A 12-year Study of Vegetation and Mammal Succession on a Reconstructed Tallgrass Prairie in Iowa

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ABSTRACT: Change within the plant and small-mammal communities of a hayfield planted to five grasses native to the tallgrass prairie was observed for 12 years. Three developmental stages were discerned: (1) a 3-year Herbaceous Weed Stage characterized by common weed species, a standing crop average of 511 g m^{-2}, and an abundance of house mice; (2) a 5-year Perennial Grassland Stage characterized by *Bromus inermis* and other cool-season grasses, a standing crop average of 403 g m^{-2}, an irruption of white-footed mice, and an increase in abundance of voles and short-tailed shrews, and (3) an Early Prairie Stage in which the standing crop of native prairie grasses (average 493 g m^{-2}) was 60% of the total living phytomass (822 g m^{-2}), and continued increase of vole and shrew densities. We hypothesized that the reconstructed prairie was suboptimal habitat for common prairie mammals because of low forb abundance, low diversity and high phytomass. The frequent capture of low weight, nonbreeding small mammals leads us to believe that the area received dispersers from other surrounding habitat.

INTRODUCTION

Simultaneous studies of vegetation succession and changes in diversity and density of small mammals have been reported for seral stages of vegetation following land abandonment from farming (Beckwith, 1954; Pearson, 1959; Smith, 1940), strip mining (Hansen and Warnock, 1978; Sly, 1976; Verts, 1957) and burning (Crowner and Barrett, 1969). In most of these studies, several stages were surveyed for a brief time to construct a composite of biotic change; few employed a long-term study design. We report here a 12-year study relating vegetation succession and changes in diversity and abundance of small mammals for a reconstructed tallgrass prairie. Specifically we describe:

(1) The vegetation succession of an abandoned hayfield from the year prior to prairie reconstruction through the next 11 years.

(2) The changes in species and abundances of small mammals as the vegetation changed.

(3) The correlations between vegetation composition and the species and abundances of small mammals.

(4) The age-mass composition of voles and shrews during the 1st 2 years of the early prairie vegetation stage.

MATERIALS AND METHODS

The 5-ha Tallgrass Prairie Preserve is located on the University of Northern Iowa (UNI) campus in metropolitan Cedar Falls, Black Hawk Co., Iowa. It is bounded on the N by a city street and residential area beyond, on the W by a street and vacant field beyond, and on the S and E by a small tree-lined stream. In July 1973 the land was plowed, disked and harrowed, and seeded with big bluestem (*Andropogon gerardi* Vitman), little bluestem [*Schizachyrium scoparium* (Michx.) Nash], Indian grass (*Sorghastrum avenaceum* (Michx.) Nash), side-oats grama (*Bouteloua curtipendula* (Michx.) Torr.) and switchgrass (*Panicum virgatum* L.). A limited number of native forbs were seeded or transplanted into the prairie. Reconstruction management also controlled invasion by woody species, particularly *Acer negundo* L., *Fraxinus pennsylvanica* Marsh and *Prunus* spp.

In early autumn 1972 the vegetation was sampled by 20 randomly established clip-quadrats (0.1 m^2) to assess species composition and aboveground, peak-standing crop biomass (dry weight, 24-36 hr at 65 C). Each succeeding autumn through 1982 quadıts sampled were from the same approximate areas of the prairie and were within the nall mammal grid described below. Treatments to enhance native prairie plant growth ıd to eliminate nonnative or weedy native species included spring burning, summer ıowing or hay removal, and herbicide application (Table 1).

Each year, from 1972-1981, within 2 weeks of vegetation sampling, small mammals ere sampled using a 10 by 10 trap-grid with Sherman live traps spaced at 10-m interals (Table 1). The traps were opened for 2 or 3 consecutive nights and examined early ıe following mornings. Data recorded for each small mammal captured included spees, sex (except for shrews), body mass, location on the grid, capture history and reroductive condition.

