

Influence of Grazing by Bison and Cattle on Deer Mice in Burned Tallgrass Prairie

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ABSTRACT.—We studied the influence of grazing by bison (*Bos bison*) and by cattle (*B. taurus*) on deer mice (*Peromyscus maniculatus*) in tallgrass prairie at the Konza Prairie Biological Station in 1997 and 1998. Small mammals were sampled by one 10-station trapline in each of four bison-grazed enclosures, four cattle-grazed enclosures and four ungrazed sites. Enclosures were 4.9 ha and the biomass of grazers in each was similar. All sites were burned annually. We sampled small mammals for 4 consecutive nights in spring before fire, in spring after fire and in autumn. Deer mice were the most abundant species ($n = 285$; 83% of all small mammals) captured in all treatments and in each trapping period. Deer mice were significantly more abundant in bison-grazed and cattle-grazed sites than in ungrazed sites in spring before fire ($P < 0.01$ and $P < 0.05$, respectively), but were similar in abundance in grazed and ungrazed sites following fire. Abundance of deer mice was significantly higher in bison-grazed sites than in cattle-grazed and ungrazed sites in autumn ($P < 0.05$ and $P < 0.001$, respectively). Bison and cattle differ in grazing and nongrazing behaviors (e.g., wallowing by bison) that result in differences in vegetation structure. It is likely that differences in deer mouse abundance between bison-grazed and cattle-grazed treatments were due to differences in vegetation structure caused by the two types of grazers.

INTRODUCTION

An estimated 30 million bison (*Bos bison*) lived in the Great Plains before settlement by Europeans (McHugh, 1972). By the late 1800s, introduced cattle (*B. taurus*) had replaced bison as the predominant ungulate grazer (Hartnett *et al.*, 1997). Grazing by bison and cattle induces significant changes in the physical structure and nutritional dynamics of vegetation, both of which strongly influence populations of other animals (Hartnett *et al.*, 1997). Large grazers can directly and indirectly affect populations and communities of small mammals. Direct effects of large grazers on small mammals include trampling of burrows, compacting of soil and competing for food resources, whereas indirect effects include altering of vegetation structure and composition which influences microhabitat selection by small mammals (Hayward *et al.*, 1997).

The effect of cattle grazing on populations and communities of small mammals has been examined in tallgrass prairie (Phillips, 1936; Grant *et al.*, 1982; Clark *et al.*, 1989). Cattle grazing induces changes in abundance and composition of populations and communities of small mammals primarily by altering the physical structure, but not the composition, of the vegetation (French *et al.*, 1976; Grant *et al.*, 1977; Grant and Birney, 1979; Grant *et al.*, 1982; Bowland and Perrin, 1989; Clark *et al.*, 1989; Schulz and Leininger, 1991). We are unaware of studies that have assessed the effects of bison grazing on populations or communities of small mammals. If cattle and bison alter the structure of the vegetation in similar ways, populations of small mammals should respond similarly to the grazing effects of both ungulates.

Cattle and bison differ in dietary, physiological and behavioral attributes and grazing by these ungulates creates differences in vegetative structure. Cattle forage more selectively

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and invest more time searching for patchily distributed high-quality forb and browse forages than bison (Plumb and Dodd, 1993). In contrast, bison selectively graze sites with high grass-to-forb cover and tend to create large homogeneous patches (Plumb and Dodd, 1993; Vinton *et al.*, 1993). As a result of these behavioral and dietary differences, grazed patches should be larger for bison than for cattle when stocking rates are similar. Additionally, bison seldom use the tongue in a horizontal plane as cattle do for forage prehension (Hudson and Frank, 1987). Bison use their lips, which allows them to graze closer to the ground than cattle, resulting in closely cropped patches of vegetation (Hartnett *et al.*, 1997). Bison also spend less time grazing, but more time engaged in nonfeeding activities than cattle. Wallowing, pawing and rolling by bison create saucer-like depressions in soil that are denuded of vegetation (Hartnett *et al.*, 1997; McMillan *et al.*, 2000); cattle do not exhibit these behaviors.

