Management and Conservation Article

Prairie Dogs: An Ecological Review and Current Biopolitics

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ABSTRACT In recent years, people have interpreted scientific information about the black-tailed prairie dog (*Cynomys ludovicianus*) in various, and sometimes conflicting, ways. Political complexity around the relationship among black-tailed prairie dogs, agricultural interests, and wildlife has increased in recent years, particularly when prairie dogs occur on publicly owned lands leased to private entities for livestock grazing. Some have proposed that estimates of prairie dog (*Cynomys* spp.) numbers from 1900 are inflated, that prairie dog grazing is not unique (other grazers have similar affects on vegetation), and that prairie dogs significantly reduce carrying capacity for livestock and wildlife. We address all these issues but concentrate on the degree of competition between prairie dogs and ungulates because this motivates most prairie dog control actions. We conclude that the available information does not justify holding distribution and numbers of prairie dogs at a level that is too low to perform their keystone ecological function. We further conclude that it is especially important that prairie dogs be sufficiently abundant on public lands to perform this function. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2801–2810; 2007)

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In recent years, people have interpreted scientific information about the black-tailed prairie dog (*Cynomys ludovicianus*) in varying ways. We expect this in review papers, as the authors often interpret the work of others and base conclusions on inconclusive historical data. With high-profile species, these differences can fuel contentious political battles. We discuss the ecological role of a politically charged species, the black-tailed prairie dog, and the relationship between prairie dogs, other wildlife species, and livestock. As conservation biologists, we seek a broader scientific understanding for use by resource managers.

In recent years the political complexity has increased over the relationship among black-tailed prairie dogs, agricultural interests, and wildlife (see Hoogland 2006). This is particularly true on publicly owned land leased to private entities for livestock grazing. Biologists agree that prairie dogs greatly declined in numbers over the last 2 centuries but disagree over the magnitude of the decline (Vermeire et al. 2004, Forrest 2005, Proctor et al. 2006). Interests responsive to agricultural concerns tend to emphasize evidence that minimizes the level of decline, whereas interests concerned with the ecological role of prairie dogs frequently emphasize evidence supporting higher levels of decline (up to 98%; Proctor et al. 2006). Some advocates of the agricultural industry actively promote management of public lands in ways designed to benefit the livestock industry (South Dakota Department of Game, Fish, and Parks and South Dakota Department of Agriculture 2002, Johnson-Nistler et al. 2004, Cooper and Gabriel 2005). Conversely, conservationists propose reduced livestock grazing on public lands in the interest of conservation of native wildlife species.

Vermeire et al. (2004) concluded that estimates of prairie dog (*Cynomys* spp.) numbers from 1900 are inflated because of overgrazing by cattle and drought during the 1880s and 1890s. Because tall, dense vegetation impedes prairie dog colony expansion (Snell and Hlavacheck 1980, Cable and Timm 1988), these conditions permitted prairie dog colonies to grow given the low vegetation cover. These authors contend that lower (uninflated) estimates justify maintaining lower numbers of prairie dogs today, that prairie dog grazing is not unique among herbivore species (i.e., other herbivores could substitute for prairie dog grazing), and that prairie dogs reduce carrying capacity for livestock and other wildlife. In rebuttal of the first point, Forrest (2005; see also Proctor et al. 2006) provided evidence that historical estimates of prairie dog numbers were not inflated. Several researchers convincingly contradicted the second point, that prairie dog grazing is not unique (Whicker and Detling 1988, Sharps and Uresk 1990, Kotliar et al. 1999, Kotliar 2000, Miller et al. 2000).

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Resolutions adopted by the Society of Conservation Biology (1994) and the American Society of Mammalogists (1998) also acknowledge the importance of prairie dogs. We mainly address the third point, the level of competition between prairie dogs and large ungulates, and we offer some information on costs vs. benefits of poisoning. Additionally, we also discuss the first 2 points primarily as they refer to the issue of competition.

COMPETITION BETWEEN PRAIRIE DOGS AND LARGE UNGULATES

Ecological Effects of Competition

We follow Ricklefs and Miller (2000:384) in defining competition as resulting "when many species seek the same resources, and the depressing effect that each one has on the availability of the shared resources adversely affects the others." Cattle and black-tailed prairie dogs exhibit a high dietary overlap—up to 60% in a mid-grass prairie and 64% in a short-grass prairie (Hansen and Gold 1977; Uresk 1984, 1986). Competition, however, does not necessarily occur simply because 2 species use the same resource. Competition exists when species A is worse off because of the activities by species B, and vice versa. Thus, cattle and prairie dogs may seek the same resources, but diet overlap alone does not prove that either species is adversely affected.

