The Prairie Dog Story: Do We Have It Right?

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As public and scientific interest in black-tailed prairie dogs has grown, views about their ecological role have become polarized. We evaluated three claims frequently made concerning the status of black-tailed prairie dogs and their interactions with other species: (1) that black-tailed prairie dogs historically occupied 40 million to 100 million hectares (ha) and now occupy only 1 to 2 percent of their former range, (2) that large ungulates preferentially forage on prairie dog colonies, and (3) that prairie dogs do not reduce carrying capacity for large herbivores. The conclusion that prairie dogs historically occupied up to 100 million ha is not supported by the literature, and the more conservative figure of 40 million ha is based on estimates from the early 20th century, when prairie dog populations were artificially high as a result of human activities. Prairie dog activity is not unique in facilitating grazing by large herbivores; and selection of prairie dog colonies for foraging is limited to specific conditions, including colony age, proximity, and season of the year. Finally, prairie dogs reduce carrying capacity for large herbivores by consuming forage, clipping plants to increase visibility, building mounds, and changing plant cover and species composition.

Keywords: carrying capacity, Cynomys, *distribution, herbivory, population estimates*

Prairie dogs (*Cynomys* spp.) and their management have been topics of great concern for more than a century. Initial interest focused primarily on controlling prairie dog populations to reduce rangeland degradation and competition with livestock. More recently, there has been a movement to protect black-tailed prairie dogs (*Cynomys ludovicianus*). In February 2000, the US Fish and Wildlife Service determined that black-tailed prairie dogs warranted listing under the Endangered Species Act, but action was precluded because other species had higher priority. Concurrently, black-tailed prairie dogs were classified and managed as pests by numerous state and federal agencies throughout their range, with many state wildlife departments permitting unlimited harvests.

Black-tailed prairie dogs are the most studied, widespread, and numerous species of the genus *Cynomys* (Hall 1981, Hoogland 1995). Yet opinions about their role in grassland ecosystems are polarized, with some researchers (e.g., Kotliar et al. 1999) concluding that prairie dog influences on other vertebrates have been greatly overstated. We believe that some of the discrepancies have been caused by varied interpretations of data and, in some instances, by selective disregard of literature on the basis of personal values. Although we are strong advocates of prairie dog conservation, we believe that management should be based on an objective evaluation of all applicable scientific findings. To do otherwise could only weaken public trust, further politicize the issue, and potentially work to the detriment of natural resources we hope to protect. In light of this, our objectives are to evaluate three claims commonly made in the scientific literature and popular press: (1) that prairie dogs occupied 40 million to 100 million hectares (ha) of shortgrass and mixed-grass prairie before the settlement of the American West, and the occupied area has since declined 98 to 99 percent; (2) that prairie dogs cause unique improvements in forage quality that attract large ungulates to colonies for grazing; and (3) that prairie dogs do not reduce carrying capacity for large herbivores.

Current versus historical status of black-tailed prairie dogs

Some researchers have considered the accuracy of past prairie dog estimates unimportant (Wuerthner 1997), but the use of such estimates to justify protection of prairie dogs requires that they be as accurate as possible. Many of the figures associated with prairie dog population and range are questionable, but we believe that careful review of cited sources and the application of logic can clarify the issue. Repeated claims have been made that prairie dogs have been reduced 98 to 99 percent during the 20th century, based on their supposed historic occupation of 40 million to 100 million ha of shortgrass and mixed-grass prairie. We do not doubt that the number of prairie dogs and the extent of their colonies were reduced during the 20th century, but the scientific literature and logic support only the lower historic estimates; furthermore, both literature and logic indicate those estimates were probably biased upward because of their timing.

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Nelson (1919) and Anderson and colleagues (1986) reported an estimate of about 40 million ha of prairie dogs at the beginning of the 20th century. However, we found no support for estimates of 81 million ha (NWF 1998) or 100 million ha (Miller et al. 1994). In fact, the National Wildlife Federation provided no original sources for their 81-million-ha estimate in the petition to list black-tailed prairie dogs (NWF 1998), and we could find none to support their claim. Similarly, we found no support for the 100-million-ha estimate of Miller and colleagues (1994), although they cited Marsh (1984) and Anderson and colleagues (1986) as their sources. Marsh (1984) provided no original estimate of prairie dog colony area, but cited Nelson (1919) as the authority for an estimate of 40.5 million ha (including all prairie dog species). Anderson and colleagues (1986) provided an original estimate of prairie dog colonies (across species) at 41.9 million ha (about 104 million acres). Miller and colleagues (1994) may have misinterpreted the unit of area for the estimate reported by Anderson and colleagues (1986) as 104 million ha rather than 104 million acres.

