

On Prairie Dogs and Coexistence with Other Species

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Abstract

On North American grasslands, the prairie dog (*Cynomys* spp.) has been held in contempt for the last hundred years by most ranchers and farmers, and actively exterminated wherever possible. A comprehensive review of the literature in 1994, backed by on-site scrutiny, suggested that, contrary to past expectation, not only do prairie dogs serve a key role in soil nutrient building and maintain habitat for other wildlife species, but they also may directly augment, rather than reduce, the rates of weight gain in livestock and native ungulates. A key mechanism for this was proposed, whereby fewer apparent pounds of forage can produce more growth among larger grazing animals of particular interest to humans, through both increased overall nitrogen availability and better amino acid balance during the parts of the season when these items are otherwise limited in their diets. That change is initiated by continued, selective utilization by prairie dogs, which keeps plants in a responsive state of growth, and is reflected in larger animals' grazing preferences. Restraint in stocking rates of all grazing animals, however, is required to realize this potential without concurrent resource damage, including a strong presence of native predators to limit prairie dog populations to sustainable levels. A closely related, more complex pattern of harvest and land use, including the preparation of value-added products, could create economic opportunities in areas that allow prairie dog habitat development. Updated to the present, and more generally, consequences of prairie dog presence will vary with many factors, which are typically overlooked in particular scientific studies, and interpretations must thoroughly consider more influences of both space and time to become more effectively predictive.

Background

This distillation was originally prepared in 1994, but did not find an appropriate publisher. During the period between then and 2005, prairie dogs (*Cynomys* spp.) approached wider preservation as formally endangered species. However, with an extended drought leaving some ranchers looking for others to blame for landscape deterioration, the colony-building animals have recently reentered an active persecution phase. Scientists are among those who remain divided about the issues. Contrast Miller and Cully 2001, "As prairie dogs are a keystone species of prairie ecosystems, their decline bodes ill for the conservation of associated species", with Vermeire et al. 2004, "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"; along with sharp arguments about keystone species status among Stapp 1998, Miller et al. 2000, and Kotliar 2000). Public interpretations of supporting data are even more widely controversial (e.g., Thacker

2001, Lydbeck et al. 2002, and Davis 2003, for just three among many examples). The need seems to have reappeared for what is sketched in the following.

The original compilation of information grew from intensive background research on the range management and ecological implications of prairie dog control during preparation of an Environmental Impact Statement (EIS) for the Rosebud and Cheyenne River Lakota Sioux Nations, under a contract from the Bureau of Indian Affairs, Aberdeen, South Dakota to Galli Associates of Bountiful, Utah. Prairie dogs were not an issue about which we had special prior knowledge or attitudes. The conclusions reached during the assessment process did not appear to be commonly appreciated, even among the scientific community, and thus seemed worth sharing more widely. This article was intended to be a summary, and not an exhaustive literature review. It therefore explicitly includes only a portion of the information resources that were evaluated during its development.

Introduction

“A man receives only what he is ready to receive, whether physically or intellectually or morally...We hear and apprehend only what we already half know...Everyman thus tracks himself through life, in all his hearing and reading and observation and travelling. His observations make a chain. The phenomenon or fact that cannot in any wise be linked with the rest which he has observed, he does not observe.” Henry David Thoreau, quoted in A. D. Richardson’s introduction to *Faith in a Seed*.

The traditional Lakota relationship with the blacktailed prairie dog (*Cynomys ludovicianus*) is intrinsic within the translation of their word for these animals, i.e., *peespeesas*, “little brothers”. Within Navajo myth, their activity was perceived as critical in preventing drought (Mollison 1991). For contemporary daily life, prairie dogs offer many tribes a considerable economic return from hunting permits, an attraction for tourists to lands where they are found, international sales as pets (where values reportedly reached as high as \$300 per animal), while they continue to provide a food source among traditional Native Americans (Bureau of Indian Affairs 1994).

Nevertheless, more than a few individuals in the tribal groups agree with the fierce viewpoint of the state of South Dakota, which legally defines these same animals as “pests... detrimental to production of crops or livestock or to welfare of persons” (State Law 38-22), against which private land owners can have a lien placed against their property for the costs of extirpation if they do not terminate every prairie dog themselves.

