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Control of Ecosystem Processes by Prairie Dogs and Other Grassland Herbivores[1]

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Abstract.--Black-tailed prairie dogs in the mixed-grass prairie at Wind Cave National Park, South Dakota, create habitat patches characterized by altered species composition, lower standing crops of plants, but higher forage quality. Native wildlife species such as bison, pronghorn, and elk preferentially feed on these prairie dog colonies and likely derive nutritional benefits from doing so.

INTRODUCTION

The impact of animals on ecosystem functioning received limited attention in older ecological literature. However, more recently, plant-animal interactions, particularly herbivory, have received widespread attention (Harper 1977, Crawley 1983, Strong et al. 1984). Herbivores in most ecosystems remove a very small amount (<10%) of plant production (Chew 1974), but in grasslands, estimates of 30 to 50% removal of aboveground net primary production are common (Wiegert and Evans 1967, Lacey and Van Poollen 1981, McNaughton 1985). Although amount of plant production removal is an indication of the effect that animals may have, it does not fully explain the complex interactions that herbivores have with their environment. Herbivores can influence rates of primary production, nutrient cycling, structural change, and decomposition which, in turn, may affect behavior and nutritional ecology of other animals. Our research focuses on prairie dogs as native herbivores in grassland ecosystems, and also addresses some fundamental questions regarding herbivory.

Prairie dogs are often viewed as pests in western rangelands. As a result, much prairie dog research has focused on their potential as competitors with cattle (Koford 1958, Hansen and Gold 1977, O'Meilia et al. 1982, Collins et al. 1984, Uresk 1985). Such studies have described prairie dog diets and have indicated how their activities change composition of plant communities. Although there have been comprehensive studies on prairie dog behavior and ecology (Clark 1986), their role as herbivores in natural ecosystems has received little attention.

Our research has been conducted on black-tailed prairie dogs (Cynomys ludovicianus) in the mixed-grass prairie at Wind Cave National Park, South Dakota. We have studied structure and function of plant populations and communities on and off prairie dog colonies, and the influence of prairie dog activity on distribution, behavior, and community composition of such diverse animals as bison and nematodes. We have also measured prairie dog-induced changes in the physical environment. This review summarizes our work in a population, community, and ecosystem context.

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PRAIRIE DOG-PLANT INTERACTIONS

Plant Population Parameters

Morphological and physiological changes often occur in intensively grazed plants. For example, plants grazed by domestic herbivores are often shorter and more prostrate than ungrazed individuals (Hickey 1961). Grazing-induced changes in morphology sometimes quickly disappear following release from grazing (Quinn and Miller 1967), or they may persist, indicating genetic differentiation into distinct ecotypes.

We have investigated differences in populations of western wheatgrass (Agropyron smithii) from an intensively grazed prairie dog colony and from within a large, permanent grazing exclosure (Detling and Painter 1983, Detling et al. 1986). Sod blocks containing western wheatgrass were collected on and off prairie dog colonies and were transplanted to a common greenhouse environment. After nine months, significant morphological differences persisted in plants from the two populations. Plants from the prairie dog colonies had more tillers per plant, fewer leaves per tiller, smaller leaves, higher blade/-sheath ratios and were more prostrate than plants from ungrazed populations. The polymorphism and persistence of these characteristics suggested that these populations were genetically distinct. Grazing has apparently modified the selection pressures and competitive balance that existed in the ungrazed populations, thereby causing a shift in dominance to an ecotype that may be more grazing resistant or, because of its shorter stature, be less intensively grazed.

Several responses of the two ecotypes to simulated grazing were also compared (Detling and Painter 1983). Photosynthetic rates were similar and partial defoliation equally enhanced net photosynthesis in the remaining leaves in the two populations. However, perhaps because of greater photosynthetic rates of leaf blades than sheaths, and greater blade/sheath ratios in the prairie dog colony population, net primary production (relative to undefoliated plants) was essentially unaffected by defoliation in plants from the prairie dog colony, but decreased by 20% following defoliation of exclosure plants. Therefore, although they are less productive, these "grazing morphs" may be more resistant to subsequent grazing than those plants seldom grazed.

Another response to grazing is increased accumulation of silica in leaves of grasses. It has been suggested (McNaughton et al. 1985), based on studies in the African savanna, that this may be a defense against herbivores, because silica decreases digestibility and palatability and promotes tooth wear (Van Soest 1982). We (Brizuela et al. 1986) found silicon concentrations were consistently higher in tillers of A. smithii and Schizachyrium scoparium from heavily grazed prairie dog colonies than from lightly grazed areas. However, repeated defoliation did not increase silicon concentration. Thus higher whole tiller concentrations from colony plants may be explained by higher silicon concentrations in leaf blades compared to sheaths (Cid 1985) and the higher blade/sheath ratios in on- versus off-colony plants (Detling and Painter 1983).