This error has since been reproduced by others. For example, Mulhern and Knowles (1995) cited Miller and colleagues (1994), Anderson and colleagues (1986), and Marsh (1984) as sources for overall estimates that prairie dogs occupied 40 million to 100 million ha in the early 20th century. Mulhern and Knowles (1995) then provided state-by-state estimates from their own study of cumulative area occupied by prairie dogs for the same period. They estimated that 7 of the 11 states that have, or once had, black-tailed prairie dogs had a total of 32,872,460 ha of colonies (including Gunnison's prairie dogs [*Cynomys gunnisoni*] in New Mexico) before 1920. Despite their own data, Mulhern and Knowles (1995) listed the US colony area for the early 20th century at 40 million to 100 million ha. The remaining four states, with no pre-1920 data (Arizona, Nebraska, Oklahoma, and Wyoming), would have had to contribute an unlikely 67 million ha to bring the total to 100 million ha. Given the distribution of prairie dogs (Hall 1981) and the assumption that prairie dogs were equally represented on a per-unit-area basis in the census and noncensus states, the total area would sum to 41.6 million ha, with the noncensus states comprising 21 percent of the area. The fact that these estimates include multiple species should be noted as well. The estimated area of occupation by black-tailed prairie dogs may have been closer to 31 million ha, since the range of black-tails comprises about 75 percent of the *Cynomys* species' range.

Whereas most estimates are based on area occupied, Seton (1929) estimated the number of prairie dogs to be 5 billion in the late 1800s, and on a regional level, Merriam (1902) reported a 6.5-million-ha colony in West Texas estimated to support more than 400 million prairie dogs. Seton's estimate would require about 21 prairie dogs per hectare for the entire area of all five species' ranges, and Merriam's would require 62 prairie dogs per hectare over the entire 6.5 million ha of the Texas colony. Although it is possible to have 21 or even 62 prairie dogs per hectare, it is extremely doubtful they could attain such averages across their range or even across large areas within their range because of limited habitat availability.

Not only are upper-range estimates of historical prairie dog populations excessive, the lower-range estimates were made in the late 1800s and early 1900s, when abundance and distribution were elevated by anthropogenic habitat changes. Reports from the early 1900s detail sharp increases in prairie dog numbers and colony sizes at the turn of the century. Merriam (1902) reported anecdotal evidence of rapid colony expansions throughout the West from 1886 to 1901. Smith (1899) stated that prairie dogs and jackrabbits had increased rapidly from 1874 to 1899 and were continuing to do so. These historic accounts clearly indicate the area of prairie dog colonies in the early 1900s was greater than previously experienced. In fact, Miller and colleagues (1994) cited Marsh (1984) for a turn-of-the-century estimate of 40.5 million ha but disregarded the preceding paragraph, in which Marsh stated that prairie dogs had increased in number and extended their range eastward into tallgrass and mixed-grass prairie as a result of landscape modification by European settlers.

The causes of prairie dog colony expansions in the late 1800s were listed as predator control, drought, and overgrazing (Smith 1899, Koford 1958). Predator control probably affected prairie dog expansions, but the extent of this influence is unclear. The most important factors were probably drought and overgrazing. Such conditions are known to facilitate colony expansion and increase prairie dog natality and survival (Knowles 1986a). In contrast, tall vegetation reduces colony expansion (Osborn and Allan 1949).