Much of that negative attitude within agriculture can be traced to a 1902, intended-to-be scientific, publication by C. H. Merriam, which simplistically contended that because prairie dogs clip and eat grass, and since their heaviest concentrations were found in visually denuded areas, they must be a destructive competitor for other users of grasses. Therefore, they should be regarded as highly detrimental to cattle, other large grazing animals, and crops. Those who still condemn the prairie dog based on Merriam’s conclusions, however, consistently have failed to note that livestock grazing pressures that he observed on the turn-of-the-century pastures were at least four times what even a moderately conscientious range manager would allow today (Koford 1958). Merriam, and many who followed, did not

pursue possible multi-sided relationships between human-imposed grazing intensity, prairie dog populations, and consequent rangeland damage (Figure 1). Even more importantly, few have considered the possibility that what initially might be perceived as destructive competition might instead, at least in some circumstances, be constructive.

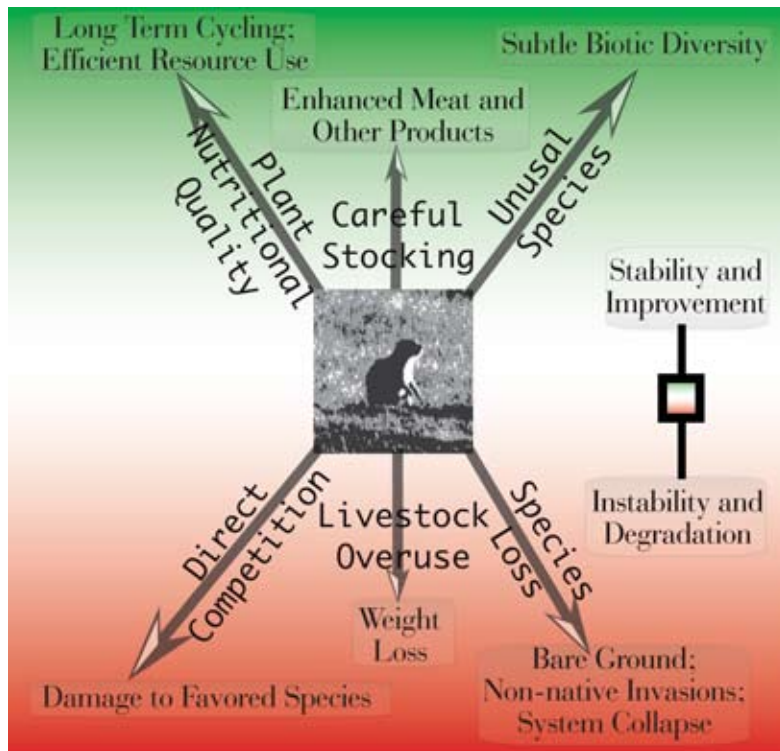


Figure 1. Larger scale interactions in which prairie dogs can be central. On the left are some of the flows directly related to plants, in the center to livestock, and on the right to diversity, with the slider reflecting all components' interactions, with colors for human and natural values.

It does not seem to overstate the case to describe careful scientific study of prairie dog-livestock relationships as “a frightfully difficult enterprise”. A thorough investigation requires the quantitative examination of large acreages, which have highly variable macro- and micro-environments, at every level in both time and space, with constantly changing plant/animal interactions for many other reasons as well (Figure 2, below). Together, these factors make replication (in its most rigorous sense) both within and among experiments simply impossible. Even attempting such inherently complex studies entails an investment of years, and a substantial number of dollars, in an era when both have been in short supply to in-the-field biological research. Political pressures, subtle and otherwise, further restrain possibilities for either funding or successfully completing meticulous investigations of this issue in the rural areas where problems with prairie dogs are asserted to exist. Hence, the body of reliable data is thin, at best.



Figure 2. Some system driving variables that may change with location and/or time. Some of the bold-faced general situation conditions that can affect and can be affected by prairie dog populations are encircled in turn by examples of each.

Nevertheless, considerable effort has been expended in pursuing the question: might the associations with prairie dogs Merriam and his followers condemned not have been the cause, but rather a symptom, of grazing management problems? In addition to looking at specific evidence, the pattern of the following re-examination may serve a further purpose. It can act as a model for other biological resource situations that have been widely thought to be competitive, but where, instead, the presence of additional species may result in fully compensating (if not greater) increases in efficiency of utilization for both material and energy. A key part of that goal is to elucidate testable mechanisms for potential or apparent increases in system efficiency in utilization of solar energy, precipitation, and soil nutrients.