Demonstrating competition is difficult in natural systems. First, there is an issue of scale. High competition may occur in localized cases (e.g., a single ranch), but when considering larger landscapes the actual level of competition may become insignificant. Second, although prairie dogs clearly reduce plant biomass, debate remains about the impact to other grazers because of increases in forage quality as a result of prairie dog activities. It appears that the degree of compensation is highly situational (see Curtin 2006, Derner et al. 2006, Detling 2006). Third, presence and level of competition among species can vary across geographical area (e.g., differences in productivity), across vegetation types (mid-grass, short-grass, or desert grasslands), among seasons, and among years (by variation in rainfall). Because we often lack data over the full range of these conditions, a useful guideline may be that in areas of low biomass productivity, competition is more likely than in areas of high biomass productivity (Detling 2006). Competition is also more likely at higher stocking levels than at light levels (see review by Holechek et al. 2004). The larger public policy question is whether competition justifies poisoning prairie dogs on publicly owned lands to benefit cattle grazing by private leasees.

Proponents of holding prairie dogs at low numbers claim such management is necessary to maintain wild ungulates and economically viable numbers of domestic livestock (Stoltenberg et al. 2004, Vermeire et al. 2004). They frame competition around a negative effect on large ungulates by prairie dogs, and typically define competition as overlapping resource use. Even if prairie dogs compete with large ungulates, the fact remains that coexistence is possible as millions of bison (*Bison bison*), pronghorn (*Antilocapra americana*), and elk (*Cervus elaphus*) lived for millennia with prairie dogs before European settlers introduced domestic livestock to the Great Plains.

In North America, individual bison cows and yearlings appear to benefit from grazing on prairie dog colonies, as opposed to grazing only away from those colonies (Vanderhye 1985, Detling 2006). Seasonal weight gain of bison varies directly with the time they spend grazing on prairie dog colonies (Detling 2006). For wild ungulates, competition with high densities of livestock may present a larger problem than competition with prairie dogs. When researchers calculated livestock competition based on diets, cattle grazing reduced bison numbers by 72% and elk numbers by 40% (Wydeven and Dahlgren 1985, Uresk 1986, Holechek et al. 1989).

At the beginning of the 20th century, Merriam (1902) estimated the effects of prairie dogs on grazing lands. Some people cite his work as justification for poisoning prairie dogs to benefit cattle grazing (see Vermeire et al. 2004). Furthermore, Merriam used an unstated formula to claim that 256 prairie dogs consume as much grass as one cow, and failed to correct for dietary overlap or to account for prairie dog food that is not livestock forage (Koford 1958). Merriam (1902:258) concluded "Hence, it is no wonder that the annual loss from prairie dogs is said to range from 50 to 75 per cent of the producing capacity of the land." Modern standards of evidence cannot support this assertion, which recent studies contradict.

O'Meilia et al. (1982) estimated competition between cattle and prairie dogs in Oklahoma, USA, and found no statistical difference in weight gain between steers raised on and off of prairie dog colonies. A reanalysis by Vermeire et al. (2004) of O'Meilia's data agreed with the original conclusion that no statistical difference in weight gain of steers occurred over the entire year, but they found a difference during winter. However, reduced winter weight gains are irrelevant for most western ranchers, because cattle typically do not free-range during winter (particularly on public lands) and ranchers supplement cattle in winter with stored foods. The O'Meilia et al. (1982) study comprised small sample sizes, so we should cautiously interpret both the original conclusion and the reanalysis (Detling 2006).

After reintroducing black-tailed prairie dogs to the Gray Ranch in southwestern New Mexico, vegetation was shorter on the prairie dog colony (Brown 2003; Curtin 2003, 2006). Vegetation diversity was lower on the colonies, but biomass was slightly higher than on random control plots, perhaps because grasses became more bunched (Curtin 2006). Soils probably played some role in the biomass results because prairie dogs colonized the richer areas (C. Curtin, Massachusetts Institute of Technology–United States Geological Survey Science Impact Collaborative, personal communication). Most importantly, large grazers do not find the tabosa grass (*Hilaria mutica*) of the region palatable, so livestock did not use the grass away from prairie dog colonies; livestock only ate tabosa grass after prairie dogs clipped it (C. Curtin, personal communication).

A study in New Mexico also reported that cattle walked miles from water across open terrain to graze on prairie dog colonies (Brown 2003, Curtin 2003). Curtin (2003:91) observed, "In short, prairie dogs have a positive interaction with native and non-native grazers." We should not extrapolate this example from southwestern grasslands across the prairie dog's range. In short-grass steppe habitat in northeastern Colorado, USA, cows showed no preference for grazing on or off colonies (Guenther and Detling 2003, Detling 2006). In a northern mixed-prairie, bison showed a decided preference for grazing on prairie dog colonies (Coppock et al. 1983*b*, Detling 2006).

Using actual data and linear programming Uresk and Paulson (1988) estimated competition between cattle and prairie dogs at 4% to 7% in South Dakota, USA. Data included diets, consumption rates, plant production, stocking rates (20% to 80% forage utilization), densities of black-tailed prairie dogs (up to 40 ha of prairie dogs at 44 prairie dogs/ha in a 2,100-ha pasture), and plant seral stages. They analyzed vegetation from 4 treatments: 1) neither cattle nor prairie dogs, 2) prairie dogs only, 3) both cattle and prairie dogs, and 4) cattle only (Uresk and Bjugstad 1983; Collins et al. 1984; Uresk 1985, 1987).