Large-scale overgrazing of the Great Plains began in about 1880 (Smith 1899, Stewart 1936) and continued through the 1930s. Smith (1899) described the grasslands as a "pastoral paradise" with luxuriant growth before the 1880s, but there was widespread deterioration by the end of the decade, with the taller grasses replaced by less desirable grasses and annuals. Cattle numbers in the 17 western states skyrocketed from about 8 million in 1870 to just under 22 million in 1890 (Stewart 1936). Montana, New Mexico, Texas, and Wyoming alone had more than 22 million sheep, enough to start local wars between cattlemen and sheep herders. Severe droughts struck various parts of the region during the same period (Stewart 1936), further reducing tallgrass and midgrass cover in favor of shortgrasses and annuals. Prairie dogs occupied portions of tallgrass and eastern mixed-grass prairie where they had not occurred before settlement and heavy livestock grazing (Merriam 1902, Schaffner 1926, Virchow and Hygnstrom 2002). A contrasting view is presented by Knowles and colleagues (2002). Much of the prairie dog range depicted by Hall (1981) included tallgrass prairie from Nebraska through Texas. The 40-million-ha estimate of total prairie dog colony area is approximately 34 percent of the total shortgrass and mixed-grass prairie region. Had more than one-third of the land been occupied by prairie dog colonies, we doubt livestock producers would have rushed into the Great Plains as they did in the 1800s.

More recently, black-tailed prairie dogs were estimated to occupy 607,000 ha throughout their range in 1960 (Summers and Linder 1978), 566,000 ha in 1971 (Cain et al. 1972), and 550,000 ha, excluding Colorado, in the 1980s (Mulhern and Knowles 1995). If Colorado trends were similar to those Mulhern and Knowles (1995) reported for other states, the adjusted 1980s estimate, including Colorado, would be 597,000 ha. These figures indicate about 30 years of stability on a range-wide scale, yet some authors suggest prairie dogs are experiencing continued declines. Miller and colleagues (1994) and Mulhern and Knowles (1995) reported that two prairie dog complexes with a combined area of more than 295,000 ha were eliminated in the 1980s and that the Animal and Plant Health Inspection Service eliminated 80,000 ha per year. If so, black-tailed prairie dogs would have been extinct 3 to 4 years after the complexes were poisoned. This suggests the area occupied was underestimated, the success of control efforts was overestimated, or both errors occurred. In some discussions of prairie dog control efforts, we believe the terms *eradication* and *elimination* have been incorrectly used as substitutes for *control.* Prairie dogs have returned to their precontrol populations in only 3 to 5 years after control efforts had reduced their population by 95 percent (Knowles 1986b).

Estimates that prairie dogs occupied 40 million ha during the early 1900s may be accurate, but that is hardly a good reason to use those estimates for comparisons with current populations. Consider the potential area of black-tailed prairie dog occupation. The combined range of all five prairie dog species is roughly 240 million ha and the range of black-tailed prairie dogs is about 137 million ha, as depicted by Hall (1981). Black-tailed prairie dogs are typically confined to shortgrass and mixed-grass prairies, which are estimated to cover 118 million ha, not excluding farmland, human developments and interspersed woodlands. The potential area of colonization within this area would be further limited by black-tailed prairie dogs' preference for elevations lower than 1830 meters (m) (Hoogland 1995) and deep, well-drained, productive soils with minimal flooding potential and 2 to 5 percent slopes (Koford 1958). Additionally, prairie dogs tend to use roads and well-established trails for dispersal in mixed-grass prairie and colonize areas that are intensively grazed or otherwise disturbed (Koford 1958, Knowles 1986a). Therefore, we conclude that the estimate of 40 million ha most likely represents the maximum potential area occupied by prairie dogs under the ideal conditions (i.e., severe drought and large-scale overgrazing) of the late 1800s and early 1900s.

Prairie dog colonies and grazing by large herbivores

Coppock and colleagues (1983a, 1983b), Wydeven and Dahlgren (1985), Knowles (1986a), and Krueger (1986) have been cited as reporting preferential foraging of prairie dog colonies by cattle, bison (*Bison bison*), pronghorn (*Antilocapra americana*), and elk (*Cervus elaphus*). This information has been offered as conclusive evidence that the relationship between prairie dogs and large herbivores is symbiotic rather than competitive (Miller et al. 1994, Wuerthner 1997). Data from the foraging studies mentioned above certainly show that some large herbivores are at times attracted to colonies. However, we suggest that prairie dogs are not unique in their effects on foraging site selection by large herbivores and that the level of foraging facilitation by prairie dogs has been extrapolated far beyond the conditions of the studies and to species not shown to select colonies.

Examination of these studies reveals support for preferential foraging only by bison and pronghorns. Coppock and colleagues (1983b) found that if bison herds were in the vicinity of a colony, they selected portions of colonies occupied 8 years or less over uncolonized sites, but herd movement and habitat use were not controlled by the presence or absence of prairie dogs. During nine periods between May and October, bison selected for prairie dog colonies four times and against them three times. Detling (1998) stated that bison also avoided colonies early and late in the growing season, when biomass was low and most plants were senescent. Others reported selection of colonies by bison during summer (Wydeven and Dahlgren 1985, Krueger 1986). Krueger (1986) considered the association between prairie dogs and bison to be facultative mutualism, since indices of foraging efficiency were greater for both species in areas of common use.

