomass (high density with and without mammals: 6.0 \pm 0.9 to 3.7 \pm 0.8 g/sample; low-density: 1.5 \pm 0.8 to 0.1 \pm 0.1 g/sample; $F_{1,30} = 7.706$, $P < 0.01$), and *Echinacea purpurea* biomass (high density: 2.8 \pm 1.0 to 1.6 \pm 0.4 g/sample; low density: 1.2 \pm 0.6 to 0.1 \pm 0.1 g/sample; $F_{1,30} = 5.447$, $P < 0.05$ [all data reported are means ± 1 SE]). For *E. purpurea*, a significant bird \times density interaction ($F_{1,30} = 7.875$, $P < 0.01$), reflecting

FIG. 1. Bird effects on seedling density per species (means \pm 1 SE). Bird granivory decreased plant densities of *Desmanthus illinoensis* ($F_{1,30} = 6.136, P < 0.05$), *Echinacea purpurea* ($F_{1,30} = 20.019, P \ll 0.001$), *Panicum virgatum* ($F_{1,30} = 8.318, P < 0.01$), and *Rudbeckia hirta* ($F_{1,30} = 9.561, P < 0.01$), with a significant density \times bird interaction for *R. hirta* ($F_{1,30} = 7.157, P < 0.05$) reflecting greater impact at high than at low densities. Bird granivory did not affect *Heliopsis helianthoides*.



heavy bird consumption of seeds in high-density plots, suggests that the vole effect was limited to low-density plots. Voles had no general influence on overall numbers of plants, but depressed forb biomass by 35% in high-density plots and 57% in low-density plots. Vole herbivory did not significantly alter species richness, but it re-

duced the more inclusive measure of diversity (D ; Fig. 3) by accentuating dominance of non-preferred grass and forb species.

DISCUSSION

Either granivory or herbivory can alter the composition of plant communities (Huntly 1991). Seed or seedling pred-

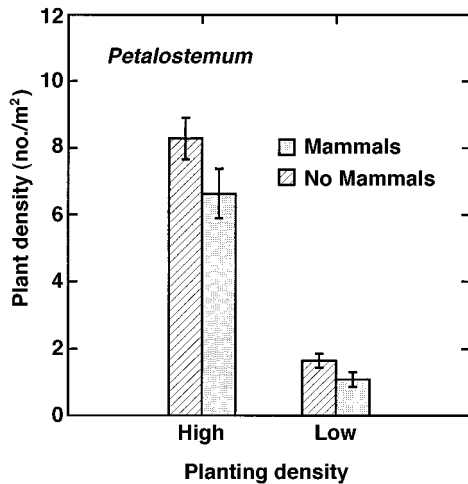


FIG. 2. Vole effects on *Petalostemum purpureum* seedling densities (means \pm 1 SE). Vole herbivory decreased densities of this species ($F_{1,30} = 19.068, P < 0.001$), with a significant density \times mammal interaction ($F_{1,30} = 4.554, P < 0.05$) reflecting greater proportional impact at low than at high seeding densities.

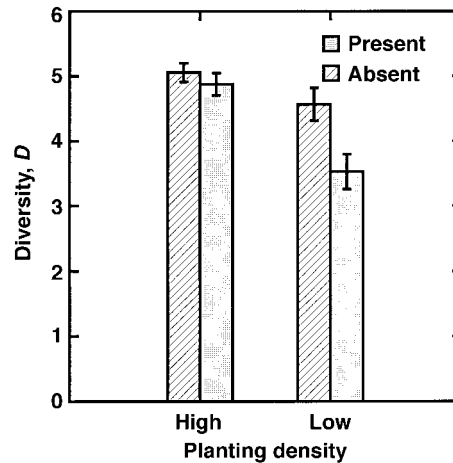


FIG. 3. Vole effects on plant diversity (Simpson's D [mean \pm 1 SE]) at high (350 seeds \cdot m⁻² \cdot species⁻¹) and low (35 seeds \cdot m⁻² \cdot species⁻¹) seeding densities. Seeding density increases ($F_{1,10} = 11.384$), and mammal access decreases ($F_{1,30} = 10.656$, both $P < 0.01$) diversity, with a significant density \times mammal interaction ($F_{1,30} = 5.273, P < 0.05$) reflecting greater impact at low (-25%) than at high (-4%) seeding densities.

ators selectively remove individuals of some species more than others, thereby giving a competitive edge to the less preferred species. An example is heavy seed predation by heteromyid rodents in an Arizona desert, which leads to replacement of large-seeded forbs by small-seeded grasses (Brown and Heske 1990). Herbivory can also be a powerful influence on succession. Seedling predation by meadow voles may eliminate maple (*Acer rubrum* [Aceraceae]) and ash (*Fraxinus americana* [Oleaceae]) recruitment, and reduce abundance of other tree species by 60–80% (Ostfeld and Canham 1993, Ostfeld et al. 1997). It is clear that seed or seedling predation may stall or even redirect succession.