Grazing by large ungulates influences the structure and function of tallgrass prairie (Hobbs, 1996; Hartnett *et al.*, 1997; Knapp *et al.*, 1999) as well as the community composition and abundance of small mammals that occur in tallgrass prairie (Phillips, 1936; Grant *et al.*, 1982; Clark *et al.*, 1989). Most studies of small mammals that examine grazing effects have used single areas exposed to or excluded from grazing (*i.e.*, unreplicated analyses of grazing effects; Hayward *et al.*, 1997). Although indirect effects of cattle grazing on small mammals have received some attention, the effects of bison grazing have not. Implementation of grazing regimes to maintain natural ecological processes as well as current interest in grassland conservation and restoration (Plumb and Dodd, 1993; Hartnett *et al.*, 1997) require the elucidation of any relationships that occur between bison grazing and small mammals or other animals. Use of bison, which currently number 150,000 to 225,000, as the large grazer on private and public grasslands also is increasing on the Great Plains (Hartnett *et al.*, 1997; Steuter and Hiding, 1999).

We examined the indirect effects of grazing by bison and cattle on small mammal populations in annually burned tallgrass prairie. We sampled small mammals in areas of tallgrass prairie grazed by bison, grazed by cattle and left ungrazed. We hypothesized that conditions created by grazing of both bison and cattle would alter abundances of small mammals when compared to ungrazed areas. We also were interested in whether the indirect effects of bison grazing on abundances of small mammals were different from those of cattle grazing. Because bison and cattle differ in grazing behavior, we expected abundances of small mammals to differ between bison-grazed and cattle-grazed prairie.

METHODS

We conducted this study in upland tallgrass prairie on the Konza Prairie Biological Station a 3487 ha research preserve located in the Flint Hills of northeastern Kansas. In 1995 bison and cattle each were assigned randomly to four of eight 4.9 ha enclosures (Fig. 1). Each of the eight enclosures was stocked either with four cattle or with four bison at the beginning of the growing season (about 1 May) during 1995–1998. Animals were selected so that total biomass of grazers when placed in the enclosures in spring was similar for each enclosure (approximately 907 kg/enclosure). To attain similar biomass of grazers, 2-y-old male bison and 1-y-old male cattle were used. This stocking rate would be considered moderate for season-long stocking in tallgrass prairie. Bison and cattle were removed from enclosures at the end of the growing season (early October). Both cattle and bison grew while in enclosures at a rate typical of growth in cattle in tallgrass prairie (about 0.8 kg/individual/d; G. Towne, pers. comm.). An ungrazed control was located adjacent to the grazing enclosures (Fig. 1). All sites were burned in April (1995–1998) before grazers were introduced.

All sampling sites contained vegetation typical of frequently burned tallgrass prairie and

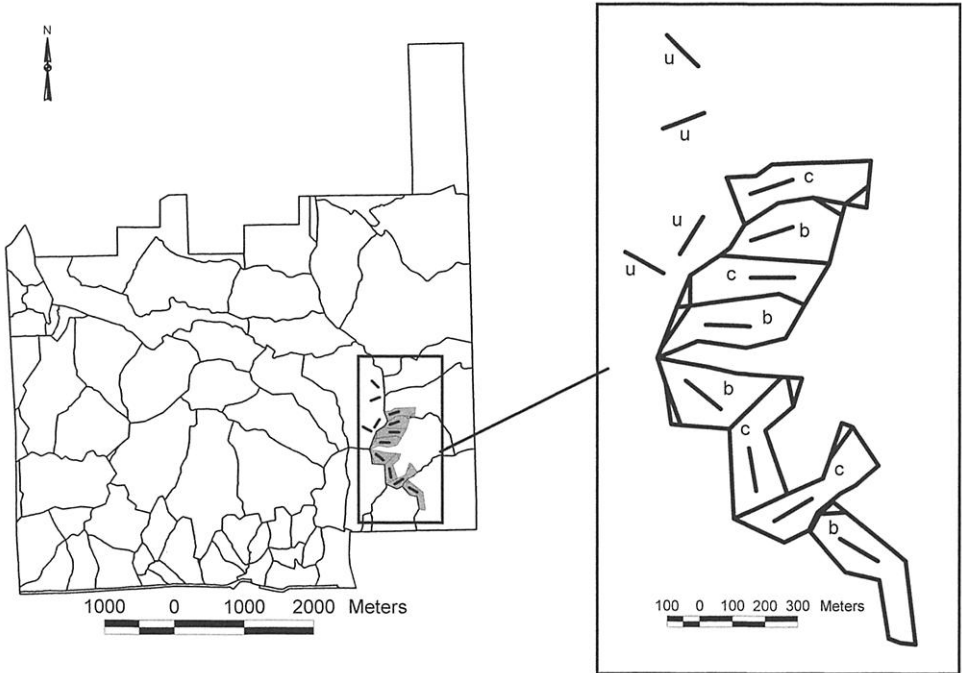


FIG. 1.—Location of trap lines in bison-grazed (b), cattle-grazed (c) and ungrazed (u) treatments on Konza Prairie Biological Station

were dominated by big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*) and indiangrass (*Sorghastrum nutans*). Annual spring fire favors warm-season grasses, such as big bluestem and indiangrass, but has a negative effect on many forbs (Hartnett and Fay, 1998). Litter was absent on all sites because all sites were burned annually. Grazed sites were more heterogeneous in composition and contained a much higher proportion of forbs than did ungrazed sites. This occurs because grazing by large mammalian herbivores, in contrast to fire, favors forbs over most grasses (Vinton *et al.*, 1993).