From October 1982 through November 1983 a more detailed study of small mamıals was conducted on treated areas A, B and C (Table 1). A 10 by 15 trap-grid of herman live traps spaced at 10-m intervals was operated which covered the original rid and 50 m to the E. This arrangement covered the three prairie treatment areas ith 70 traps in section A, 40 traps in section B, and 40 traps in section C. Information ecorded was identical with that recorded earlier.

Changes in the small mammal fauna and vegetation were analyzed by catch per nit effort and biomass of vegetation. The vegetation graphs provide annual values for eak standing crop of individual plant groups, a composite biomass for all groups standing crop) and total phytomass, the summation of standing crop and litter. The reationship of mammals to vegetation was determined by a forward, stepwise multipleorrelation analysis (BMDP2R) with catch per unit effort for each mammal species as he dependent variable. Significant partial correlation coefficients of each independent egetation variable were reported just before the value was entered into the model, and he cumulative R-value was obtained.

Vole and shrew masses for 1983-1984, after testing for significant differences beween years, were pooled to obtain population age structure assuming an age-to-mass orrelation. Vole age-mass classes are those reported by Getz *et al.* (1979).

RESULTS

Vegetation succession.—The old hayfield in 1972 was dominated by foxtail (*Setaria* pp.), red clover (*Trifolium pratense* L.), ragweed (*Ambrosia artemisiifolia* L.), alfalfa (*Mediago sativa* L.) and thistle (*Cirsium* spp.), in rank order of biomass with foxtail biomass qual to that of the forbs. We will discuss the reconstructed prairie vegetation and nammal composition in three stages that we perceived during the 12-year study (Fig. 1): (1) Herbaceous Weed Stage-Soil disturbance in 1973 to sow the prairie grasses (Tale 1) was followed by a 3-year weed stage dominated by several hayfield forbs and foxail [*Setaria lutescens* (Wieg.) Hubb. and *S. viridis* (L.) Beauv.]. The more common forbs n rank biomass sequence included ragweed, red clover, horseweed (*Conyza canadensis* L.) Cronq.) and knotweed (*Polygonum* spp.). Standing crop biomass during this stage averaged 511 g m^{-2} annually. (2) Perennial Grassland Stage-Cool season grasses (Fig. 1), including bromegrass (*Bromus inermis* Leyss), western wheatgrass (*Agropyron smithii* Rybd.) and wild-rye (*Elymus canadensis* L.), in respective biomass rank, replaced the weed stage vegetation and dominated for 5 years. During this grassland stage standing crop dropped to an annual average of 403 g m^{-2}, while forbs annually averaged only 33 g m^{-2}. (3) Early Prairie Stage-In 1981 the grassland succeeded to an early prairie stage with the prairie grass group alone exceeding all other plant biomass. The prairie grasses attained an annual average of 493 g m^{-2}, nearly 60% of the standing crop, whereas litter attained an average of 289 g m^{-2}. Few "weedy' forbs then occurred in the prairie; *Bromus inermis* was still the prevalent cool-season grass.

Composition and habitat relations of small mammals.—Capture rates from 1972 to 1981 showed a transition from house mice (*Mus musculus*) and meadow voles (*Microtus pennsylvanicus*) initially, a dominance of white-footed mice (*Peromyscus leucopus*) in 1977, and a dominance of meadow voles and shrews (*Blarina brevicauda* and *Sorex cinereus*), thereafter

(Fig. 2). The monthly capture rates (1982-1983) showed a dominance of meadow voles and short-tailed shrews with only incidental captures of other species.

The numbers of mammals captured reflected the recency and impact of treatments to enhance prairie vegetation. From October 1982 through November 1983 there was an average of 0.77 captures per row per trap period in section A which was mowed in 1981 and burned in 1983. This contrasted with a 2.25 captures in section B, treated with herbicide in 1980, and 2.35 captures in section C, burned in April 1981. The number of captures per row in sections B and C were significantly greater ($F_{1,148} = 23.4$, $P<0.01$) than the number captured in section A.