Many ranchers follow the adage "take half and leave half" of the vegetation (Lacey and Van Poolen 1981). When reviewing studies of stocking rates, Holechek et al. (2004) reported that heavy grazing used an average of 57% of primary forage species, moderate grazing used 43%, and light grazing used 32%; over long time frames, moderate grazing levels maintained vegetation productivity for arid and semi-arid grasslands. Using Uresk and Paulson's (1988) model, Detling (2006) suggested that when cattle consume 60% of the vegetation in a pasture and prairie dogs occupy 2% of that pasture, cow-calf capacity declines by 3.3%. Looking at different scales, individual pastures may include more than 2% of their area occupied by prairie dogs, but prairie dogs still occupy about 2% of their former range (Proctor et al. 2006). Holechek et al. (2004) promoted a moderate stocking rate (about 45% utilization) for range health, and stocking at that rate should also reduce competition between livestock and prairie dogs.

More recently, Derner et al. (2006) looked at interactions between cattle and prairie dogs on the short-grass steppe of the Pawnee National Grasslands, Colorado. Over 6 years, the weight of cattle declined with increasing area occupied by prairie dogs, but at a rate proportionately lower than the increasing percentage of pasture occupied by prairie dogs ($Y = 98.71 - 0.21X$). When prairie dogs occupied 20% of the pasture, cattle weight gain declined by 5.5%; when prairie dogs occupied 60% of the pasture, cattle weight gain declined by 13.9% (Derner et al. 2006). Annual precipitation was below average in 4 of the 6 years, and mean weight gain of cattle on and off of colonies was significantly different (which the authors defined as $P < 0.10$) in 3 of 5 years (2 of which experienced below average precipitation) for which the authors analyzed weight gain (Derner et al. 2006). One of those years demonstrated highly significant differences ($P < 0.001$) and that year involved the pasture with a prairie dog colonization level of 63% and below average precipitation. During the wet year, only one site with prairie dogs (4.3%) was lower in cattle weights than other sites with and without prairie dogs (Tukey's Multiple Comparison Procedure, $\alpha = 0.01$). Over the entire study, mean seasonal weight gain of cattle on pastures without prairie dogs was 6% higher than on pastures with prairie dogs; mean area occupied by prairie dogs was 24%, with a range from 4% to 63% (Derner et al. 2006).

Contrary to statements by Vermeire et al. (2004:692), Uresk and Paulson (1988) did not "limit" prairie dogs to an early seral stage. Prairie dogs simply did not occur on the 58% of the 2,100-ha pasture that occurred at or near climax; the authors did not assume this (Uresk and Paulson 1988). Prairie dogs inhabited areas of the pasture that fell within the remaining 3 seral categories: early, early-intermediate, and a few in late-intermediate seral condition. Due to many years of heavy livestock grazing, areas of the grasslands existed in early seral stages of plant succession with buffalo grass (*Buchloe dactyloides*) being the dominant plant (Johnson et al. 1951, Lewis et al. 1956). However, with livestock reductions and poisoning of black-tailed prairie dogs, plant succession progressed to later seral stages (Uresk 1987, 1990). We recognize that plant succession does not always proceed in an orderly fashion; when disturbance is severe enough to push a system across a threshold, nonlinear responses can dominate.

All prairie dog towns sampled in the Badlands National Park, Buffalo Gap Grasslands, Thunder Basin Grasslands, and Ft. Pierre Grasslands contained prairie dog colonies in early or intermediate seral stages of plant succession (Koford 1958, Uresk 1985, Cincotta et al. 1989, Severson and Plumb 1998). In mixed-grass and tall-grass prairie, managing for a long-term, climax stage by reducing livestock-grazing increases vegetation height, and thus reduces the number of prairie dogs, which do not colonize in climax vegetation (Koford 1958, Snell and Hlavachick 1980, Snell 1985, Uresk 1987). Disturbance is indeed equated with seral status, and prairie dogs seek areas of disturbance or early seral condition (Koford 1958; Uresk 1987, 1990; Uresk and Paulson 1988; Cincotta et al. 1989). Prairie dogs do alter the vegetation for structure and composition, generally in association with another large herbivore, but the short grasses and the mid grasses are well adapted to herbivory (Uresk 1987, Winter et al. 2002).

Researchers estimate dietary overlap at 60% and 64% for cattle and prairie dogs in a mid-grass and short-grass prairie, respectively (Hansen and Gold 1977; Uresk 1984, 1986). Both livestock and prairie dogs independently and synergistically induced changes in plant species composition. Koford (1958) and Knowles (1982) found that prairie dogs began clipping mid grasses at approximately 15 cm or higher. Without grazing by livestock, or with light livestock grazing, clipping by prairie dogs generally occurs to maintain the colony in short vegetation (Koford 1958, Snell and Hlavachick 1980, Snell 1985, Uresk 1987). However, Heady and Child (1994) reported that plant biomass can decline by 1% to 5% from the hoof action of cows and soil compaction, and this decreases plant biomass available for livestock. The negative effects of soil compaction increase as stocking rates increase (Holechek et al. 2004).