We did not measure vegetation conditions in our 12 sites, but we did make descriptive observations during the different sampling periods. Amount and vertical structure of vegetation were quite different between our ungrazed and grazed sites both in autumn and in spring before prescribed fires. This difference was due to removal of vegetation by bison and cattle in grazed sites that did not occur in ungrazed sites. In autumn and the subsequent spring before fire, standing biomass was much less in our grazed sites than in ungrazed sites. In grazed sites, vegetation was less than 5 cm in height in many areas and averaged much less than 25 cm overall. During autumn sampling on ungrazed sites in both years, standing vegetation typically was greater than 50 cm in height over most of the area and at least 25 cm throughout each site. In spring before fire, part of the standing dead vegetation had broken over in ungrazed sites and, therefore, was shorter and more compact than in autumn.

After fire, vegetation conditions were similar in ungrazed and grazed sites as fire removed nearly all mulch and standing vegetation from ungrazed and grazed sites. The primary differences between ungrazed and grazed sites were that some small, scattered patches of

heavily grazed prairie in grazed sites were not burned due to an absence of fuel (vegetation only a few cm in height). Following fire, most of these unburned patches would have resembled burned prairie because of the absence of any standing vegetation over a few cm in height. In contrast, a few small and scattered patches with relatively tall vegetation were left unburned in some ungrazed to moderately grazed patches because fire did not always carry across short vegetation in grazed patches to ignite these heavy fuel loads.

Scattered shrubs occur in some prairie sites on Konza Prairie. In our ungrazed sites, shrubs were uncommon and, therefore, we expected them to have little effect on small mammals. However, shrubs were present in some of the eight grazed enclosures and their number and distribution varied widely among enclosures. When we placed our sampling lines, we avoided shrubby areas as much as possible so that shrubs would have little influence on our trapping effort to capture small mammals associated primarily with grassland habitats. However, we had to place sampling lines across a narrow ravine (<10 m wide) with shrubs in two bison enclosures because of lack of space to do otherwise. Further, the presence of shrubs within the overall area of our study made it more likely that white-footed mice (*Peromyscus leucopus*), a woodland species, would occur in our sampling.

We sampled small mammals in spring before (March–April) and after (April–May) sites were burned and in autumn (October–November) from spring 1997 through autumn 1998. These time periods were chosen so that sampling was conducted before grazers were stocked in the enclosures (spring) and after they were removed (autumn) to avoid influencing the behavior of grazers. We trapped all treatments simultaneously with the exception of spring sampling periods after experimental fire. Due to weather and site management, treatments were burned on different dates. We trapped 2–3 wk following experimental fires to control for time since fire. Starting dates for sampling after fire in spring were never >18 d apart.

To sample small mammals, we placed one trap line in each of the 8 grazed enclosures and 4 trap lines in a nearby ungrazed site (Fig. 1). Each trap line consisted of 10 stations with a 15 m interstation interval. At each station we placed 2 large ($7.6 \times 8.9 \times 22.9$ cm) nonfolding Sherman live traps baited with peanut butter and rolled oats. We set traps on four consecutive nights during each sampling period. We marked rodents with ear tags to allow recognition of individuals. We hair-clipped shrews to count the total number of shrews captured during each sampling period.

For deer mice (*Peromyscus maniculatus*), we report relative abundances as number of individuals per 10-station trapline. We analyzed differences in relative abundance among treatments by using analysis of variance (ANOVA) as a split-split plot design with grazing treatment as the whole plot, year as the split plot and period within year as the split-split plot. We analyzed data by using ANOVA as a mixed model with year as a fixed effect and also with year as a random effect. The former model allowed a narrow inference, whereas the latter model allowed for broader inference to be drawn with respect to year.