General Context

Figures 3 and 4 are not intended to be definitive, but should reflect problems with common observation of prairie dog activity as reducing net productivity, standing crop, and/or cover. In fig. 3 below, of a private ranch in South Dakota, notice three levels: (1) closest to the camera, outside the fence, with neither prairie dogs nor livestock; (2) inside nearer, with livestock but no prairie dogs; and (3) in the distance with both active.



Figure 3. Prairie dog town with cattle grazing. On private land in west-central South Dakota, fall 1992, with tallest plants closest to the camera where they are protected from most grazing by the fence, and in the background an active prairie dog colony.

In fig. 4, from Wind Cave National Park, South Dakota, in a later season, of a long-established prairie dog town regularly visited by bison, differences were less distinct, with the exception of individual clearings around family group mounds. This comparison is targeted not to be another condemnation of livestock grazing, but to underline the impacts of combinations, and of artificial restraints by ecologically arbitrary fencing and choices in human-controlled stocking rates of any type of grazing animal.



Figure 4. Prairie dog town with bison grazing. In Wind Cave National Park, South Dakota, fall 1992, with the entire area open to bison use, noting how plant height does not change into the distance.

Weather and climatic variations are among the many factors that can exacerbate differences. Even Wind Caves does not have all the species that have historically evolved to coexist and interact with prairie dogs. Figure 2 suggested just some of the considerations that can affect system interactions on any particular site. The Ptolemaic epicycle structure

of that figure is intentional. No personal observation, research paper, or summary has considered all of these issues, but yet each – and the ones we have left out – plays some role in full appreciation and prediction of prairie dog impacts on any particular site. As just one example, all ranchers are worried about control of numbers, yet what is the history and presence or absence of the animals evolved predators? No individual observation in space or time can appropriately be generalized across all circumstances, despite the temptation to view one's own research as so carefully chosen as to become definitive.

Changes in Vegetation Structure and Productivity

In very localized situations, prairie dogs, along with their rodent compatriots, indeed have been measured to consume as much as 60% to 80% of the annual plant production (Sieg 1987). However, small mammals' ability to physically reach the overall production is limited by such factors as the height of plant growing points and the soil qualities required for successful burrowing. Sieg concluded that as a class, they rarely achieve a 20% impact at the ecosystem level, and more typical consumption is less than 5% of total aboveground plant growth. At those modest impact levels, small mammals seem unlikely to be a consistent competitively negative factor. Instead, in many instances they may achieve a net stimulatory effect on plant production, because of their selective removal of dead or dying tissue (Detling and Painter 1983).

This basic assumption of small mammal near-invisibility to net plant availability for other creatures was tested by Collins et al. (1984), who found that total vegetation production (in the Conata Basin in southwest South Dakota) did not significantly vary on and off studied prairie dog towns. There were shifts among the species that comprised the total biomass, but absolute gain in forage availability for livestock by completely eliminating prairie dogs averaged just 50 kg/ha (i.e., less than 5% of that from control plots), primarily from grama/buffalograss [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths/*Buchloe dactyloides* (Nutt.) Engel.] and western/crested wheatgrass [*Agropyron smithii* Rydb./*A. cristatum* (L.) Gaertner] categories.

Meanwhile, both total plant species diversity and livestock use of plant species was found to be generally greater on, rather than off, prairie dog towns in Colorado (Bonham and Lerwick, 1976). Similar trends were found in comparisons on other locations by Hansen and Gold (1977), Archer et al. (1987), and Coppock et al. (1983).

Whicker and Detling (1988a) got to the heart of a key perceptual difficulty: the difference between the most noticeable changes to the human eye and what, more precisely, is happening ecologically. Although a lower standing cover was visible on the studied dog towns observed on any single day, they found no statistical correlation between the intensity of prairie dog use and the yearly sum of the aboveground net primary (i.e., plant) productivity. Growth increments were simply utilized more quickly and completely as densities rose, and not left as standing dead or decadent material. Thus, in studying prairie dog impacts, it becomes particularly important not to rely just on a single observation of vegetation (e.g., peak biomass).

In a related concern, standing dead shoots may please a human observer by giving the appearance of a fuller vegetation cover, but are mostly composed of much less digestible

dry material, which tends to be ignored or avoided by most grazing animals. Dead shoots also represent a fire hazard and restrain further active growth by the plant in question. Whicker and Detling (1988b) have emphasized how grazing removal of lower-productivity, aging leaves stimulates compensatory growth among grasses that regrow from their bases. Polley (1987) confirmed, more specifically, that western wheatgrass on prairie dog colonies responded more effectively to grazing, achieving “high rates of resource capture”, including a higher total nitrogen uptake, when compared to plants growing outside prairie dog utilization areas.