Vermeire et al. (2004) concluded that the presence of prairie dog burrow-mounds reduced vegetation, which reduced livestock carrying capacity. Mounds account for 2.5% to 6% of the ground area on a prairie dog colony (Farrar 2002, Detling 2006). However, as moisture runs off these mounds, the adjacent areas harvest the water and nutrients for plant growth. As a result, the aboveground biomass of plants associated with mounds increases in native vegetation (Gold 1976, Severe 1977). This increase in aboveground biomass can variably offset the loss of vegetation on the prairie dog burrow-mounds.

Vermeire et al. (2004:694) also stated "...habitat occupied by prairie dogs shifts, over time, from one suited for grazers to one better suited for browsers." Johnson-Nistler (2004) reported the opposite. In some grasslands where woody plant encroachment is a problem, prairie dogs limit woody species and help maintain the dominance of herbaceous species. Everett (2002) found shrub cover was 7.5 times higher outside of prairie dog colonies than inside of colonies on Thunder Basin National Grassland in Wyoming, USA. Similarly, mesquite (*Prosopis* spp.) increased from 27% to 61% of the cover in the first 23 years after prairie dogs were removed from an area in Texas, USA (Weltzin et al. 1997). In Chihuahua, List (1997) documented a 14% increase in mesquite in the first 8 years after a prairie dog colony was poisoned. When prairie dogs were reintroduced on the Gray Ranch in southwestern New Mexico, USA, they clipped and girdled mesquite plants immediately after release (Brown 2003, Curtin 2003).

Economic Effects of Competition

Stoltenberg et al. (2004) indicated that total forage removed on prairie dog colony-sites (cattle + prairie dogs) was nearly 2 times greater than the forage removed by cattle (based on a forage estimation study). Stoltenberg et al. (2004) stated that prairie dogs removed an average of 852 kg/ha (760 pounds) of forage in June and July. Achieving this amount of forage consumption would require 457 prairie dogs/ha (185 prairie dogs/acre). One prairie dog consumes about 0.93 kg (2.05 pounds) of forage per month (Hansen and Cavender 1973). Furthermore, prairie dogs should have engaged in minimal clipping to enhance visibility on the study sites. Stoltenberg (2004) reported average vegetation heights ranging from a low of 7.4 cm to a high of 9.7 cm, but clipping for visibility does not generally occur until heights reach approximately 15 cm or greater (Koford 1958, Knowles 1982). The results of this study are difficult to evaluate with the limited information that Stoltenberg et al. (2004) and Stoltenberg (2004) presented. Prairie dogs and cattle apparently removed nearly equal amounts of forage during the 2 months, even though prairie dogs colonized 7.9% of the 701-ha study site. The authors do not describe stocking rates of livestock and prairie dog densities, and the methods used to estimate and compare forage weight are unclear. We could not calculate forage disappearance (consumption + clipping) based on the information available.

Vermeire et al. (2004) analyzed the effect of prairie dogs on livestock using a 1:1 competition rate via direct forage reduction, but livestock and prairie dogs do not compete for forage at a 1:1 ratio. Furthermore, the calculations of Vermeire et al. assume a full year of grazing by prairie dogs, cows, steers, and sheep, but livestock generally graze public lands over a 6-month period (or less), and prairie dogs do not always come aboveground during the winter months (Hoogland 1995). Thus, Vermeire et al. (2004) estimated that, at prairie dog densities ranging between 8/ha and 46/ha, 12 and 67 cow-days were lost and 76 and 435 sheep-days were lost, respectively. We estimated forage reduction for cows and sheep based on 6 months of grazing, and we adjusted for dietary overlap with prairie dogs using information from Alexander et al. (1983) and Uresk (1984, 1986). At the same prairie dog densities as above (8/ha and 46/ha), over 6 months 4 and 20 cow-days were lost and 8 and 48 sheep-days were lost, respectively (Table 1). Similarly, we estimated reduction in numbers of cows and sheep on a 1,000-ha grazing allotment (Table 2). Eight prairie dogs per hectare (low densities) would require a reduction of one cow or 3 sheep on a 1,000-ha allotment (carrying capacity of 2.4 ha per 1 animal-unit-month [AUM] for cows). Eighteen prairie dogs per hectare ($\bar{x}$ densities on the prairie) would require a reduction of 2 cows or 7 sheep on the allotment. Extreme densities of 46 prairie dogs per hectare required a reduction of 6 cows or 18 sheep on a 1,000-ha allotment.

