

## MASSIVE AND DISTINCTIVE EFFECTS OF MEADOW VOLES ON GRASSLAND VEGETATION

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**Abstract.** We ask whether vole herbivory in experimental grassland plots is sufficient to create an unpalatable community. In a six-year experiment, meadow voles (*Microtus pennsylvanicus*) reduced plant standing crop between 30% and 72%, well within the range of ungulate effects. Moreover, meadow voles reduced their available forage species by changing the plant community composition: four grass species and a legume upon which they foraged declined sharply in cover and/or number of individuals, five forbs avoided by voles increased, and two forbs neither declined nor increased with either measure. Reductions of diversity occurred when voles first defoliated the plots in 2000 but disappeared as plant species avoided by voles replaced vulnerable plants. Within six years, meadow voles created plant communities dominated by species that they did not eat.

**Key words:** experimental restoration; herbivory; *Microtus*; plant–animal interactions; tallgrass prairie; vole herbivory.

### INTRODUCTION

Climate defines the structure of regional plant communities, while plant-eating animals often determine which plant taxa thrive or fail (Huntly 1991). Large ungulates strongly influence grassland plant abundance and species composition (McNaughton et al. 1991, Milchunas and Lauenroth 1993, Knapp et al. 1999). Far less recognized are rodents as “cryptic consumers” that potentially eat almost as much grassland vegetation as ungulates when large animals are fenced out (Keesing 2000). This has implications for central North America, where grazing ungulates no longer exist on relicts of once-vast native prairies (Noss et al. 1995). If small mammals affect grasslands in distinctive ways, contemporary grasslands may differ from those once dominated by a grazing megafauna. We report that herbivory by ubiquitous meadow voles (*Microtus pennsylvanicus*) creates consistent, ungulate-level effects on the standing crop, but distinctive effects on species composition of tallgrass prairie plants in experimental plantings. An earlier report (Howe et al. 2002) predicted that voles would ultimately produce communities of noxious plants that they would not eat. They did so within six years.

How do much smaller (<60 g) “cryptic consumers” influence grasslands? In contrast to ungulates, small herbivorous rodents are ubiquitous and often abundant in sites where ungulates choose not to go or have been exterminated. Populations of voles (*Microtus pennsylvanicus* and *M. ochrogaster*) fluctuate widely, but do not cycle regularly in temperate climates and are rarely

absent altogether (Taitt and Krebs 1985). In central North America, voles settle in abundances of 100 to 250 animals/ha if cover is protected from ungulate grazing, mowing, and fire (Kaufman et al. 1990, Lin and Batzli 2001). Might ubiquitous voles, in the absence of ungulates, shape the character of North American grasslands? As a first step, in this paper we ask whether meadow-vole herbivory so alters the plant assemblages that it creates unpalatable communities dominated by plants that voles fail to eat.

### METHODS

#### *Experimental plantings*

We monitored aboveground standing crop, abundance, and cover of plants in experimental prairie restorations in a converted hayfield at the Morton Arboretum in Lisle, Illinois, USA, from 1998 through 2003. The experiment consisted of 24 14 × 14 m small-mammal exclosures 1.23 m high with hardware cloth sunk 0.6 m into the soil, arranged in a 4 × 6 grid on a backhoed and disced hayfield. Experimental treatments planted in June or December 1997 included 18 grasses and forbs sown at low density (35 seeds/m<sup>2</sup> per species) or high density (350 seeds/m<sup>2</sup> per species) in exclosures that either admitted or excluded voles (Howe and Brown 1999). Each 14 × 14 m plot was divided into four 7 × 7 m subplots, two of which were randomly selected to admit or exclude voles. Exclusion subplots lacked gates and had aluminum flashing bent over the top as an outside overhang of 20 cm. Rodents were allowed access to half of the subplots with similar fences perforated by four ground-level 5 × 5 cm gates. For details of experimental design and first season (1997) effects of selective herbivory on vegetation, see Howe and Brown (1999).