Eight significant, partial correlation coefficients were found that showed mammal abundances were changing with vegetation composition (Table 2). The herbaceous weed stage showed house mice abundance positively correlated and white-footed mice abundance negatively correlated with the biomass of foxtail. The perennial grassland stage had less litter than other stages, and the abundance of white-footed mice during this stage might be related to this factor. Later, as bromegrass and prairie grasses developed,

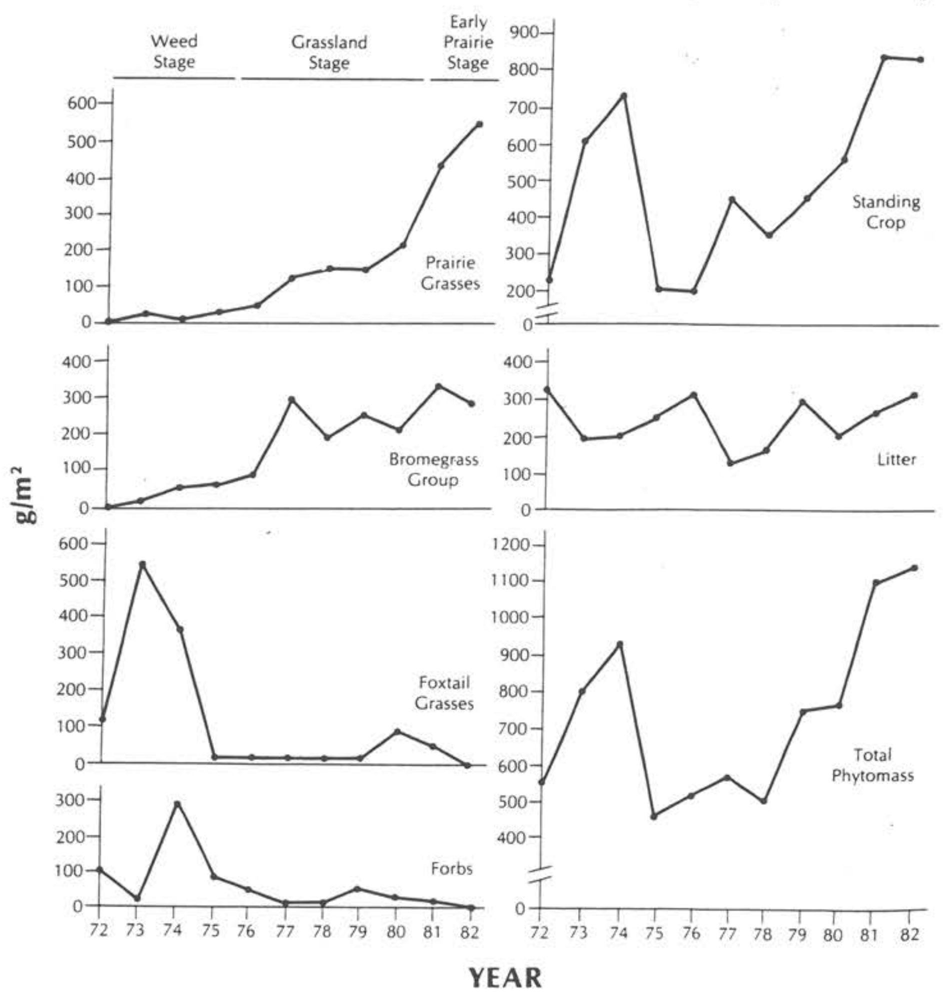

Fig. 1. – Vegetation elements (g m-2) on the UNI Prairie Preserve from 1972-1982

ıeir masses were positively correlated with the abundances of meadow voles and both ırew species (Table 2).

Age-mass composition of voles and shrews.—The age-mass pyramid for meadow voles ·om 1982 to 1983 showed few adult, breeding individuals (Fig. 3). The pyramid for ıort-tailed shrews similarly showed the heavier—26 to 30 g—mass classes to be less bundant (Fig. 4), and few shrews were observed in reproductive condition.