Wydeven and Dahlgren (1985) conducted the only study evaluating elk use of prairie dog colonies. Their data show the percentage of elk observations on colonies was less than or similar to the percentage of open prairie sites colonized (i.e., neutral or negative selection). Furthermore, elk used colonies primarily for rutting activities, not foraging. Mule deer (*Odocoileus hemionus*) were observed on prairie dog colonies less often than expected throughout the year (Wydeven and Dahlgren 1985). Pronghorn, by contrast, selected prairie dog colonies during all seasons except winter (Wydeven and Dahlgren 1985) and selected colonies most during summer (Krueger 1986). Pronghorn favored the forb-dominated areas of colonies, but the presence of prairie dogs was considered to have a slightly negative effect on pronghorn foraging behavior (Krueger 1986).

Contrary to reports of others citing him (Miller et al. 1994, Wuerthner 1997), Knowles (1986a) actually reported prairie dog preference for sites disturbed by humans and livestock, rather than a preference by cattle for prairie dog colonies. Most colonies were in areas heavily grazed by cattle, with about 97 percent near roads and trails and 62 percent near water developments. Ease of travel and frequent proximity to disturbed sites could explain the apparent affinity for roads and trails (Knowles 1986a). The use of trails may be less important in shortgrass plains. Cattle were observed more often near prairie dog colonies, but Knowles (1986a) concluded that this was because of their proximity to water and that colonization occurred after heavy use by cattle. Prairie dog selection of disturbed sites may not represent a preference as much as a requirement. Deferment of cattle grazing has reduced colony area and rate of colony expansion (Osborn and Allan 1949). In summary, only two of the five large herbivores studied have shown a foraging preference for colonies, and these were on specific portions of colonies under specific conditions.

Coppock and colleagues (1983b) hypothesized that the mechanism attracting bison to prairie dog colonies was improved forage quality, which is related to changes in herbage dynamics, species composition, and nutrient cycling (Coppock et al. 1983a). Prairie dog colonies contain much less lower-quality, mature standing herbage, and the low-seral plant communities on colonies are characterized by forbs, half-shrubs, and annual grasses, which are typically high in crude protein and digestibility (Coppock et al. 1983a). However, these effects are not unique to the activities of prairie dogs. Cid and colleagues (1991) found that relative to ungrazed herbage, nitrogen content was 0.11 percent and 0.14 percent greater, respectively, in herbage grazed by prairie dogs and bison. Willms and colleagues (1988) showed sites selectively grazed by cattle had reduced litter and standing dead plant material, altered species composition (toward seral, or nonclimax, species), and increased soil nitrates, ammonium, and available phosphorus. Long-term, intensive use by any grazer will cause comparable changes in plant communities.

Continuous, selective grazing of patches is well documented for grazers and intermediate feeders and occurs, in part, because the animals are avoiding excessive litter and standing dead material, which reduce forage quality. Patch grazing is also known to increase as forage supply increases relative to demand. A less apparent but strongly influential condition in the studies conducted in Wind Cave National Park (Coppock et al. 1983a, 1983b, Wydeven and Dahlgren 1985, Krueger 1986) is that there was no livestock grazing, and grazing use by wild ungulates was light. Whicker and Detling (1988) reported that large herbivores in the park utilized only 5 to 30 percent of the aboveground net primary production. Grazing pressure on uncolonized sites was so light that grazed and ungrazed plots had the same amount of live, dead, and total herbage and supported similar cover values for all plant species (Detling 1998). Uncolonized sites had 1345 kilograms (kg) per hectare of litter and 2837 kg per hectare standing herbage; 33 percent of the standing forage was dead. Under these conditions, one would expect animals to strongly select previously grazed sites (including prairie dog colonies), even though Wydeven and Dahlgren (1985) reported preferred forages were more abundant in uncolonized areas. Selective grazing of previously grazed patches is well documented in grazing literature. In the absence of prairie dogs, the dominant herbivores would selectively use grazed patches they had created themselves. The primary potential difference would be the size and distribution of patches, which are controlled by stocking rate and site characteristics that affect animal grazing distribution.