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Generally, vole densities ranged from 80 through 220 animals/ha. Periodic censuses showed that vole populations were uncharacteristically low (4 animals/ha) in early 1998, but recovered thereafter. The meadow vole (*Microtus pennsylvanicus*) was the sole microtine rodent in these plots from 1997 through 2001. Coincident with recovery of vegetation from a massive meadow-vole-induced defoliation in 2000 (Howe et al. 2002), prairie voles (*M. ochrogaster*) appeared in June 2002 (1.4% of total), became common by November 2002 (22%), and accounted for almost half of the voles live-trapped in 2003, the final year of vegetation sampling (47–48%). By the last vole census in September 2005, two years beyond the plant community study reported here, 93% of the voles trapped were prairie voles. Aside from seed-eating mice (*Peromyscus leucopus*) and birds, no other vertebrate herbivores frequented the site. Bird granivory, controlled initially, had no detectable effect beyond 1998. During the course of the study, Arboretum staff vigorously controlled deer (*Odocoileus virginianus*) for other purposes. Weeds that reached the canopy were aggressively removed.

#### Sampling

Standing crop, plant number, and cover were sampled in October and November each year. Biomass of standing crop best reflects the resources assimilated the previous season, as one estimate of previous competitive effect of life form and total use of the habitat. A measure of standing crop was determined with three randomized 0.25-m<sup>2</sup> clippings per subplot, where aboveground plant material was clipped to the ground, bagged, dried to constant mass, sorted as grass or forb, and weighed to the nearest 0.1 g. This is not sufficient for estimates of species responses, but is for total aboveground biomass or grass and forb response. Counts offer some reflection of prior competitive ability, but more importantly include species too small to reach the canopy, and juvenile individuals that reflect capacity to respond to disturbance. Counts and cover were determined from five permanent 1 × 1 m plots in each of 96 subplots, allowing species-specific comparisons. Counts were of individual plants in noncloning species or distinct rosettes or clumps of stems (e.g., three stems of *Solidago rigida* or six of *Phalaris arundinacea* emerging from a base would be counted as a single plant in each case). Either because of hard clay soils or time (seven years from planting to end of plant sampling), other grasses showed no sign of clonal growth. Cover indicates what the plots look like, and reflects competition for space of species whether or not they accumulate much biomass (e.g., some species, such as *Phalaris arundinacea*, aggressively dominate space over competitors that would otherwise have much higher biomass in the same space; e.g., Howe 1995). Cover was estimated with a 1-m<sup>2</sup> frame placed over the permanent sampling plots and a drawing of the area of each species drawn to scale; these areas were later determined by digitizing with a

Leico planimeter (Howe and Lane 2004). The minimal area included for a plant species was at least 10 × 10 cm of continuous canopy. In these recent plantings, little integration of individual stems was evident, as would occur in native prairie, allowing inclusion of plant area of species that reached the canopy. Cover of the 11 focal species accounted for >99% of the cover of planted species, and 86% of the total plant cover. Volunteer plants, including those native to North America, accounted for 14% of cover overall, mostly by small individuals of low biomass that occupied open areas (e.g., *Poa pratensis*) or individuals or clumps of taller species that survived control measures (*Solidago altissima*).

Simpson's diversity index ( $D$ ) was adapted as proportional diversity of cover ( $D_{pr}$ ):

$$D_{pr} = 1 / \sum p_i^2$$

where  $p_i$  is the proportion of a m<sup>2</sup> occupied by species  $i$  among species in the square meter. This is not strictly diversity, which is calculated from counts (e.g., Howe et al. 2002), but serves as an index of heterogeneity applicable to the cover analyses used here for species composition (Howe and Lane 2004). Proportional diversity was calculated using the five permanent 1-m<sup>2</sup> samples in each enclosure, thereby avoiding values of monocultures at the canopy level, which are informative for cover or counts but distort derivative calculations. Species richness was the number of species in the same cover samples of five permanent 1-m<sup>2</sup> sample plots in each enclosure. In this sample 26 (of 576 possible instances) plots produced outlier  $D_{pr}$  values (>20.0, or >2 SD above the mean) in some year. Most high outliers were in vole-access plots, but outliers added too much variance for credible statistical analysis and were excluded.