RESULTS

Eight species of small mammals were captured in one or more of the three grazing treatments (Table 1). Deer mice ($n = 285$) were the most abundant small mammal in all treatments and during each time period. The deer mouse was the only species abundant enough to allow statistical analysis. Abundance of deer mice was influenced by a significant grazing treatment by time period interaction (year as fixed effect: $F = 4.38$, $df = 4, 36$, $P = 0.0055$; year as random effect: $F = 4.15$, $df = 4, 53$, $P = 0.0054$). Deer mice were significantly more abundant on bison-grazed sites than on cattle-grazed or ungrazed sites in autumn ($P < 0.05$ and $P < 0.001$; Fig. 2). Deer mice were significantly more abundant

TABLE 1.—Number of small mammals captured in tallgrass prairie that was grazed by bison, grazed by cattle and ungrazed. Each site was sampled during spring before controlled fire, during spring after controlled fire, and during autumn on the Konza Prairie Biological Station, Kansas, from spring 1997 to autumn 1998

Species	Spring before fire			Spring after fire			Autumn		
	Bison	Cattle	Un-grazed	Bison	Cattle	Un-grazed	Bison	Cattle	Un-grazed
Deer mice	50	33	14	7	14	33	65	40	29
White-footed mice	7	2	1	4	0	1	9	2	2
Prairie voles (<i>Microtus ochrogaster</i>)	0	0	0	1	0	0	4	2	4
Elliot's short-tailed shrews (<i>Blarina hylophaga</i>)	0	0	0	0	1	0	3	1	4
Western harvest mice (<i>Reithrodontomys megalotis</i>)	2	1	2	0	0	0	0	0	1
Thirteen-lined ground squirrels (<i>Spermophilus tridecemlineatus</i>)	0	1	0	0	1	0	0	0	0
Eastern wood rats (<i>Neotoma floridana</i>)	0	0	0	0	0	1	0	0	0
Least shrews (<i>Cryptotis parva</i>)	0	0	0	0	0	0	0	0	1

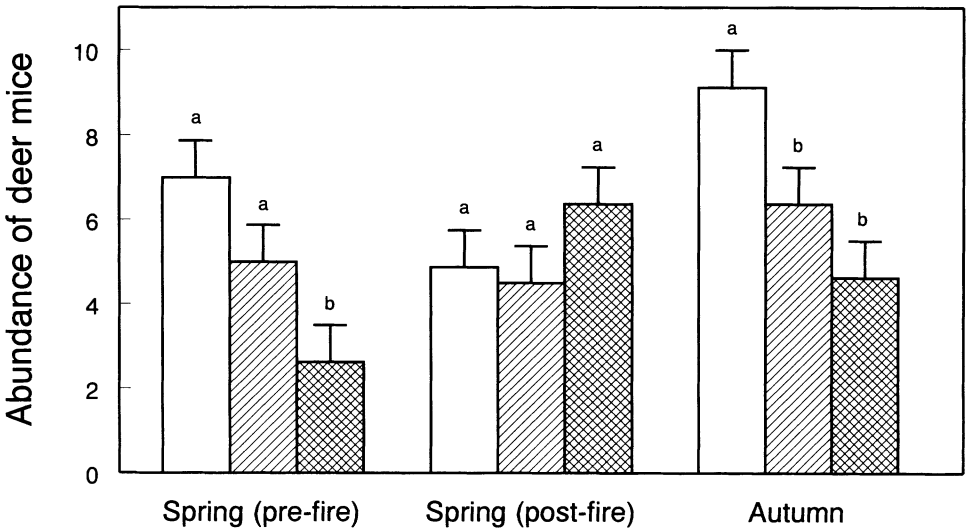


FIG. 2.—Relative abundance (individuals/trapline) of deer mice (+1SE) in tallgrass prairie grazed by bison (open bar), grazed by cattle (hatched bar) and left ungrazed (double hatched bar). Within each time period, means with different letters are significantly different at $\alpha = 0.05$

on grazed sites (both bison-grazed and cattle-grazed) than on ungrazed sites in spring before fire ($P < 0.01$ and $P < 0.05$, for fixed and random effects, respectively). However, abundance of deer mice did not differ among the three treatments following fire in spring ($P > 0.05$ and $P > 0.05$).

Eleven deer mice moved among sampling sites during the period between prefire and postfire sampling in spring. Five deer mice (45% of those that moved) moved from grazed to ungrazed sites, but no deer mice moved from ungrazed sites to grazed sites following fire. Further, two mice (18%) moved between grazed sites and four individuals (36%) between ungrazed sites.