In general, as plants mature their nutritive value declines (Van Soest 1982). However, grazing removes aging leaves and may stimulate growth of new tissue, which usually has a higher nitrogen concentration and greater digestibility than that of an ungrazed plant (McNaughton 1984). Part of our research at Wind Cave involved examination of the effect of prairie dog colonization and grazing on plant nutrient dynamics (Coppock et al. 1983a). A prairie dog colony was divided into three ages, or states of colonization: (a) an older area, colonized more than 25 yr, (b) a young area, occupied 3-8 yr, and (c) a recently (<2 yr) colonized edge. The (d) uncolonized prairie was used as a baseline, control site. During the growing season, live material of six grass species (three cool season species and three warm season species), a composite of forb species, and a dwarf-shrub, Artemesia frigida, were collected monthly in each site and analyzed for nitrogen concentration and digestibility.

In general, shoot nitrogen concentrations were lowest in plants from the uncolonized grassland, and increased with the length of time an area had been occupied. Similar results for western wheatgrass were also observed (Krueger 1986). On an average, cool season grasses had higher nitrogen concentrations throughout the season than did warm season species for each state of colonization. Digestibility of grasses followed a pattern similar to nitrogen concentration: digestibility declined as the season progressed; grasses from the uncolonized area had lower digestibilities than those from the edge or young colony; cool season grasses were more digestible than warm season ones. These

results indicate that prairie dogs have a directional effect on plant nutrition and positively influence forage quality by their grazing.

Plant Community Parameters

When prairie dogs invade an area, they crop the vegetation to a height of a few centimeters and maintain it in that state. This can create microclimatic changes within the canopy and soil. Archer and Detling (1986) observed significant increases in soil temperature and as great or greater soil moisture content on prairie dog colonies as off. These abiotic changes can directly influence such things as rate of microbial activity, nutrient cycling, plant water balance, and plant production. These effects can further change the microhabitat, and thus the plant community. Cause and effect rapidly become obscured, but it is clear that grazing, directly or indirectly, modifies either the competitive balance of plants within the colony or modifies the environment such that some plants are better adapted than others.

Following occupation by prairie dogs, overall canopy height decreases and grasses are replaced by forbs. In one of our research colonies, the mean canopy height decreased 62% in the first two years of colonization, and changed little thereafter (Archer et al. 1987). Change in canopy structure can be achieved in several ways: (1) plants that are clipped repeatedly never reach full growth; (2) genetically determined taller morphs are replaced by grazing tolerant, shorter, prostrate ecotypes of the same species (Detling and Painter 1983); and (3) the plant community changes such that many of the taller species are replaced by shorter species (Koford 1958, Coppock et al. 1983a, Archer et al. 1987).

These same factors may contribute to concomitant decreases in standing crop following colonization. In one site, the greatest peak live standing crop (190 g/m^2) was found in uncolonized prairie, where grasses comprised 85% of the biomass (Coppock et al. 1983a). Similar biomass levels were found in the oldest portion of the colony; however, less than 3% of that was grasses. The grass-dominated young area of the colony only had about one-third the live standing crop as the uncolonized area. However, there was a greater proportion of live material relative to standing dead in the colonized areas compared to the uncolonized prairie. Because prairie dogs are continually clipping the vegetation, very little of it matures and dies; thus,

standing dead material does not accumulate in large quantities. As a result, the amount of material that eventually falls to the ground as litter is reduced, and bare ground increases (Coppock et al. 1983a). For example, Archer (et al. 1987) found that rapid changes occurred in the first two years following colonization, but by the third year, bare ground had stabilized at 35% (compared to ⁻10% initially) and litter cover had decreased to less than 10% (⁻20% initially).

Change in plant species composition after prairie dog occupation has been widely noted (Osborn and Allen 1949, King 1955, Koford 1958, Bonham and Lerwick 1976), but its rate of change has not been documented in detail. In separate colonies, Coppock et al. (1983a) and Archer et al. (1987) studied the rate of plant species change, replacement, and diversity. The rate of change, controlled in part by grazing pressure of prairie dogs and other herbivores, initial community composition, soil type, and weather, varied between colonies, but the trends were similar. In the most recently colonized areas (<2 yr), there was little change in plant species composition relative to uncolonized prairie. In areas of the colonies that had been impacted more than 3 yr, shifts in plant dominance and composition had begun (Coppock et al. 1983a) or had rapidly progressed (Archer et al. 1987). The dominant species in the uncolonized prairie, the midgrasses, were replaced by shortgrasses and annual forbs. Species diversity was highest in parts of the colonies occupied an intermediate length of time. Diversity in the oldest portions of each colony declined to levels similar to the uncolonized prairie due to the final dominance by a few species of forbs or dwarf shrubs.