Discussion

The vegetation sequences and changes in small mammal diversity and numbers of ıe UNI reconstructed prairie superficially paralleled that seen on abandoned farms 3eckwith, 1954; Pearson, 1959; Smith, 1940) and mine spoils (Hansen and Warnock, 978; Sly, 1976; Verts, 1957). The initial weed stage reported for all studies, and lasting -7 years,was dominated by *Peromyscus maniculatus*, except in New Jersey where *P. leuco-us* dominated the stage (Pearson, 1959). Mine spoils succeeded in 7-12 years to mixed erbaceous-woody seral stages dominated by *P. leucopus*. Intermediate perennial grass :ages persisted for decades on abandoned farmlands in New Jersey (Pearson, 1959) nd Oklahoma (Smith, 1940) before succeeding to forest and tallgrass prairie respec-vely. In the intermediate stages of all seres numbers of *Microtus pennsylvanicus* and/or *M. :hrogaster, Sorex cinereus* and *Blarina brevicauda* increased, but occurrences of *Mus musculus* ecame fewer and more erratic as the early weed stage disappeared. The stream and ıe adjacent urban area may have sufficiently isolated the prairie preserve from *P. mani-ılatus* and *Microtus ochrogaster* which one would anticipate in a developing prairie.

Table 1.—Year, treatments to assist prairie development, and trapping dates from 1972 to 983

Year	Treatment	Trapping dates
·972	None	28, 29 September
·73	Plowed, Prairie grasses sown, July	26-28 September
1974	Mowed, June	6, 7 September
1975	Hayed, July	15-17 October
1976	None	13, 20, 21 October
1977	Mowed, burned, April	28, 29 September
1978	Burned, Spring; Mowed, Summer	25, 26 October
1979	Mowed, June	5, 6 October
1980	Treatment sections: A. Burned, May B. Herbicide, June C. Mowed, August	29-31 October
1981	A. Mowed, July B. None C. Burned, April	23, 24 October
1982	None	Throughout year
1983	A. Burned, May B. None C. None	Throughout year

Vegetation and mammal changes. — (1) Herbaceous Weed Stage — The 3-year herbaceous weed stage of the reconstructed prairie possessed many of the commonly reported adventive species. The high abundance of the annual foxtail may have been a consequence of its abundance in nearby disturbed sites. The commonly reported assemblage of composites that sometimes dominate late in this stage, especially *Aster, Erigeron, Helianthus* and *Solidago*, was not found here. The average standing crop of 511 g m^{-2} exceeded those for two young abandoned fields dominated by *Setaria glauca* (L.) Beauv. (120 g m^{-2}) and *Aristida basiramea* Engelm. (120 g m^{-2}) in Minnesota (Bray *et al.*, 1959), and a dry old field dominated by *Poa pratensis* L. (149 g m^{-2}) also in Minnesota (Bernard, 1974).

House mice were abundant before and the 1st year after prairie plants were sown. This species was virtually absent in subsequent years. The initial abundance of house mice was positively correlated with foxtail which was abundant prior to prairie grass planting and the following 2 years. The numbers of house mice were negatively correlated with forb and bromegrass abundance reflecting their intolerance of seral stages beyond the initial weed stage. In a weed field in S-central Iowa, house mice were common (Voight and Glenn-Lewin, 1979), and Fleharty and Navo (1983) reported cropland in W-central Kansas as ideal habitat for house mice. In contrast, house mice were not re-