DISCUSSION

Deer mice were the most common rodent on our study sites, whereas other species of rodents and shrews were relatively uncommon. The numerical dominance by deer mice in all study sites was not unexpected because all of the treatments were burned annually. Deer mice respond positively to conditions created by fire in tallgrass prairie and this results in their abundance being greater in burned than in unburned prairie (Kaufman *et al.*, 1983; Kaufman *et al.*, 1988b; Snyder and Best, 1988; Kaufman *et al.*, 1990; McMillan *et al.*, 1995). Additionally, deer mice moved from unburned prairie to nearby burned locations following prescribed fire (Kaufman *et al.*, 1988a; Clark and Kaufman, 1990).

Deer mice were more abundant on grazed sites (both cattle and bison) than on ungrazed sites in autumn and in spring before fire, and this difference was significant for spring before fire for both grazers, but only for the bison-grazed treatment in autumn. Consistent with our overall results of a positive effect of grazing, deer mice were most abundant on moderately overgrazed pastures in Oklahoma (Phillips, 1936). In tallgrass prairie on and near Konza Prairie, deer mice avoided ungrazed unburned sites, but used grazed unburned sites (Clark *et al.*, 1989). Total biomass of deer mice also was greater in grazed unburned than in ungrazed unburned tallgrass prairie in Oklahoma (Grant *et al.*, 1982). The similarity of use of our grazed and ungrazed sites in spring after fire was due to fire overriding the grazing effects seen in autumn and spring before fire and was caused in part by movements from grazed to ungrazed sites.

We detected no difference in abundances of deer mice between grazing treatments in spring after fire; this likely was due to fire creating conditions in ungrazed sites that were favorable for deer mice. Grazed sites are relatively open and are, therefore, suitable for deer mice before spring fire. Grazed sites also have areas that remain unburned because fuel is removed by grazing, whereas ungrazed sites are opened up because litter and standing dead vegetation is burned completely. Deer mice choose areas with a high proportion of exposed soil and little or no litter in tallgrass prairie (Kaufman *et al.*, 1988b). Thus, the similarity in patterns of abundance of deer mice in grazed and ungrazed sites following fire likely is the result of selection by deer mice for areas in which little litter occurs and the soil surface is open. When given a choice in laboratory trials, deer mice removed more seeds from experimental patches that had sparse plant litter covering seeds as compared to patches with dense litter over seeds (Kaufman and Kaufman, 1990). Changes in foraging efficiency, therefore, may underlie the relationships we observed between deer mice and grazers and fire.

Patterns of abundance of deer mice (bison-grazed > cattle-grazed > ungrazed) in our study sites during autumn, and the following spring, suggest that grazing by bison and cattle differ in their effects on deer mice. Greater abundance of deer mice in bison-grazed sites than in cattle-grazed sites likely is due to spatial and structural differences in vegetation that results from differences in grazing patterns and nongrazing behaviors of the two un-

gulates (Plumb and Dodd, 1993; Vinton *et al.*, 1993; Hartnett *et al.*, 1997; McMillan *et al.*, 2000). For example, bison create larger grazing patches with shorter vegetation than do cattle (Vinton *et al.*, 1993; Hartnett *et al.*, 1997). Presence of wallows in bison enclosures also increased patches of bare ground not present in cattle enclosures. Interspecific differences in both grazing and wallowing result in more suitable sites (*e.g.*, more bare soil and little vertical plant structure) for deer mice in areas grazed by bison than by cattle. The preference of bison for grasses over forbs (Plumb and Dodd, 1993; Vinton *et al.*, 1993) also may result in a higher production of forb seeds on bison-grazed areas than on cattle-grazed areas.

The presence of white-footed mice in bison enclosures as compared to cattle enclosures was related to the placement of the trapline in two bison enclosures. These traplines had to be placed across a wooded ravine because of space limitation in the enclosure. If these lines are excluded, the captures of white-footed mice in bison enclosures were 2, 2 and 2, in autumn, spring before fire and spring after fire as compared to captures of these mice of 2, 2 and 0 in cattle enclosures for these three seasons, respectively. Therefore, the pattern observed for white-footed mice in Table 2 should not be interpreted as a bison-effect in future studies.

All of our study sites were burned annually; an impact that leads to the dominance of deer mice. Decreasing the frequency of fire in tallgrass prairie will favor species of small mammals other than deer mice (*e.g.*, western harvest mice and prairie voles; Kaufman *et al.*, 1983; Kaufman *et al.*, 1990). Additional studies are needed to elucidate the influence of grazing by bison and cattle on small mammals under various fire regimes that include reduced frequency of fire because grazing that occurs with periodic fire should continue to have a negative effect on small mammals that require a litter layer by reducing the depth of or essentially eliminating the litter layer.

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