We report vole effects over time for each species with adequate data. Repeated-measures ANOVAs tested for differences in biomass values between mammal exclusion and mammal exposure plots, and the interaction year with the vole treatment (the significance values of  $F_{5,445}$  in each case). We performed separate analyses for 11 species sufficiently common for complete analyses of abundance and cover. We tested for significant interactions of voles with planting density and planting season. Comprehensive examination of all effects and interactions will be presented elsewhere. Counts were square-root transformed, and cover as a proportion was arcsine-square-root transformed to better approximate normality. Bonferroni adjustments were made to provide a conservative correction of the experiment-wise error rate for the separate ANOVAs (e.g., 11 species for counts provide conservative estimates of statistical significance). These adjustments were made (1) to the main effects of voles, planting density, planting season and their interactions; (2) to the univariate repeated-measures  $F$  tests of interactions between year and voles, planting density, and planting season; and (3) to the

multivariate Wilks' lambda for determining whether to accept as significant any of the five polynomial contrasts. Significance values reported are Bonferroni adjusted (e.g., an uncorrected value of  $P < 0.005$  is reported as a corrected experiment-wise error rate of  $P < 0.05$ ,  $P < 0.001$  as  $P < 0.01$ ). Means are accompanied by standard errors. Statistics were performed with SYSTAT 11 (SPSS 2004).

## RESULTS

### *Effects on standing crop, plant number, and cover*

Over time, voles had substantial effects on standing crop, number, and cover of plants. Repeated-measures analysis of variance (ANOVA) teased out effects in each variable that can be attributed to vole herbivory from 1998 to 2003, as contrasted with differences in starting values or other factors (Fig. 1). By 2003 with vole access, the aboveground biomass declined 38% (to  $526.5 \pm 29.9$  g/m<sup>2</sup> where voles were excluded and to  $325.8 \pm 24.4$  g/m<sup>2</sup> where voles were admitted); plant number increased 9% ( $30.7 \pm 5.1$  to  $33.6 \pm 4.8$  plants/m<sup>2</sup>); and cover fell by 8% ( $90 \pm 1\%$  to  $82 \pm 2\%$ /m<sup>2</sup> (all data mean  $\pm$  SD);  $P < 0.05$  to  $P \ll 0.0001$ ). The increase in numbers came mostly from smaller individual plants. Standing crop in 2003 recovered substantially from the 72% reduction in 2000 ( $443.3$  g/m<sup>2</sup> without voles to  $122.9$  g/m<sup>2</sup> with voles present), reflecting replacement of plants preferred by *M. pennsylvanicus* by species that they did not eat. Weeds increased in number on mammal-access plots ( $22.1 \pm 6.8$  to  $37.2 \pm 10.9$  plants/m<sup>2</sup>), with inconsistent effects of season ( $P < 0.05$ ). These were mostly small individuals (e.g., *Poa*) too small to reach the canopy; there were no significant differences in weed biomass or cover as a function of vole access.

Vole herbivory affected native grass and forb performance (Fig. 1). By 2003, overall native-grass standing crop, counts, and cover were reduced in vole-access plots (biomass,  $98.2 \pm 16.8$  g/m<sup>2</sup>; individuals,  $5.3 \pm 0.4$  ind./m<sup>2</sup>; cover  $16 \pm 3\%$ ) as compared with vole-exclusion plots ( $278.8 \pm 35.0$  g/m<sup>2</sup>;  $9.8 \pm 1.8$  ind./m<sup>2</sup>;  $46 \pm 4\%$ ). All were significant direct effects ( $P < 0.01$  to  $P < 0.001$ ), most evident 1998–2002. Vole and season effects interacted 1999–2000 and 2002–2003, with especially sharp reductions in June plantings ( $P < 0.01$ ). By 2003, repeated-measures ANOVA showed native-forb biomass was less in vole-access plots ( $227.6 \pm 21.4$  vs.  $247.7 \pm 26.9$  g/m<sup>2</sup>;  $P < 0.05$ ), but there were more forb individuals ( $27.2 \pm 5.7$  ind./m<sup>2</sup> vs.  $16.4 \pm 6.1$  ind./m<sup>2</sup>;  $P < 0.01$ ), and forb cover was greater ( $66 \pm 4\%$  vs.  $43 \pm 4\%$ ;  $P < 0.01$ ). The net effect of vole herbivory was a sharp reduction in grass standing crop, cover, and number by 65%, 54%, and 30%, respectively, reduction of forb biomass by 8%, and increases in forb numbers and cover by 48% and 53%, respectively.