Black-tailed prairie dogs and the carrying capacity of large herbivores

It has been suggested that prairie dogs do not reduce the carrying capacity of large herbivores because competition is minimal (Miller et al. 1994), or because improved forage quality nullifies negative effects of reduced herbage (Wuerthner 1997). However, the sources cited by Miller and colleagues (1994) and Wuerthner (1997) do not support their conclusions, and we believe the conditions for reduction of carrying capacity by prairie dogs can be demonstrated.

Forage reduction by prairie dogs was estimated to be 18 percent at a density of 7.3 prairie dogs per hectare (Hansen and Gold 1977) and 33 to 37 percent at densities of 21 to 30 prairie dogs per hectare (O'Meilia et al. 1982). At similar densities, 29 percent of total herbage and 63 percent of grass standing crop were removed by prairie dogs, and competition for grass among prairie dogs, elk, and cattle was confirmed (Knowles 1986a). In two cases that show the extreme range of such calculations, Merriam (1902) estimated the carrying capacity of large ungulates was reduced 50 to 75 percent by prairie dogs, whereas Miller and colleagues (1994) estimated only a 4- to 7-percent reduction using data from Uresk and Paulson (1988). Both estimates could be correct under specific conditions. Reductions of 50 to 75 percent appear reasonable, given the expansive colonies and high prairie dog densities noted by Merriam (1902), and the reductions of 4 to 7 percent reported by Miller and colleagues (1994) are equally possible if the area colonized is small relative to the uncolonized area. However, the 4- to 7-percent estimate warrants discussion because it has been commonly cited in recent years with little consideration of the conditions for which it is applicable.

The estimate of a 4- to 7-percent reduction in carrying capacity for large herbivores is derived from a modeling exercise with data collected from a 2100-ha pasture in the Conata Basin, 27 kilometers south of Wall, South Dakota (Uresk and Paulson 1988). Data included the diet composition of cattle and black-tailed prairie dogs, prairie dog densities, and forage production. Simulations limited prairie dog effects on livestock carrying capacity to sites in low seral stages, on the assumption that prairie dogs do not occur in or near climax vegetation because they prefer disturbed sites. However, disturbance should not be equated with seral status, because prairie dog attraction to disturbed sites is based on reduced plant height and density (i.e., increased visibility). Short-term disturbances, such as intensive grazing, can reduce plant height without changing species composition. In addition, the model accounted only for forage consumed by prairie dogs, but prairie dogs are known to clip considerable amounts of forage taller than 5 to 10 centimeters (cm) to increase their ability to spot predators (Koford 1958, Hoogland 1995). Uresk and Paulson (1988) determined that, with no prairie dogs, a pasture would support 40 to 161 cow–calf pairs (animal units), allowing for 20 and 80 percent utilization, respectively. With a 40-ha colony in the pasture, carrying capacities at 20 percent and 80 percent utilization were estimated to be 37 and 157 animal units, respectively. These numbers represent a 4- to 7-percent reduction in stocking capacity with less than 2 percent of the area colonized. However, Miller and colleagues (1994) did not consider that these reductions in carrying capacity grow as the colonized portion of the pasture increases. Concluding that 2 percent is the maximum proportion of pastures that prairie dog colonies occupy is unrealistic. Even with the conservative conditions applied by Uresk and Paulson (1988), extrapolations from these data suggest that livestock carrying capacity at 20 and 80 percent utilization levels would reach zero when prairie dogs occupied 25 and 77 percent of the pasture, respectively.

Miller and colleagues (1994) and Wuerthner (1997) both cited O'Meilia and colleagues (1982) as proof that cattle weight gains are unaffected by prairie dogs. Indeed, O'Meilia and colleagues (1982) found no statistical differences in cattle weight gains between pastures with and without prairie dogs. However, a series of limitations and errors should be considered with these results. First, prairie dogs were transplanted into the treatment pastures 4, 3, and 2 years before the response variables were measured. Therefore, responses are applicable only to the short-term effects of young colonies, which have the least impact on vegetation structure and composition (Coppock et al. 1983a). Second, prairie dogs moved into uncolonized treatment pastures and had to be controlled. Third, cattle were stocked at very heavy rates, utilizing 80 to 92 percent of the available herbage independent of prairie dog use. Weight gains are typically reduced or eliminated at such high levels of utilization. Therefore, the cattle could not express their genetic potential for growth, and the potential for further reductions in herbage by prairie dogs was minimized.