In our enclosure experiment, initial effects of granivory and herbivory by small vertebrates are generally consistent with expectations, but the interaction of animal activity with seeding densities suggests potentially important direct and indirect effects on later succession. With respect to initial predictions:

1) As predicted, bird granivory suppressed two species with seeds of intermediate size, switchgrass (*Panicum virgatum*; seed 0.57 mg) and black-eyed Susan (*Rudbeckia hirta*; seed 0.51 mg), with a substantially stronger effect on *R. hirta* at high than low planting densities. Perhaps because our plots attracted larger granivores than expected (e.g., blackbirds and doves) or because large seeds are more easily encountered than small ones (e.g., Getty and Pulliam 1993), avian granivores also depressed large-seeded bundleflower (*Desmanthus illinoensis*; seed 5.32 mg) and purple coneflower (*Echinacea purpurea*; seed 4.05 mg), with the latter impact at high seeding densities. Because these birds digest seeds rather than disperse them (e.g., Blockstein et al. 1987), reduction of plant densities is due to mortality rather than migration of seeds through seed dispersal.

2) Contrary to expectations, rodent granivory was not evident. Meadow voles (*Microtus pennsylvanicus*) common at our site modify foraging behavior when the perceived risk of predation is high, avoiding open areas (e.g., Kaufman et al. 1990) or perhaps leaving foods at higher residual densities under higher predation threat in the open than under cover (see Brown and Morgan 1995). Vole activity was not seen in the plots until late August, when enough vegetation had emerged to offer cover and food. Perceived predation risk probably precluded effective vole use of a potentially rich seed resource.

3) Consistent with predictions, neither bird nor rodent granivory depressed plants with seeds below optimal foraging size (<0.2 mg/seed).

4) Consistent with expectations, vole herbivory depressed dicots, but had no direct effect on grasses. The selective nature of this herbivory depressed plant diversity (*D*) by accentuating dominance of non-preferred species, particularly at low planting densities.

In this study, birds and rodents had additive effects on the density and biomass of plants, with a notable

lack of bird \times mammal interactions. Interaction effects between taxa could occur if those taxa amplify or diminish each other's impact. Amplification might happen if heavy seed predation is followed by heavy seedling herbivory of the same species; reduction of effects could occur if depletion of a resource by one taxon reduces availability of and preference for it by another. Here differences in timing of plot use (birds early, voles late) and form (granivory by birds, herbivory by voles) make birds and voles potent and complementary forces at the outset of restorational succession.

Seedling predation that follows heavy seed mortality has a greater direct effect on the ultimate composition of plant communities than does granivory alone. In our plots, a surviving seedling of switchgrass (*P. virgatum*) in low-density plots is worth 6 seeds, while one in high-density plots is worth 25 seeds. A lucky surviving seedling of native yarrow (*Achillea millefolium* var. *lanulosa*) may be worth 300 seeds in low-density plots, 2500 in high-density plots. All things being equal in these examples, a vole that eats a seedling from a high-density plot is 6 to 2500 times as influential as a sparrow that eats a seed of the same plant species in the same plot.

Beyond direct effects of granivory and herbivory, birds and mammals are likely to initiate a series of indirect effects among plant species (Belsky 1986, Brown and Heske 1990, Thompson et al. 1991). Species may be eliminated, allowing ecological release of competitors or negative effects on mutualists. It is too early in the present experiment to predict particular outcomes of indirect effects, but controlled manipulation reveals powerful effects of planting density, bird granivory and mammal herbivory, and their interactions that plausibly could occur in uncontrolled restoration projects and natural systems. We see two likely consequences:

First, ecological release is a likely indirect effect of bird granivory. General suppression of grasses by seed-eating birds could release forbs in subsequent years, and general suppression of common forbs may encourage uncommon grasses and forbs (Cornell and Lawton 1992). In this scenario plant diversity is likely to increase over time in high-density plots where bird effects are most obvious.

Second, vole-driven suppression of otherwise prominent forbs is likely to alter ongoing secondary succession. The most likely outcome in low-density plots where vole effects are strongest is a reduction of diversity through drastic reduction of three potential dominants, and release of the non-preferred dominant switchgrass (*P. virgatum*).

Large and additive effects of bird granivory and vole herbivory have implications beyond this experiment. Continual attrition of seeds through bird or rodent granivory may go unnoticed in established grasslands, where annual recruitment of seedlings under tallgrass canopies is often <1 seedling/m², unless fire, mowing, or ungulate

grazing stimulates germination and establishment from seed (Glenn-Lewin et al. 1990, Howe 1995). The obvious effects may be episodic, even if granivory is long term. Fire and grazing severe enough to bare soil have their own direct impacts on vegetation, and may additionally create open ground accessible to intense bird granivory. Episodic seed eating by birds, in addition to chronic granivory by birds and rodents, may have substantial but unrecognized direct and indirect effects on established prairie vegetation, and will have a strong potential impact on restorations that employ broadcast seeding.

Small-rodent herbivory may also be a potent but unnoticed force in established and restored tallgrass communities. Preference of meadow voles for dicots is well established in both native grassland and agricultural habitats (Lindroth and Batzli 1984), although their impact on total biomass and diversity has not been noted previously. We expect that recruitment of dicot seedlings in established native vegetation and in restorations may be strongly affected by vole herbivory in central North America. If so, vegetation in widely scattered tallgrass remnants may be affected by uncommonly large or small vole populations, while trajectories of vegetative succession in tallgrass restorations are likely to be influenced by the sizes of ambient vole populations within a few months of planting.

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