Among all plant species, annual nitrogen incorporation into aboveground plant tissue increased by fully 50% as prairie dog use rose from none to light, rather than decreasing because of their clipping activity (Whicker and Detling, 1988a). That highly significant increase in total nitrogen was sustained as the intensity of prairie dog impacts became heavier.

An overall compositional change from dominance by perennial grasses to a mixture of perennial and annual forbs (i.e., broader-leaved flowering plants) in this vegetation followed substantial prairie dog colonization within three years (Archer et al. 1987). The most sensitive grasses were the needlegrass (*Stipa*) and bluegrass (*Poa*) species. Concurrently, a shift within 12 years after prairie dog arrival on livestock pastures was suggested from “tall” to “dwarf morphs” (ecotypes) of several grass species (Whicker and Detling 1988a). The latter are apparently either more tolerant to grazing or less intensively grazed because they are harder to reach. Notably, however, in assessing net impacts of prairie dog activity, these grass ecotypes’ shorter stature also makes them more likely to be overlooked in by-eye surveys of vegetation status.

A shift from grasses to forbs and dwarf shrubs over time on prairie dog towns that was described in Archer et al. (1987) was confirmed by Cincotta et al. (1989), but the latter suggested that the rate of change slowed when an initial short-grass understory was present. Here, perennial mid-grasses, e.g., sand dropseed [*Sporobolus cryptandrus* (Torrey) A. Gray], green needlegrass (*Stipa viridula* Trin.), and needle-and-thread (*Stipa comata* Trin. & Rupr.), tended to disappear first, in as little as 2 years with heavy use. These species appeared to be stressed by prairie dog clipping for predator avoidance, in addition to active consumption. Short grasses, e.g., buffalograss [*Buchloe dactyloides* (Nutt.) Engl.], took longer than 10 years to be similarly reduced. An intermediate “resilient period” of 4 to 7 years was also emphasized by Cincotta et al. (1989), where little change takes place in the shorter grasses until their root carbohydrates were depleted, and less than 75% cover remained, at which point sharp compositional changes occurred.

This phenomenon may be related to a root biomass decline, and to an increase in nematode populations, which were noted in measurements on prairie dog colonies by Whicker and Detling (1988a). These factors could limit long-term aboveground grass yields, especially in times of environmental stress (e.g., drought), and to selectively favor more broad-leaved plants (i.e., forbs) with less extensive fibrous-mat root systems, which can respond more quickly to smaller inputs of precipitation.

Percentages of bare ground did not differ ($P < 0.05$) on and off prairie dog colonies in areas measured in Colorado and Kansas by Winter et al. (2002). These authors concluded,

“Prairie dogs undoubtedly alter vegetation structure and composition in shortgrass prairie, and likely have a great influence on landscape heterogeneity, but our results suggest that shortgrass prairie is well adapted to the herbivory and soil disturbing activities of prairie dogs.”

Aboveground biomass was more than 2 times greater in off-colony sites than on-colony sites, primarily due to the near elimination of grasses on prairie dog colonies, within a South Dakota comparison by Fahnestock and Detling (2002). Similarly, standing crop biomass, plant species richness, litter, standing crop crude protein, sagebrush canopy cover, and density were greater ($P < 0.05$) on uncolonized areas compared to colonized areas, while bare ground and crude protein concentration were greater ($P < 0.05$) on areas colonized by prairie dogs compared to uncolonized areas (Johnson-Nisler et al. 2004). However, like many others, these authors measured only standing crop at limited intervals, and did not consider the relationship of those standing crops through utilization to more complete measures of productivity of either vegetation or among trophic levels.

In a not easily quantified personal observation, several South Dakota locations appeared to have an interesting correlate to a loss of standing dead grasses, one which may play an additional role in perceptions of denudation in prairie dog towns. As the species balance shifts from grasses to forbs, there is a distinctive consequent shift in color as perceived by the human eye, especially late in the year. Grasses cure to a yellowish-white tone, which can easily be distinguished from a darker background of earth, while forbs cure to a more reddish-brown color, which visually can blend into the soil behind them when looked at from distances further than a few feet away. This apparent disappearance effect is particularly striking when the primary view is from a shallow angle, e.g., from a vehicle window on a not-so-nearby road. When examples of first-glance-barren, heavily-livestock-grazed prairie dog towns were examined on foot, i.e., at a more nearly vertical angle from closer distances, the percentage of ground with plant cover tended to be more similar to neighboring, burrowing-rodent-free plots than had been anticipated from more currently typical, lower angle, further-removed inspections from a vehicle.