### *Changes in community composition*

Species composition changed substantially. Over time, most species increased or decreased significantly with

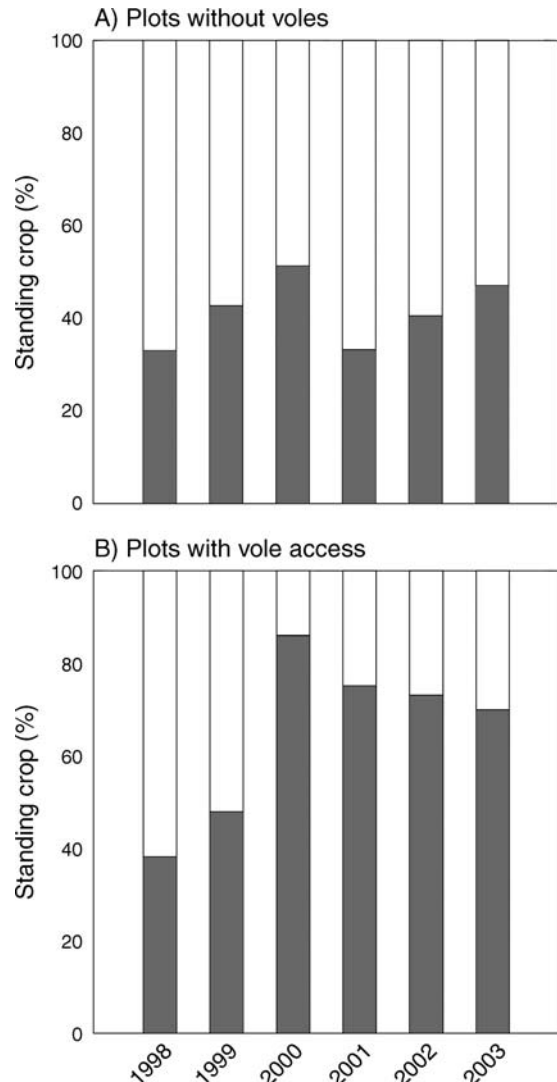


FIG. 1. Percentage standing crop for forbs (gray bars) and grasses (open bars), with and without voles, in experimental plantings at the Morton Arboretum in Lisle, Illinois, USA.

exposure to voles (Fig. 2). All grasses declined. Of the grasses, *Phalaris arundinacea* was the least affected. This grass attains 6% silica by dry mass at maturity (Van Soest 1982). One common legume (*Desmanthus illinoensis*) declined, while four forbs increased in numbers or cover and three were unaffected (Table 1; repeated-measures ANOVA,  $P < 0.05$  to  $P < 0.001$  where applicable). Not shown in Table 1 is *Dalea purpurea*, a legume that did not reach the canopy, which declined in number with vole access ( $P < 0.01$ ). *Echinacea pallida*, *E. purpurea*, and *Rudbeckia hirta* (a biennial) recovered from almost-barren mats of rosettes, the only vegetation left in some plots denuded by meadow voles in 2000, but extreme variance in *E. purpurea* precluded a statistical effect. Increases in *Penstemon digitalis* and *Solidago rigida* registered statistically as strong direct effects despite initial scarcity in some vole-access plots. With

recovery from the year 2000 defoliation, dominant vegetation in plots accessible to voles was of species not eaten by *M. pennsylvanicus*.

Some interactions with other variables were evident. *P. digitalis* numbers reflected the vole interaction with season, and additionally increased in low-density plantings. *Panicum virgatum* decreased in abundance with vole access in June plantings. Cover of *Penstemon digitalis* and *S. rigida* showed significant interactions of vole access with planting season, with increases in December plantings, while *Heliopsis helianthoides* and *Panicum virgatum* had inconsistent interactions of vole access with season. *R. hirta* cover increased in low-density plantings with vole access.

Voies increased diversity but did not consistently affect plant species number per square meter over six years. The interaction of  $D_{pr}$  (proportional diversity of cover [see *Methods: Sampling*, above]) with rodent access was significant ( $F_{5,365} = 3.039$ ,  $P = 0.01$ ), with  $D_{pr} = 8.05 \pm 1.35$  by 2003 where voles had access and  $4.57 \pm 0.46$  where they were excluded (Wilks' lambda at  $P = 0.005$ ). Overall the samples showed 1–11 species of experimental plants/m<sup>2</sup> (in 2001 and 2003,  $6.8 \pm 0.2$  and  $6.3 \pm 0.2$  plants/m<sup>2</sup>, respectively) with no consistent influence of voles from repeated-measures ANOVA. Only in the year 2000, when voles defoliated the plots (Howe et al. 2002), were there fewer species in vole-access plots ( $4.8 \pm 0.2$  species/m<sup>2</sup>) than in protected plots ( $5.7 \pm 1.9$  species/m<sup>2</sup>;  $F_{1,94} = 6.22$ ,  $P < 0.025$ ).