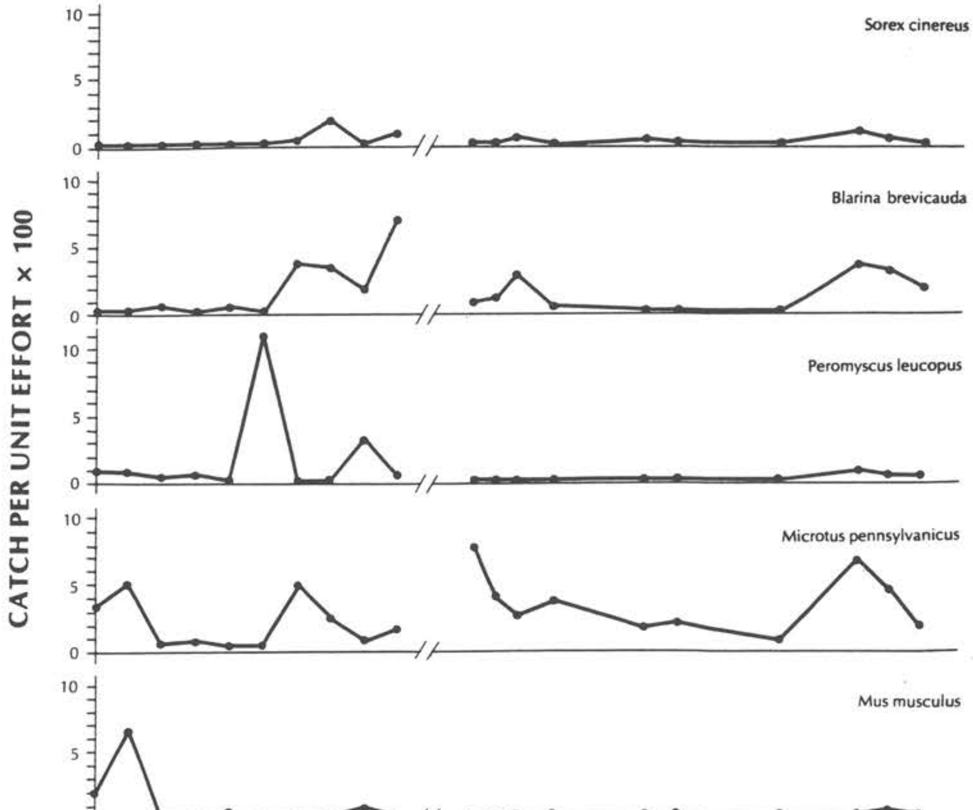

Fig. 2. — Small mammals (captures per 100 trap nights) on the UNI Prairie Preserve from 1972-1983

..ued in studies of small mammals in tallgrass prairies (*e.g.*, Getz *et al.*, 1979). Since 973, only three house mice were captured on our study site, and they were probably nmigrants from nearby residences.

The meadow vole was the dominant species during the course of prairie restoration, nd it was relatively abundant before and immediately following planting of prairie rasses. Geier and Best (1980) reported meadow vole abundance at a prairie site in uthrie County, Iowa, to be greatest in areas with high forb cover.

(2) Perennial Grassland Stage—*Bromus inermis*, a cool-season, weedy European extic, dominated the prairie for the next 5 years and resembled in habit the *Aristida-ragrostis* stages of Oklahoma and Kansas (Smith, 1940). Foxtail grass increased late in ıe stage (1980), in response to treatment with herbicide to control bromegrass on aproximately one-third of the prairie. The annual average of 620 g m^{-2} total phytomass ɔr the perennial grass stage, even with litter reduced by fire management, is still an nderestimate because cool-season grasses attain peak standing crop before the autumn ample date.

The white-footed mouse was present in early stages of prairie development with an pparent "irruption" in 1977. It was subsequently less abundant. Its abundance was egatively correlated with foxtail in the early weed stage of prairie reconstruction, and it lso was negatively correlated with litter. The greatest abundances of *Peromyscus* followed ne mowing and burning treatments of 1977 and the burn and herbicide treatments of 980. These treatments provided more open habitat commonly associated with the inreased abundance of white-footed mice. This species was also reported to be present in arly successional stages of old fields in New Jersey while perennial forbs were present; hen it reappeared in later successional stages (Pearson, 1959). In contrast, the whiteɔoted mouse has been reported widely as a late successional stage species associated vith more diverse and structurally complex woody plant habitat (Hansen and Warnock, 978; M'Closkey and Fieldwick, 1975; M'Closkey and Lajoie, 1975; Shure, 1970; ahner, 1982).