One of the study's limitations cannot be detected within the manuscript. A review of archived data indicates that the livestock data were improperly analyzed with respect to experimental versus sampling units (Robert Gillen, US Department of Agriculture, Agricultural Research Service, Woodward, OK, personal communication, 22 September 2003). When reanalyzed, the data show that prairie dogs reduced winter weight gains for cattle ($P < 0.03$), but gains remained similar between treatments during summer ($P > 0.84$) and over the total grazing season ($P > 0.32$). Although the results of O'Meilia and colleagues (1982) do not show overall reductions in cattle performance during recent colonization by prairie dogs, we believe the results are less conclusive than portrayed, and statistical differences would have been difficult to show since cattle performance data have only two replications for two treatments over 2 years. Miller and colleagues (1994) also cite Hansen and Gold (1977) as additional evidence that livestock performance was not reduced by prairie dogs. However, the only references to cattle performance in Hansen and Gold (1977) were statements that prairie dogs probably reduced habitat suitability for cattle, and cattle in pastures with prairie dogs did not lose or gain weight over the winter grazing period.

Table 1. Direct reduction of forage (grazing days) for five large herbivores as related to forage consumption by three densities of prairie dogs.

Prairie dogs per hectare	Grazing days per hectare lost annually to prairie dog grazing				
	Cow	Steer	Sheep	Bison	Elk
8	12	16	76	6	17
18	26	35	170	15	37
46	67	90	435	37	95

Note: Values for grazing days are based on daily dry matter intake rates of black-tailed prairie dogs (Hansen and Cavender 1973) and large herbivores.

Table 2. Colony area required for three densities of prairie dogs to consume 1 grazing-year equivalent of forage for five large herbivores.

Prairie dogs per hectare	Prairie dog colony area required to consume 1 grazing year (hectares)				
	Cow	Steer	Sheep	Bison	Elk
8	31.3	23.4	4.8	56.5	22.0
18	13.9	10.4	2.1	25.1	9.8
46	5.4	4.1	0.8	9.8	3.8

Note: Values for grazing years are based on daily dry matter intake rates of black-tailed prairie dogs (Hansen and Cavender 1973) and large herbivores.

Prairie dog effects on herbivore carrying capacity depend on numerous interacting factors that must be considered with any given estimate. Three factors undeniably affecting stocking capacity of herbivores are the amount, type, and quality of forage available. Prairie dogs reduce the amount of available forage by consuming it directly, clipping plants, denuding mounds, and causing changes in species composition. Daily dry matter consumption by prairie dogs is estimated at 31 to 46 grams (Merriam 1902, Hansen and Cavender 1973, Hansen and Gold 1977). If consumption rates were all that affected carrying capacity, then effects could be estimated simply and directly based on daily intake requirements for the herbivores of interest, prairie dog density (table 1), and the area colonized (table 2). However, these estimates would greatly underestimate the reduction in carrying capacity by excluding the effects of burrowing, clipping, and changes in plant species composition.

The impact of mound building may reduce plant biomass considerably, since mounds are predominantly bare. However, the reduction would vary with mound size and density. Mounds are typically 1 to 3 m in diameter (Hoogland 1995) and density may increase with colony age (Archer et al. 1987). Bare ground between mounds in mixed-grass prairie has been shown to increase from about 10 percent on uncolonized sites to 35 percent after 3 years of colonization (Archer et al. 1987) and from 16 percent to 59 percent after 26 years of colonization (Detling 1998). Clipping effects on biomass will increase with increasing site productivity. Shortgrasses are already near the 5- to 10-cm plant height commonly found on colonies (Archer et al. 1987, Weltzin et al. 1997), so little clipping is required to maintain visibility. However, a large percentage of individual midgrasses and tallgrasses must be clipped to achieve the same visibility, resulting in greater reductions of biomass.