#### DISCUSSION

##### *Vole effects on vegetation*

Impacts of rodents on grasslands are in some ways similar to those of ungulates. In grasslands, ungulates regularly consume 15–92% of the standing crop, often with profound impacts on ecosystem dynamics (McNaughton 1985, 1992, McNaughton et al. 1991). In this experiment, voles cut >30% to 72% of the vegetation, reducing standing crop well within the range achieved by ungulates, and voles strongly shape species composition estimated by relative abundance and cover. However, in other ways rodents are unlikely to create the degree of heterogeneity reported for ungulates. Voies often fail to consume cut vegetation, are small in body size (<60 g), and are unlikely to move or concentrate nitrogen waste to the degree seen in ungulates (see Hobbs 1996). Voies cut as much vegetation as ungulates, but the smaller voies leave extensive litter, do not redistribute much organic matter, and are unlikely to produce heterogeneous high- and low-N habitats to the degree that is common for large mammals.

The different scales on which rodents and ungulates forage affect vegetation in different ways. In favored places bison (*Bison bison*) increase plant species diversity by grazing, trampling, and wallowing, but use other apparently suitable habitat much less intensively, if at all (Collins 1987, Senft et al. 1987). In addition, predation risk dramatically changes the foraging landscape for

ungulates. In some landscapes elk (*Cervus elaphus*) are 12% less likely to occur in grasslands where wolves occur than in those from which wolves are absent (Creel et al. 2005), and wolf presence releases willow forage that elk otherwise suppress (Ripple and Beschta 2004). Voies do not trample large areas or create wallows, nor do they obviously avoid vegetated habitats because of predation risk, although predator risk undoubtedly affects foraging (Pusenius and Ostfeld 2000). Instead voies adjust numbers in grassland habitats, approximating a fluid ideal-free distribution (Lin and Batzli 2001). The smaller scale at which the voies forage implies that their effects, whatever they may be, are more uniformly distributed than those of ungulates.

##### *Consequences of contingent selectivity*

Foraging by mammals is contingent, with selection of a particular food influenced by intrinsic nutritional quality, handling properties (including plant defenses), risk of predation, and what else is available (Schoener 1971, Brown 1999, Preisser et al. 2005). On first principles, voies should be selective feeders (Howe and Westley 1992). Small mammalian herbivores with small gut volumes and limited gut flora should be more selective than larger ungulates, with the ubiquity of the smaller animals imposing consistent suppression of preferred forage species and release of nonpreferred species (Ostfeld et al. 1997), while much larger ungulates can eat a wider array of maturing vegetation. Effects of vole herbivory on plant communities vary in time and space because the relative value of forage varies in time and space. For instance, in one Wisconsin (USA) experiment, no effects of herbivory were detected because voies preferred forage outside the plots over the mix of species planted in them (Howe and Brown 2001). Two-hundred meters away, planted mixes that included a preferred grass and legume that dominated when voies were fenced out were dramatically altered when voies were admitted (Howe and Lane 2004). Vole effects are most obvious where edible plants are common. In our experiment, vole reduction of biomass decreased from 72% in 2000 to 38% in 2003 as unpalatable forbs replaced grasses and a legume species that were strongly suppressed by rodent herbivory. These effects were easily detected because initially dominant but edible vegetation was easily sampled.

In short, particular consequences of vole herbivory on plant communities are context dependent. With small mammals vulnerable to subtle differences in plant defenses and nutritional quality, effects on plant communities vary with circumstances, with the most influence where vegetation is edible and far less influence where distasteful or even toxic dominant vegetation limits rodent use of habitat. Where palatable forage is common, vole depletion of vegetation can be dramatic (Batzli and Pitelka 1970, Howe et al. 2002). Because voies are less abundant in native prairies than in human-made pasture and forage-crop habitats, they may have

