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Vole Herbivory Shapes Vegetation in Experimental Tallgrass Prairie Restorations (Illinois and Wisconsin)

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It is widely acknowledged that cattle and bison influence plant diversity in grasslands, but rodents may have even more pervasive effects. To test the idea that meadow voles (*Microtus pennsylvanicus*) shape tallgrass communities, Joel Brown and I created experimental tallgrass restorations in exclosures in Illinois and Wisconsin. We asked: 1) Does seed-size selection shape what comes up; 2) Does vole herbivory determine which plants survive seedling establishment, and 3) Does vole herbivory on mature plants alter tallgrass composition? Here, I present a brief synthesis of our investigations, which together confirmed Hulme's (1996) claim for English meadows: Grassland vegetation is what rodents choose not to eat.

To answer the first question, we established 18 2-m x 2-m exclosures at a site near Viola in southwestern Wisconsin (Howe and Brown 2000, 2001). In October 1997, we broadcast seeds of 16 forbs at 100 seeds/m²/species. By limiting vole access into six of the exclosures only during the growing season, into six others only during winter and allowing no access into the rest, we learned that voles had both direct and indirect effects. For example, they ignored rosinweed (*Silphium integrifolium*) plants, but relished its large seed. As a result, they reduced emerging seedlings to 32/m² in winter-access exclosures compared with 80/m² in the other exclosures. Lower rosinweed density released other plants, increasing diversity by 33 percent. Thirty months after completely excluding voles from all plots, adult rosinweed self-limited to 20-30/m² and still suppressed other plants. But

rodent effects persisted, with echoes of suppression on densities of large-seeded vetch (*Astragalus canadensis*) and tick-trefoil (*Desmodium glutinosum*), and indirect release of small-seeded yellow coneflower (*Ratibida pinnata*) and goldenrod (*Solidago rigida*), and unpalatable purple coneflower (*Echinacea purpurea*). Plant diversity remained 27 percent higher where voles had foraged 30 months earlier than where they had not.

In 1997, we addressed our second question at the Morton Arboretum near Chicago by establishing 14-m x 14-m plots divided into vole access and exclusion treatments and planted with 18 grasses and forbs (Howe and Brown 1999, Howe and others 2002). Predation fear of open spaces prevented vole granivory. With knee-high vegetation, selective vole herbivory reduced forbs by 57 percent in some treatments. In 2000, the voles—which had reached a population density of 383/acre (155/ha)—ate almost everything. Densities of most grasses and forbs fell 16-98 percent, with some plots reduced to mats of unpalatable purple coneflower rosettes. Black-eyed Susan (*Rudbeckia hirta*), a native opportunist, increased more than 1,000 percent. Voles ate as much vegetation as ungulates, but by favoring less dominant plants they decreased plant diversity by 37 percent.

For our final question, I planted 16 species of grasses and forbs at 50 seeds/m²/species in 18 4-m x 4-m exclosures, all closed to mammals for 26 months, in wet ground at the Viola site (Howe and Lane in review). Once vegetation was head high and flowering in August 1998, I cut openings in nine exclosures. During 36 months of exposure to vole herbivory, otherwise abundant tick-trefoil (*Desmodium canadense*) and Virginia wild rye (*Elymus virginicus*) were eliminated, while voles accelerated succession to dominance by unpalatable mountain mint (*Pycnanthemum virginianum*) and perennial black-eyed Susan (*R. subtomentosa*). By eating mature plants, voles changed the successional process.

If few vole effects are found in native prairies (Gibson and others 1990), it is probably because they have long since eaten the palatable plants.

Restorationists can take practical approaches to overcome vole herbivory. For example, traps, poison, fences, areas exposed by mowing, or underground vibrators might have surprising benefits for large-seeded plants, such as *Silphium*. Because vole herbivory usually decreases plant diversity while ungulates increase it, restorations should include dominance-reduction measures that favor subdominants, such as mowing, grazing, or growing-season fire (for example, see Howe 1999, Copeland and others 2002). Otherwise, they will suffer the consequences of ubiquitous rodents selectively eliminating less common plants.

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Small Mammal Responses to Tallgrass Prairie Restoration from Fescue Pastures (Kansas)

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The practice of over-seeding grasslands with tall fescue (*Festuca arundinacea*) for cattle grazing has altered 680,000 acres (275,000 ha) of tallgrass prairie in Kansas. Although fescue—a vigorous, cool-season perennial—may benefit cattle growers by providing green forage during months when native warm-season grasses are dormant, the structurally dense fescue grasslands formed through annual nitrogen fertilization are thought to pro-

vide poorer wildlife habitat than structurally diverse native prairie pastures (Sole 1995).

We examined small mammal community responses to a passive method of converting tall fescue pastures to native tallgrass vegetation on 1,482 acres (600 ha) at the Kansas Army Ammunition Plant (KSAAP) in Labette County. These grasslands have been managed for cattle grazing since the 1940s, at which time the grazing allotments were over-seeded with tall fescue. Annual applications of nitrogen fertilizer and year-round grazing favored the growth of fescue, which mostly replaced the native vegetation. During the same period, grazing was excluded from a number of small areas that were set aside as native prairie and have been maintained by annual mowing and haying. In 1996, KSAAP's natural resources manager began restoring two allotments (381 acres [154 ha]) by removing cattle, stopping fertilization, and conducting spring burns. No prairie species were planted.

Our study sites, ranging from 132 acres (53 ha) to 416 acres (168 ha), represented five treatments: 1) Grazed controls—two allotments with ongoing, year-round grazing during 1998, which became the 1999 restoration sites, and two new allotments in 2000; 2) 1997 restoration—cattle removed from two allotments on December 31, 1996; 3) 1998 restoration—cattle removed from two allotments on December 31, 1997; 4) 1999 restoration—cattle removed from two allotments on December 31, 1998; and 5) ungrazed controls on four allotments. We trapped small mammals along four transects in each treatment using two Sherman live-traps at each of 20 trap stations spaced 50 ft (15 m) apart. We baited the traps with peanut butter and oatmeal and trapped animals for three consecutive nights during each fall and spring from October 1998 through April 2000.

We captured 632 mammals of 11 species, including two shrews, one rabbit, and eight rodents. The most abundant species (365 captures) was the hispid cotton rat (*Signodon hispidus*), which we captured on all transects. It was most abundant on the 1997 restoration plots (152) and least abundant on the currently grazed sites (3). The deer mouse (*Peromyscus maniculatus*) was the second most abundant species (139) and was captured in similar abundances on all treatments. The least shrew (*Cryptotis parva*) preferred the ungrazed and 1997 restoration plots. No species showed clear preference for the currently grazed sites. We trapped the largest number of mammals on the 1997 restoration plots, due to the preference of hispid cotton rats for these sites.

The five most abundant plant species associated with grazed fescue pastures decreased as the restoration sites matured, while the most abundant species associated with native prairie pastures at the KSAAP increased (Cully and others in review). It is no surprise, therefore, that sites several years into the restoration process had higher animal species richness and captures than did the ungrazed or grazed sites. Our results are similar to those of Moreth and Schramm (1972), who found that restored prairie vegetation supported higher and more diversified populations of