PRAIRIE DOGS AND INTERACTIONS WITH OTHER ANIMALS

Thus far we have considered prairie dog interactions with the aboveground vegetation; however, prairie dogs are also creating patches within the ecosystem that modify densities, foraging patterns, and nutritional dynamics of other animals.

Prairie Dogs and Ungulates

Free-ranging populations of native grassland ungulates within Wind Cave National Park include about 350 bison, 60 pronghorn, and 400 elk. Early observations suggested that bison and pronghorn

were frequently associated with prairie dog colonies (King 1955, Koford 1958). More recently, Wydeven and Dahlgren (1985) reported summer use of prairie dogs colonies by bison, elk, and pronghorn. Our research has verified that there is selection for prairie dog colonies by both bison and pronghorn, and that this may incur some nutritional advantage to animals that feed on colonies (Coppock et al. 1983b, Krueger 1986, Vanderhye 1985).

In conjunction with studies on plant response to colonization, Coppock et al. (1983a,b) also investigated the parkwide selection of bison for prairie dog colonies, the pattern of use by bison within a colony, and the relationship between that and the dynamics of the plant communities on and off colonies. The park consists of approximately 6% prairie dog colonies, 74% uncolonized grassland, and 20% coniferous forest. If animals randomly use whatever habitat they encounter, the frequency of observations of those animals on a habitat will approximate the proportion of that habitat in the park. Our results showed that bison predominately use the grasslands and prairie dog colonies and, in summer, the use of colonies was much higher than would be expected by chance alone.

On an extensively studied colony, bison preferred specific sites for various activities (Coppock et al. 1983b). Over the growing season, bison used the (a) younger, grass-dominated portion of the colony for both grazing and resting (3.0 and 2.7 times expected, respectively), the (b) edge primarily for grazing (2.5 times expected), and the (c) forb/dwarf shrub-dominated older areas for resting (2.5 times expected). The amount of time spent resting on the edge of the colony and feeding in the oldest part of the colony was essentially random. They used the adjacent uncolonized prairie only 20% of the expected time for either activity, indicating that this area was avoided in preference for the colony. Similar utilization patterns have been observed on other colonies (Krueger 1986).

Although bison are relatively nonselective feeders (Schwartz and Ellis 1981), at least on the scale of a bite, they can choose the habitat in which they prefer to feed. When possible, an animal would be expected to feed in the most favorable locations, such as where nutrient levels and availability of the forage are high. As discussed earlier, prairie dogs modify grasslands such that plant material from colonies has a greater live to dead ratio (albeit lower standing crop), a higher crude protein (nitrogen) level, and a greater digestibility than from the uncolonized prairie, and this all implies greater nutrition per bite. The moderately impacted grass-dominated areas of the colonies are especially representative of these features. Thus, it seems reasonable to assume that prairie dogs have modified the environment making it a favorable feeding and resting habitat for other animals.

Vanderhye (1985) investigated nutritional benefits accrued to bison by selectively feeding on colonies by using Swift's (1983) model to simulate weight gains based on dietary information. Diet quality data were varied according to measured on and off colony values. Various patterns of colony usage, including random, typical, none, and 100%, were simulated. Averaged across all available studies, typical bison use of colonies during the growing season was estimated at 39% and random use was 12%. The model output suggested that if mature cows randomly use the colonies for feeding, they will gain an additional 2 kg (7% of seasonal weight gain) of body weight compared to not feeding on colonies at all. Typical usage of colonies confers an additional 5 kg (18%) weight gain. For yearling bison, randomly feeding on colonies could add 4 kg (14%) of body weight and typical use could add 13 kg (46%) beyond the gain expected when they avoid grazing on colonies altogether. The nutritional advantages are only realized from June through August when differences in forage quality between on- and off- colonies are maximal.

Elk (Wydeven and Dahlgren 1985) and pronghorn (Krueger 1986) also preferentially use prairie dog colonies. Krueger (1986) found that although both bison and pronghorn preferentially used colonies in summer, their location of use within the colonies differed. While bison preferentially used the grass-dominated areas, 57-97% of the pronghorn feeding on colonies were on the forb-shrub dominated centers. Within a preferred feeding area of the colony, there was a high dietary overlap between bison and prairie dogs and between pronghorn and prairie dogs. However, rather than competing for forage, the relationship between bison and prairie dogs seemed to be mutually positive, and between pronghorn and prairie dogs it was mostly neutral (Krueger 1986).