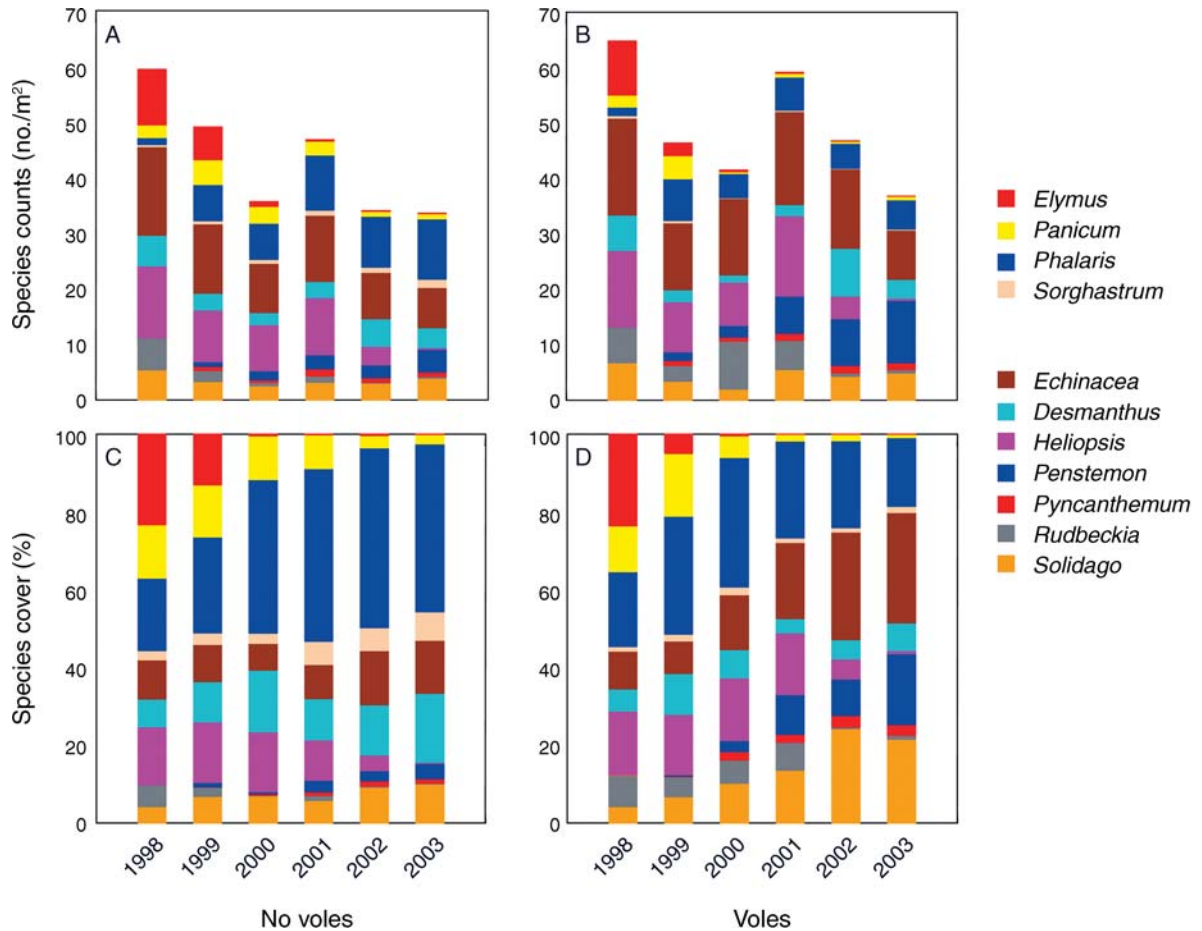


FIG. 2. Counts and percentage cover of grassland plants in experimental plantings at the Morton Arboretum in Lisle, Illinois, USA, (A and C) without voles and (B and D) with vole access. The top four taxa on the legend are grasses. Species of the indicated genera are listed in Table 1.

TABLE 1. Direct effects of change in abundance and cover due to voles, as shown by repeated-measures ANOVA.