Trying to increase forage by poisoning prairie dogs adds to expense borne by the public. In 2004, the South Dakota Game, Fish, and Parks poisoned prairie dogs on 3,110 ha of United States Forest Service lands at a cost to taxpayers of $24.58/ha (State of South Dakota 2005). Prorated over a 3-year period, at a stocking rate of one cow–calf pair per 2.4 ha—stocking rates in the general area ranged from 2 ha/AUM to 8.7 ha/AUM, depending on conditions (Uresk and Paulson 1988)—poisoning prairie dogs cost the taxpayers $19.40/AUM. An economic analysis by Collins et al. (1984) looked at prairie dog control in Conata Basin, South Dakota, where the 2004 poisoning was focused. They based their results on harvesting vegetation under 4 treatments: 1) neither cattle nor prairie dogs, 2) prairie dogs only, 3) both cattle and prairie dogs, and 4) cattle only (Uresk and Bjugstad 1983; Collins et al. 1984; Uresk 1985, 1987). Removing prairie dogs gained 51 kg/ha of forage, rendering it uneconomical to poison prairie dogs for additional livestock forage (unless subsidized by the public sector).

Similarly, Derner et al. (2006) found that declines in weight gain of cattle grazing on pastures with 20% occupancy by prairie dogs resulted in $14.95 less per steer. This translates to a 5.5% reduction. On pastures with 60% of the area in prairie dogs, the amount was $37.91 less per steer, a 14% reduction (Derner et al. 2006). In terms of

Table 1. Direct reduction of forage (grazing d for 6 months) for cows and sheep relative to forage consumption by density of black-tailed prairie dogs.[a]

Prairie dogs/ha	Grazing d/ha lost for 6 months to prairie dog grazing[b]	
	Cow	Sheep
8	4	8
18	8	19
46	20	48

[a] Data based on corrected diet similarities (dry wt composition) among the 3 herbivores.

[b] Colony area required for the given densities of prairie dogs (31 g daily dry matter intake/prairie dog; Hansen and Cavender 1973; Uresk 1984, 1986) to consume one grazing-yr equivalent of forage for cows (11.9 kg daily dry matter intake/cow; National Research Council 1984) and sheep (1.3 kg daily dry matter intake/sheep; Church 1972, Alexander et al. 1983).

Table 2. Estimated stocking rate of cows and sheep (grazing d for 6 months) for a 1,000-ha grazing allotment at different densities of black-tailed prairie dog.[a]

Colony area (ha)	Prairie dogs/ha					
	8		18		46	
	Cow	Sheep	Cow	Sheep	Cow	Sheep
0	69.0	483.0	69.0	483.0	69.0	483.0
20	68.8	482.2	68.5	481.3	67.6	478.5
40	68.5	481.4	67.9	479.5	66.1	474.1
60	67.9	480.7	67.3	477.8	64.7	469.6
80	67.9	479.9	66.8	476.0	63.2	465.1

[a] Carrying capacity of cows is estimated at 69 based on 2.4 ha per animal unit month (11.9 kg daily dry matter intake/cow; National Research Council 1984). Seven sheep are considered equivalent to one cow (1.3 kg daily dry matter intake/sheep; Church 1972, Alexander et al. 1983). Cow and sheep numbers are based on direct consumption of forage with a dietary overlap of 60% and 22%, respectively (31 g daily dry matter intake/prairie dog; Hansen and Cavender 1973; Uresk 1984, 1986). Forage utilization levels and plant standing crop for the allotment are not considered.

profit per unit of area, this translates to a loss of about $2.23/ha ($0.88/acre) at 20% occupancy by prairie dogs and about $5.58/ha ($2.20/acre) at 60% occupancy (Derner et al. 2006). According to Buhler (2006), an agronomy specialist with the Colorado State University Cooperative Extension, poisoning 76 burrows/ha (30 burrows/acre) would cost about $3.81 ($1.50/acre) using zinc phosphide and about $10.67 ($4.20/acre) using aluminum phosphide tablets. One must also consider labor, and Buhler (2006) stated that commercial applicators charge about $178/ha ($70/acre). Such large expenditures for so little gain are not profitable.

Factors that limit prairie dogs include soil types, slope, aspect, vegetation, and plague (Koford 1958, Reading 1993). Within those physical limits, reproductive success varies with social and demographic factors, such as population numbers, and maternal body mass (Hoogland 1995). High population levels or low maternal body mass inhibit reproductive success and thus make prairie dog numbers somewhat self-limiting. Historically, prairie dogs covered about 20% of the short and mixed-grass prairie (Summers and Linder 1978), and prairie dog colonies occupy about the same percentage of a prairie dog complex (Miller et al. 1996). More recently, Cooper and Gabriel (2005) estimated that 1.1% of the Great Plains managed by the United States Forest Service holds prairie dogs. Thus, there is little detriment to the livestock industry as a whole. We contend that it is scientifically and economically irresponsible to further reduce prairie dog populations on publicly owned lands because of competition with livestock.

HISTORICAL NUMBERS AND POLITICS

Historical estimates for numbers of prairie dogs help guide present management goals. Virchow and Hygnstrom (2002) and Vermeire et al. (2004) suggested that an estimate of 40,000,000 ha of prairie dogs in 1900 was unnaturally high because prairie dogs expanded in the face of drought and overgrazing by domestic livestock during the 1880s and 1890s. If the presence of roughly 23,000,000 cattle around 1900 led to inflated numbers of prairie dogs, what would have prevented prairie dogs from becoming equally numerous in the early and mid-1800s, when 30,000,000 bison inhabited the plains and similar environmental conditions prevailed (Forrest 2005)?