Prairie Dogs and the Belowground Ecosystem

Much of the plant system's dynamics occurs belowground and prairie dogs may influence the belowground responses of both plants and animals. It has been estimated that most of the energy flow in grassland systems occurs belowground (Coleman et al. 1976) and soil invertebrates, largely nematodes, may consume as much or more plant biomass as cattle on the mixed grass prairie (Smolik 1974). Because the root system provides a link for transport of materials from the soil to the shoot system, factors which affect the root system generally influence the aboveground plant dynamics as well.

Grazing typically reduces root biomass (Schuster 1964) because of reduced production and reallocation of material from roots to the regrowing aboveground shoots. There is marked decline in total root biomass from off prairie dog colonies to older parts of the colonies. In one study (Ingham and Detling 1984), soil cores were taken monthly from beneath A. smithii and S. scoparium on a heavily impacted section of the colony and in uncolonized prairie. Roots and nematodes were extracted from the cores. The seasonal mean root biomass from the colony was 70-80% of that off the colony, and total nematode densities were 45% higher on the colony than off. Nematode densities may reflect changes in soil microclimate or soil or plant chemistry caused by grazing. Annual net root production (ANRP) on the colony was about 60% of that off the colony; however, the percent of ANRP that nematodes consumed was estimated as 2.5x higher on the colony as off. Therefore, combining lower root production, higher nematode densities, and total consumption of roots on the colonies indicates a substantial impact and amount of energy and material flow occurring belowground.

Some Management Implications

As part of natural ecosystems, prairie dogs enhance certain features of the vegetation and create favorable habitat patches for other animals. Thus, in situations such as those described above for Wind Cave National Park, the presence of a limited number of prairie dog colonies scattered throughout the native grassland may improve the health and increase the diversity of other wildlife species. However, extensive utilization of prairie dog colonies by large herds of ungulates such as bison may accelerate changes in the vegetation via increased consumption rates and soil disruption and compaction by trampling and wallowing. This can reduce suitability of these sites for both bison and prairie dogs. Other research at Wind Cave National Park has shown that extensive bison utilization of such areas can be reduced by creating additional suitable bison habitat with controlled burns (Coppock and Detling 1986). It is necessary, however, to conduct the burns sufficiently far from prairie dog colonies that the burned areas will not provide additional habitat for rapid expansion of prairie dog colonies.

Caution should be exercised when extrapolating from the results of our studies in natural areas managed for wildlife preservation to rangelands managed for livestock production. While prairie dogs likely improve forage quality for cattle on rangelands just as they do for bison at Wind Cave National Park, it must be remembered that the areas with the enhanced forage quality have a lower total amount of forage available for consumption by livestock. Futhermore, it is common for significant portions of prairie dog colonies to be dominated by forbs, dwarf shrubs, or grass species which are unpalatable to livestock. Thus the increased forage quality in areas of colonies still dominated by grasses comes at the expense of a sizeable reduction in total available grass forage. While this may not be a problem when managing for wildlife populations at densities well below the carrying capacity of the land, it is a potentially larger problem in ranching operations in which livestock are maintained at levels closer to the carrying capacity.

Another consideration in managing for prairie dogs is one of scale. Much of our rangeland is divided into paddocks or pastures, and the amount of land available to cattle or other livestock is often not as extensive as that available to bison and other ungulates in parks such as Wind Cave. Therefore, it is conceivable that large proportions of individual paddocks may be covered by prairie dog colonies, thus reducing available forage far more than was observed in our studies in a natural area (Coppock et al. 1983a,b; Coppock and Detling 1986; Krueger 1986). Management policies for both domestic animals and prairie dogs should consider a number of factors including how much area is confined or available, animal densities, range condition and trend, opportunities for habitat selection, season of usage, and potential patterns of interactions.

FUTURE RESEARCH

Our research suggests that prairie dogs create unique patches of biological activity within grassland ecosystems. This patch structure is dramatically different from the surrounding grasslands, the behavior of other animals is modified by the presence of the patches, and changes in certain patch characteristics proceed in a fairly regular pattern through time.

Our current research is directed at further understanding some of the key ecosystem processes that determine the rates of structural and functional changes. We know that grazing by prairie dogs and associated herbivores decreases plant standing crop; however, does this necessarily imply decreases in net primary production? New green material with high nutritive value is being continually produced during the growing season on colonies, but are the rates of nitrogen (or other essential minerals) turnover and cycling different from those in uncolonized areas? Does extensive and preferential use colonies by several species of ungulates contribute to nutrient imports onto colonies via feces and urine, or is there a net offtake of nutrients? What happens when grazers are removed? How do other mobile herbivores, such as grasshoppers, respond to a patch structure that varies in time and space? At what point does a colony or part of a colony senesce, and do processes change or reverse? Answers to these questions are important for understanding the interactions of prairie dogs and their environment, and the role of herbivory as an influential moderator of ecosystem dynamics.

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