Species†	Vole effect‡	
	Abundance	Cover
<i>Desmanthus illinoensis</i> (bundle-flower)	decrease***	decrease*
<i>Echinacea pallida</i> (prairie coneflower)	none	increase**
<i>Echinacea purpurea</i> (purple coneflower)	none	none
<i>Heliopsis helianthoides</i> (early sunflower)	none	none
<i>Penstemon digitalis</i> (foxglove)	increase***	increase***
<i>Pycnanthemum virginianum</i> (mountain mint)	none	none
<i>Rudbeckia hirta</i> (black-eyed Susan)	increase***	increase***
<i>Solidago rigida</i> (stiff goldenrod)	increase***	increase**
<i>Elymus canadensis</i> (Virginia rye)	decrease***	decrease*
<i>Panicum virgatum</i> (switchgrass)	decrease***	decrease***
<i>Phalaris arundinacea</i> (reed canary grass)	decrease***	decrease***
<i>Sorghastrum nutans</i> (Indian grass)	decrease***	decrease***

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$  (statistical significance based on Wilks' lambda).

† The last four species listed are grasses.

‡ Repeated-measures ANOVA by species for six years: "none" indicates not statistically significant; "decrease" or "increase" indicates statistically significant effects after Bonferroni adjustment for multiple comparisons, where Wilks' lambda is significant. See *Results: Changes in community composition* for interactions of mammal effects with planting season or planting density.

little impact on dominant native vegetation where preferred forage has either been culled or was not present to begin with (Lindroth and Batzli 1984, Gibson et al. 1990, Howe and Brown 2001). For instance, in this experiment sharp reductions in plant diversity occurred when voles first reached high abundances because palatable species were common (see Howe et al. 2002). However, plant diversity, if not density, rebounded as less palatable species compensated for suppression of their competition, while palatable species were reduced in number, cover, and standing crop, but were not entirely eliminated from the habitat. When palatable foliage is reduced, likely a common situation in nature, even consistent use of sparse edible vegetation by small populations of rodents may be difficult to sample and therefore detect.

#### *Creating a noxious world*

Animal activity may either increase or decrease the value of habitats to the animals themselves (Jones et al. 1997). Episodic insect outbreaks, such as chrysomelid destruction of *Solidago altissima* stands, create decimated host-plant communities and, with accumulated litter, suppress most other plant species, illustrating broad effects of suppression of one common plant species (Carson and Root 2000). On the other hand beavers (*Castor canadensis*) are classic constructive engineers in their own interests by creating ponds that favor willows upon which they feed, as well as creating habitats for other plants that would otherwise not occur in the landscape (Wright et al. 2002). In our experiment, meadow vole reduction of standing-crop biomass and change in plant species composition in cover and abundance result from direct suppression of several preferred forage species and indirect release of less palatable species. We find that meadow voles progressively degrade their own foraging environment, producing dominant vegetation that becomes largely untouched by their herbivory. One end result might ultimately be that observed by Lindroth and Batzli (1984)—lower vole densities in habitats culled by herbivory than in anthropogenic habitats planted and maintained with palatable forage species. Another possibility is creation of conditions by meadow voles that favor what might superficially appear to be close competitors. Here, both effects are evident, with prairie voles filling the second role.

This experiment was not designed to distinguish differences in use and effects of herbivory by different rodents, but it is interesting that as vegetation recovered from catastrophic meadow vole herbivory (Howe et al. 2002), prairie voles (*Microtus ochrogaster*) replaced their congeners at this site (see *Methods: Experimental plantings*, above). The obvious hypothesis is that in the transient dynamics of this system, communities degraded by meadow vole herbivory presented opportunities for prairie voles that, by virtue of slightly different diets and slightly smaller body size (e.g., Lindroth and Batzli

1984), gained a competitive advantage over their congeners. A nonexclusive alternative is that stable extended families in the monogamous social system of prairie voles better utilize low forage quality than more promiscuous meadow voles (Getz and Carter 1996), adding another advantage for prairie voles in habitats altered by meadow voles. Two years after the end of this experiment, meadow voles were all but absent from the site; prairie voles prevailed. A question for an experiment targeted for this interaction is whether the ultimate result is that found elsewhere, low vole densities in increasingly unpalatable vegetation, or an oscillation between plant species avoided by meadow voles and those avoided by prairie voles.

Meadow voles create increasingly unpalatable foraging environments for themselves. They strongly suppress grasses and forbs that they find palatable, and release competing plants that they do not. Given a larger mix of species at planting that allows a greater variety of responses to herbivory, and enough time, we predict that both vole species would so degrade their environments that experimental plantings would support far lower populations of both rodents, as in native prairies. We expect that after decades of selective herbivory by voles, native prairies are what voles choose not to eat.

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