We suggest that Vermeire et al. (2004) misinterpreted Smith (1899) when stating that overgrazing in the 1880s set the stage for unnaturally high numbers of prairie dogs in 1900. Vermeire et al. (2004:690) stated "Smith (1889) described the grasslands as a 'pastoral paradise' with luxuriant growth before the 1880s." Smith's (1889:8) statement about a "pastoral paradise" referred to a period from 1874 to 1884 in central and western Texas after the near extermination of the southern buffalo herd by 1873 and after an act of Congress removed Native Americans in 1874:

"The disappearance of the buffalo was nearly coincident with that of the Indian, and there was a period of fully ten years after the destruction of the buffalo herds before the number of cattle and sheep on any portion of the ranges equaled the great herds of game. These years, from 1874 to 1884, may be called the 'golden period' of the Southwestern stockman. ... There were also abundant rains and the seasons were mild. ... Grasses and forage plants, ungrazed, grew and thrived, reseeded themselves, and increased to a wonderful degree of luxuriance, so the stockmen on entering this pastoral paradise thought that it was not possible to put enough cattle and sheep on the land to eat down all of the rank growth of vegetation."

Smith (1889:9) also wrote:

"Newcomers who had not seen the land when it was possessed by the Indian, the buffalo and mustang, at the time when the herbage was eaten down, or kept in check by fires or drought, naturally thought that this rich profusion of vegetation was the normal condition and that the saying that it was impossible to put enough cows on the land to eat all the grass was literally true."

The more complete statement by Smith (1889) offers a different picture than indicated by Vermeire et al. (2004).

The argument that prairie dogs were expanding at the beginning of the 20th century did not consider the huge numbers of bison that were already exterminated (as mentioned in Smith 1889) or the extensive prairie dog poisoning that already occurred (Knowles et al. 2002). Furthermore, the relevant point is that the declining trends in prairie dog populations are clear. Using the United States Fish and Wildlife Service's (2004) current estimates for black-tailed prairie dogs, the prairie dog species with the greatest historical range, the declining population trend is clear whether there were once 40,000,000 ha, 30,000,000 ha, 20,000,000 ha, or 10,000,000 ha of that species. Respectively, these figures indicate declines of roughly 98%, 97%, 96%, or 92%.

A quarter century ago, prairie dogs covered only 1.6% of the Forest Service lands on the Great Plains (Schenbeck 1982). Prairie dogs currently occupy <2% of the land within the species' range in South Dakota; yet despite such low numbers, implementing the South Dakota Black-Tailed Prairie Dog Conservation and Management Plan could result in a further reduction. The Plan recommends a statewide population goal of 80,726 ha of prairie dog colonies. Surveys completed in accordance with the Plan documented that prairie dogs currently inhabit 166,503 ha in South Dakota (Cooper and Gabriel 2005). We do not mean to single out South Dakota. The situation is similar in other states throughout the range of the prairie dog; we simply had access to better documentation for South Dakota. Considering the benefits of prairie dogs to the grassland ecosystems they inhabit (e.g., sustaining wildlife, soil nutrients, and vegetation; Campbell and Clark 1981, Agnew et al. 1986, Sharps and Uresk 1990, Bevers et al. 1997, Lomolino and Smith 2003), 1.1% occupancy by prairie dogs on federally owned land seems extremely modest.

The criteria the United States Fish and Wildlife Service uses to list species under the United States Endangered Species Act are 1) the present or threatened destruction, modification, or curtailment of its habitat or range; 2) over-utilization for commercial, recreational, scientific, or educational purposes; 3) disease or predation; 4) the inadequacy of existing regulatory mechanisms; and 5) other natural or human factors affecting its continued existence (see Manes 2006 for a discussion of all 5 criteria). A species must only meet one of these criteria to merit listing. Interestingly, the sparse occupancy of prairie dogs throughout their range appears to counter one of the arguments the United States Fish and Wildlife Service used to remove prairie dogs from the candidate list in 2004 (Manes 2006), at least on federal lands where the government controls management. The United States Fish and Wildlife Service argued that prairie dogs increased over the last 40 years (Manes 2006). Proctor et al. (2006) analyzed the present area inhabited by prairie dogs and found that of the 2% of their original range that prairie dogs still occupied, 1.5% occurred on tribal lands, 0.33% occurred on federal lands, and only 0.08% occurred on private lands.

UNIQUENESS OF PRAIRIE DOG ACTIVITIES

Proponents of reducing prairie dogs argue that prairie dog grazing does not produce unique effects and stated "Long-term, intensive use by any grazer will cause comparable changes in plant communities" (Vermeire et al. 2004:692). Scientific research does not support this claim on the mixed-prairie. For example, bison grazing alone produced a small impact on plant biomass, plant species composition, and plant or soil nitrogen, but prairie dog grazing led to a large effect on these same factors (Fahnestock and Detling 2002). Indeed, no additive effect occurs when bison and prairie dogs grazed together versus when prairie dogs grazed alone (Fahnestock and Detling 2002). Bison often create conditions necessary for prairie dogs on mixed grass prairies, but prairie dogs exert the larger effect on soil and plants.