The short-tailed shrew and meadow vole became increasingly abundant during the nial grassland stage, and their abundances show positive correlations with brome- and prairie grass abundances which were rapidly increasing.

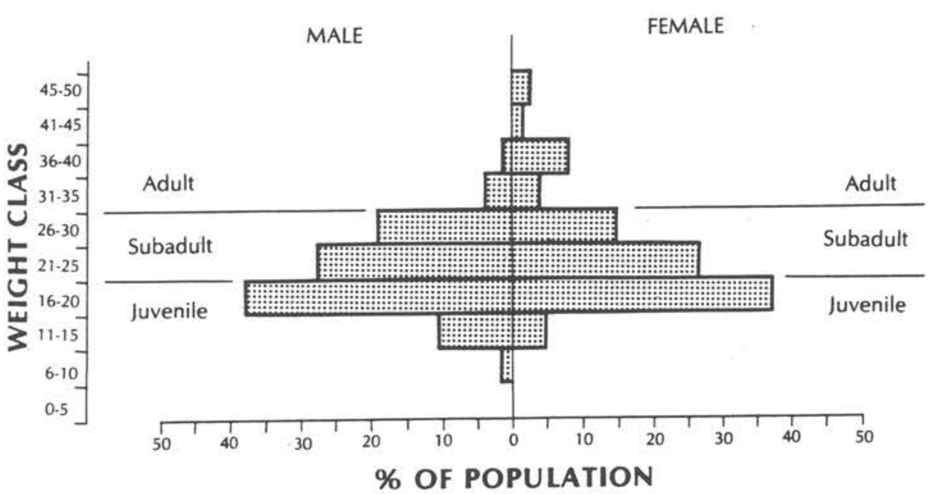

Fig. 3.—Mass-age pyramid in grams for *M. pennsylvanicus* trapped from October 1982 through November 1983. There was little difference between autumn trapping seasons when most were captured, hence the data from the entire trapping period were pooled. Age categories are from Getz *et al.*, 1979. Sample size is 80 males and 75 females

(3) Early Prairie Stage—Nine years after seeding the prairie, prairie grasses were the dominant vegetation, but the area lacked the usual diversity of prairie forbs. The average standing crop for only prairie grasses exceeded most aboveground peak live standing crop values (which averaged just below 400 g m^{-2}) reported by Risser *et al.* (1981) for several true prairie sites. The average standing crop of 837 g m^{-2} for the early prairie stage of the reconstruction clearly exceeded maximum values of 592, 566, 570 and 390 g m^{-2} reported by Risser *et al.* (1981) for prairie sites in Oklahoma, South Dakota, Missouri and Iowa, respectively.

The meadow vole populations were positively correlated with the abundance of prairie grasses; however, the abundance of prairie grasses is correlated highly with bromegrass abundance ($r = 0.79$), and in our stepwise multiple correlation only one of the two variables was entered into the model. Meadow voles, relative to other native mammals, favor high dense cover distant from woody vegetation (Bowker and Pearson, 1975; Eadie, 1953; M'Closkey and Fieldwick, 1975; Yahner, 1982; Zimmerman, 1965), and the UNI prairie reconstruction has progressed toward and perhaps beyond this dense habitat type. Voles in unmanipulated prairies with different vegetation heights and with different degrees of cover have been found to be more abundant in taller vegetation with greater cover (Birney *et al.*, 1976; Grant and Birney, 1979).

The abundance of voles reported in this study is relatively low compared to abundances in nonnative grassland, weed and old-field habitats (Gaines *et al.*, 1979; Gaines and Rose, 1976; Getz *et al.*, 1979; Krebs *et al.*, 1969). Seemingly, native prairie and restored prairie are less ideal habitats for voles than are areas where other than tallgrass prairie species predominate.