Changes in species composition caused by colonization potentially reduce forage availability by reducing total productivity or by replacing preferred forages with unpalatable plants. Prairie dogs shift perennial mixed-grass communities toward forb–annual grass mixtures and, eventually, toward domination by half-shrubs, forbs, and bare ground (Coppock et al. 1983a, Archer et al. 1987, Weltzin et al. 1997). Graminoid standing crop is generally reduced through each of these stages. Weltzin and colleagues (1997) found shortgrass standing crop was similar on colonized and uncolonized sites, but total live herbaceous standing crop was 3 to 4 times lower on colonies, and midgrass standing crop was 6 to 15 times lower. Coppock and colleagues (1983a) showed that 3- to 8-year-old colonies had half the total biomass of uncolonized mixed-grass sites. Total biomass on older portions of colonies was similar to that on uncolonized sites, but 55 percent of the colony biomass was composed of woody species. Graminoids were reduced 59 percent on the younger portions of colonies and 97 percent on the older portions. The implication is that the habitat occupied by prairie dogs shifts, over time, from one suited for grazers to one better suited for browsers.

To address the potential for increased forage quality (crude protein and digestibility) on colonies to override the effects of reduced forage, it is necessary to understand how forage quality affects the performance of ruminant animals. Weight gain for ruminant animals is generally determined by forage intake. Increased crude protein can improve gains indirectly by promoting rumen microbes that aid in digestion and become an additional source of protein for the ruminant. Increased microbial populations and forage digestibility then support more rapid rates of digestion and passage through the gastrointestinal tract, which in turn allow greater forage intake. Realizing the benefits of increased forage quality, therefore, still depends primarily on the amount of forage available. Increases in crude protein (6.25 × nitrogen concentration) on colonies are small (0.7 to 1.9 percent) (Coppock et al. 1983a, Cid et al. 1991) and limited in duration. Prairie dogs' contributions to average forage quality would also be low when small portions of pastures were colonized. Increasing the colony area would increase average forage quality, but it would also reduce the total crude protein available because of reductions in forage quantity (table 3).

Interactions between prairie dogs and large herbivores are scale and time dependent. Small colonies in large areas are not likely to reduce forage availability enough to affect animal performance or stocking capacity. Similarly, young colonies cause few changes in plant species composition that negatively affect grazers. However, forage quantity becomes more limited as colonies age and occupy greater portions of an area, leading to reduced carrying capacity in one of two ways: (1) Stocking rates are reduced to compensate for lost forage, or (2) forage utilization is increased. The latter may temporarily allow the number of animals to be maintained, but the plant community will be driven toward a lower seral stage over time, and animal performance will suffer as forage resources become more limited. Increased utilization is likely to increase the rate of colony expansion as well, compounding the adverse effects on carrying capacity. The problem is that colonies cannot be kept small and young without some form of control. Therefore, control of prairie dogs has been considered necessary to maintain carrying capacity of livestock and wild ungulates (Wydeven and Dahlgren 1985, Whicker and Detling 1988, Detling 1998).

Conclusions

We believe there is substantial evidence that

- Black-tailed prairie dogs did not occupy 100 million ha in North America before European settlement, and the 40-million-ha estimate may be representative of their maximum potential occupancy under extreme conditions.
- Selective foraging on prairie dog colonies has been demonstrated for bison and pronghorn, but only under limited conditions, and prairie dogs are not unique in their ability to increase the attractiveness of sites for grazing.
- Prairie dog colonies can reduce carrying capacity for livestock as well as other large grazers, and their impact varies with habitat type, prairie dog density, colony age, and the proportion of area colonized.

The positive and negative influences of prairie dogs have been overstated as interests have teetered between scientific

Table 3. Effects of prairie dog colonization (percentage of area colonized) on herbaceous standing crop, crude protein, and nitrogen content.

Area colonized (percentage)	Standing crop (kg per ha)	Crude protein (percentage)	Nitrogen (kg per ha)	Nitrogen (percentage of uncolonized value)
0	2000	8.0	25.6	100
20	1700	8.4	22.8	89
40	1400	8.8	19.7	77
60	1100	9.2	16.2	63
80	800	9.6	12.3	48
100	500	10.0	8.0	31

Note: Estimates assume a standing crop of 500 kilograms herbage per hectare and a 2 percent increase in crude protein on colonized sites.

and political. A certain amount of skepticism is always warranted during the review of literature, but in the case of polarized issues, such as those surrounding prairie dogs, it is essential for the good of science and management. Just as early interests in eradication rather than control of prairie dogs were an overreaction to information about the deleterious effects of prairie dogs, current interests in protection rather than conservation and management may be an equally extreme reaction based on exaggerations of prairie dogs' positive role in grassland ecosystems.

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