Any grazer creates more succulent and nutritious regrowth than ungrazed forage, and large herbivores often select those previously grazed patches (McNaughton 1984, Knapp et al. 1999). At a macro-ecological scale, grazing represents a natural disturbance to the landscape. At a local scale, however, not all grazing is the same. Different species of grazers prefer different types of plants, and they eat those plants in different ways. Some species are opportunistic, some are selective, and some are intermediate between those 2 extremes. Even for a given species of grazer, seasonal differences exist. Cattle are grazers, but confinement produces a landscape with less diversity than one grazed by wandering ungulates (Benedict et al. 1996). Bison, in contrast, wander over an immense region and particular patches of grass may have as much as a 2-year rest before the bison return (Lott 2002). Perhaps the major difference between grazing by native herbivores and domestic livestock comes when some livestock managers promote killing predators and competitors, building fences unfriendly to wildlife, making unnecessary roads, increasing exotic plants, using chemicals, altering fire regimes, or managing in ways that degrade riparian areas (Freilich et al. 2003).

For cattle to serve as an ecological substitute for bison at some level on federal lands (see Tohill and Dollerschell 1990, Thomas 1991), they should mimic the pattern of wild bison—no prairie dog poisoning and avoidance of areas with drought. The lower rate for leasing federal lands and compensation programs can compensate for not poisoning. Turning an existing, negative subsidy (poisoning) into a positive incentive for not poisoning can fund compensation (Miller et al. 1996, Miller and Reading 2006). The National Wildlife Federation followed this pattern to provide incentives to leaseholders on National Forest lands around Yellowstone National Park that retire their leases to reduce conflict between livestock and grizzly bears (*Ursus arctos*) or wolves (*Canis lupus*). This program increases habitat security for wildlife, financially benefits the rancher, and reduces management headaches for the Forest Service. Similar options may exist for National Grasslands. The Malpai Borderlands Group, and others in New Mexico and Arizona, USA, stress the need to destock an area during drought, and they use grass banks or land held in reserve for ranchers affected by drought (Sayre 2001; http://www.malpaiborderlandsgroup.org/gb.asp).

Like cattle, prairie dogs graze, but prairie dogs represent much more than just grazers (Kotliar et al. 2006). They also move soil (Detling and Whicker 1988, Detling 1998), influence nutrient cycling (Coppock et al. 1983*a*; Detling and Whicker 1988; Whicker and Detling 1988, 1993; Detling 1998), increase nitrogen content of soil and plants (Holland and Detling 1990, Detling 1998), change vegetation structure and community dynamics (Coppock et al. 1983*a*, Whicker and Detling 1988, Weltzin et al. 1997, Detling 1998, Fahnestock and Detling 2002), aerate the ground (Whicker and Detling 1988, Outwater 1996, Detling 1998), alter soil chemistry (Munn 1993), and deepen water penetration (Outwater 1996, Detling 1998). They provide a ready source of prey to many predators and burrows for shelter to other animals and insects (Goodrich and Buskirk 1998, Kotliar et al. 1999, Shipley and Reading 2006). This combination of effects gives the prairie dog its role as a highly interactive (keystone) species in the ecosystem, creating a matrix of different habitats that increases diversity across the grassland (Kotliar et al. 1999, 2006; Miller et al. 2000).

Vermeire et al. (2004:689) cited Kotliar et al. (1999) as saying that the role prairie dogs play in influencing other vertebrate species is "greatly overstated." Vermeire et al. (2004:689) added the word "greatly"; Kotliar et al. (1999) did not use it. The following quotes accurately reflect the assessment by Kotliar et al. (1999:177 and 178, respectively):

> "Despite our conclusion that some prairie dog functions may be smaller than previously assumed, collectively these functions are quite large compared to other herbivores in the system. We suggest that prairie dogs also provide some unique functions not duplicated by any other species and that continued decline of prairie dogs may lead to substantial erosion of biological diversity and landscape heterogeneity across prairie and shrub-steppe landscapes."
>
> "We conclude that although some aspects of their role have been overstated in the literature, the available science clearly indicates that prairie dogs function as a keystone species."

The Society of Conservation Biology (1994) and the American Society of Mammalogists (1998) also advanced resolutions that support the view of Kotliar et al. (1999, 2006) that prairie dogs fit the definition of a keystone species (significantly affects ecosystem structure, function, and composition in ways not wholly duplicated by other species). Vermeire et al. (2004:695) stated that just as early interests in eradication were an overreaction, interests for conservation "may be an equally extreme reaction based on exaggerations of the prairie dogs' positive role in grassland systems." However, they offered no detailed discussion about that role and why it is exaggerated, and they ignore a growing body of literature (cited above) that suggests prairie dogs play key roles in the ecological processes of grasslands.