Since 1977, the prairie supported a relatively abundant population of short-tailed shrews in the autumn in areas with greater litter cover. Masked shrews were taken occasionally, but their population was likely underestimated by the use of Sherman live traps. Both species of shrews show positive correlations with bromegrass abundance, which as noted above, is also correlated highly with the abundance of prairie grasses. Hence, the short-tailed and masked shrew were associated with the early prairie stage.

Probably the few white-footed mice captured were foraging or dispersing from the woody areas along the nearby stream.

Age structure during the early prairie stage.—The small number of breeding individuals and the predominance of juveniles and subadults contrasts with other studies (Getz *et al.*, 1979); Iverson and Turner, 1974). Voles in the mass classes found on the Preserve were like voles experimentally identified as immigrants from areas with more stable populations (Gaines and Johnson, 1984). Low mass classes may also reflect poor habitat quality (Cole and Batzli, 1979). We speculate that the area is of relatively poor quality and is inhabited by immigrants from a few pockets of weedy habitat and the vegetation adjacent to the stream.

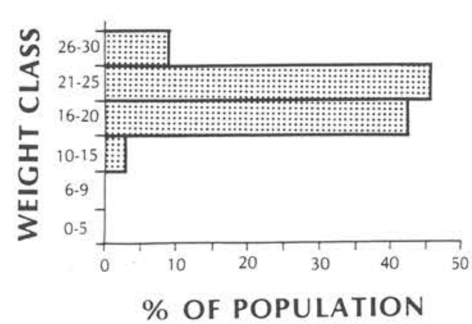

Fig. 4.—Mass-age histogram in grams for *B. brevicauda*. Sample size is 66 individuals. Data are as described in Figure 3

ther considerations.—Along with the low abundances of small mammals, nonbreed-g age structure of mammals captured and an irruption of a species not normally und away from woody vegetation, three other factors suggest that the Prairie preserve suboptimal habitat. First, the frequent fire, herbicide and mowing treatments pre-nted the accumulation of litter (Lemon and Clausen, 1984; Peterson *et al.*, 1985), and e area has become progressively a polyculture of the five perennial prairie grasses ith few other herbs, forbs or woody plants to provide habitat diversity. The significant fferences in numbers of captures per row among treatment areas showed the impact treatments on habitability for small mammals. Second, in some areas phytomass ex-eded that reported by Birney *et al.* (1976) and they suggested that high phytomass ay lower mammal densities. Third, predation is likely high. The stream that borders e Prairie Preserve is a corridor for rural and urban predators which have been fre-uently caught in large traps. Domestic cats and dogs from nearby residences enter the reserve, and frequent trap disturbance characteristic of such predators occurred.

There is interest in the initiation, development and maintenance of tallgrass prairies the midwest (Smith and Christiansen, 1982). In our experience, future development nd management should consider effective techniques to better balance native plant pecies diversity, especially forbs, and to undertake manipulations which favor the na-ve fauna. Succession was greatly compressed in time on the reconstructed prairie to e point that the land appears to be like native prairie. However, the abundance of rasses, deficiency of forbs, and the corresponding lack of structural diversity now pro-ides seeming abnormal habitat as reflected by the biology of small mammals on the udy site.

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TABLE 2.—Significant ($P < 0.05$) partial correlation coefficients from a stepwise multiple re-ression analysis. The dependent variable is catch per unit effort x 100 for the mammal species sted. The independent variables are weights of vegetation elements in grams per square me-er, as shown in Figure 1

	Partial correlation coefficients							
pecies	Forbs	Foxtail	Bromegrass	Prairie grass	Litter	Biomass	Phytomass	Cumulative R
Mus usculus	−0.81	0.80	−0.89					0.9870
Microtus ennsylvanicus				0.60				0.6031
Peromyscus eucopus		−0.82			−0.74			0.8503
Blarina revicauda			0.60					0.5986
Sorex inereus			0.56					0.5578

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