CONCLUSIONS

The issue of how much competition exists between prairie dogs and livestock is hotly disputed. In general, competition is more likely in areas of low productivity than in areas of high productivity, and light to moderate stocking rates produce less competition than high stocking rates (Detling 2006). Some members of the agricultural industry have framed the argument of competition in terms of how prairie dogs hurt cattle and large ungulates. They have not explored the effect that cattle can have on other grazers, large and small. We agree that more research is clearly required. We disagree, however, with the conclusions of Vermeire et al. (2004). We do not think the available evidence justifies holding distribution and numbers of prairie dogs at levels too low for them to perform their ecological function (Soulé et al. 2002, 2005).

We propose that the politics of the agricultural community only serve to cloak an important conservation issue. The prairie dog, a highly interactive species of grassland ecosystems, has declined greatly throughout its range to a level and distribution at which it can no longer serve its historical ecological function (Soulé et al. 2002, 2005; Proctor et al. 2006). Some people suggest that holding prairie dogs at low numbers is necessary to maintain livestock and wild ungulates. Yet, wild ungulates thrived for millennia with prairie dogs before European settlers. And, setting goals for prairie dogs based on the real or perceived needs of domestic livestock means we favor an abundant exotic species at the expense of a declining native species. In this case, the native species helped drive the evolution of the grassland system over thousands of years. To label such a species as a pest is not ecologically sound.

The best example of a species benefiting from prairie dogs is the black-footed ferret (*Mustela nigripes*). As obligate associates of prairie dogs, ferrets rely on them for about 90% of their prey and use their burrows as den sites and refugia (Miller et al. 1996). Because prairie dogs declined, black-footed ferret numbers collapsed. At one point, only 10 known individuals represented the entire species; they survived because of an intensive, and expensive, captive breeding effort (Miller et al. 1996, Biggins et al. 2006). Reintroductions of captive-raised black-footed ferrets began in 1991, but the black-footed ferret recovery effort is stalling because too few prairie dog complexes of sufficient size exist to meet the goals of the 1988 Black-Footed Ferret Recovery Plan (United States Fish and Wildlife Service 1988, Miller and Reading 2006). Bevers et al. (1997) estimated that an adult population of 200 black-footed ferrets requires a black-tailed prairie dog complex of 6,500 ha to support it. Because it takes 3 individual black-footed ferrets to make a genetically effective population (N_e) of 1 (United States Fish and Wildlife Service 1988), 200 individuals would reduce the consequences of inbreeding over the short term (by surpassing the guideline of needing an N_e of ≥ 50), but that number falls short of an N_e of 500, a number proposed for adaptive evolution in the long term (Frankel and Soulé 1981).

Constraining prairie dogs to low numbers in small, widely distributed colonies may allow them to persist, but low densities and scattered distribution will preclude them from performing their ecosystem functions (Miller et al. 2000, Soulé et al. 2005, Proctor et al. 2006). In other words, prairie dogs are functionally extinct (Soulé et al. 2005).

The day the United States Fish and Wildlife Service announced that they would remove the black-tailed prairie dog from the protection of their candidate list, the Governor of South Dakota announced a federal–state plan to "control the infestation of prairie dogs" on federal lands (Stein 2004:7). Thus 3,110 ha of prairie dogs were poisoned on the Buffalo Gap National Grasslands, parts of which occurred on the Conata Basin prairie dog complex, home to one of the most successful reintroduced populations of the endangered black-footed ferret. Other states took similar actions to poison prairie dogs. Given that prairie dogs occupy 1.1% of Forest Service lands on the Great Plains (Cooper and Gabriel 2005), how much more prairie dog control on our publicly owned lands does the livestock industry require? Kotliar et al. (1999) stated that continued decline of prairie dogs can lead to an erosion of biological diversity. What is considered an acceptable loss of biological diversity? Should we draw the line before black-footed ferrets go extinct, or should we wait for other species to become imperiled?

MANAGEMENT IMPLICATIONS

If society wants to conserve prairie dogs, the species should exist in densities and distribution that allows them to perform their evolutionary and ecological function on the grasslands. Black-footed ferret recovery could function as a benchmark for measuring the ecological function of prairie dogs. Recovering ferrets requires large complexes of prairie dogs distributed throughout their former range (United States Fish and Wildlife Service 1988). Because prairie dogs occupy 1.1% of Forest Service lands on the Great Plains (Cooper and Gabriel 2005), because poisoning is not economically feasible (Collins et al. 1984, Derner et al. 2006), and because prairie dogs support biodiversity and ecosystem processes (Kotliar et al. 1999), the implications of continued poisoning programs are clear. For cattle to serve as an ecological substitute for bison at some level on federal lands (see Tohill and Dollerschell 1990, Thomas 1991), management should strive to mimic the pattern of wild bison—no prairie dog poisoning and avoiding areas with drought. Policy makers could convert tax dollars currently allocated to a negative subsidy (poisoning) into a positive incentive for prairie dog conservation (Miller et al. 1996, Miller and Reading 2006). A grassbank system, perhaps created by holding some retired federal leases open, could help mimic bison moves during drought.

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