As further counterpoint to the expectation of prairie dogs as the most active vector, Schuster (1964) noted that cattle grazing, without other competition, also reduced grass root mass, and that this decrease was in direct proportion to their grazing intensity. More bluntly, large grazers (specifically, livestock) appeared to exacerbate changes in vegetation on prairie dog towns, and accelerate the expansion of towns into new areas (Osborn and Allen 1949). Shifts within overall plant composition varied more with “site-specific factors”, e.g., microclimate, soils, and the activity patterns of other animals, than they do with the length of prairie dog occupation was the conclusion by Whicker and Detling (1988a). Diversity, defined as absolute numbers of plant species, appeared to be maximized at intermediate levels of disturbance.

It must be emphasized that none of the more positive general statements do preclude local variations, including a shift in dominance to plants wholly unpalatable to livestock, or extensive vegetation loss on individual prairie dog towns. However, while qualitatively examining many thousands of hectares in Wyoming and South Dakota during the preparation of this article, the least vegetated areas consistently encountered were those that

had received excessive primary use by livestock (especially if horses were the dominant users) or humans (particularly those aided by machines). These most clearly damaged sites were found in general areas where prairie dogs long ago had been eliminated, or where they never had been present.

Consequential Values

The higher total nitrogen available on prairie dog towns, providing a higher relative nutritional quality, resulted in a higher nitrogen intake by grazing animals per forage unit consumed (Whicker and Detling 1988a). One practical extrapolation, which does not appear to have been suggested elsewhere from these facts, is a potential for more consistent crude protein intake by cattle throughout the entire grazing season. This would be especially important late in the season, when declining nitrogen levels in forages away from dog towns typically limits (or ends) net gains for cattle and other herbivores.

This potential fits with observations that shifts in plant composition from grass dominance towards the forbs and dwarf shrubs that accompany prairie dog colonization parallel increased, not decreased, utilization by large grazers (Whicker and Detling 1988b). Unrestrained bison (*Bison bison*) strongly selected for prairie dog towns in their activity patterns, spending up to 90% of their time there (Coppock et al. 1983). That study found that bison are 2.5 times as likely to rest in the older burrowing-rodent-use areas, and to graze in the more newly occupied zones. These choices correlated with more favorable live-to-dead vegetation ratios, and with the improved digestibility and crude protein levels in grasses and the other plants found there, all of which result from regrowth when an area has been clipped by prairie dogs.

Meanwhile, bison concentrated their grazing on the grass areas of prairie dog towns, while pronghorn antelope (*Antilocapra americana*) focused on the forb/shrub areas, being found there 67 to 97% of the time (Krueger 1986). This latter observation could have vital importance for those engaged in wildlife management, and could encourage wider use of multiple-species options for meat production.

The increased aboveground nitrogen yield available on prairie dog towns translated into an approximately 20 to 50% increase in yearling bison growth rates, as compared to animals that were not allowed access to towns, according to Vanderhye (1985). A weight gain advantage was still present for mature bison cows, albeit reduced to 10 to 20%. An interpretive caution for this data was added by Whicker and Detling (1988a), who noted that the more efficient protein utilization found in bison (when compared to cattle) may cause the benefits of additional nitrogen intake to be greater in this native animal species than for domesticated animals. Also, this growth advantage may be lost if heavily rodent-occupied zones are not balanced by access to use-free areas, as could occur in the case of extensive prairie dog coverage within a single fenced paddock.

Dietary overlap between prairie dogs and cattle does not appear to have been studied as a direct comparison experimentally, especially on a season long basis, although it would logically seem to be a key factor in assessing competition between these animals. While grasses were expected to be highly desired by both, and prairie dogs confirmed as selective feeders (Uresk 1984), just a 60% dietary overlap on a species-selected basis between prairie

dogs and cattle has been observed (Uresk 1992), whereas Koford (1958) had roughly estimated a 75% overlap. Uresk (1992) also reiterated the conclusions of Sieg (1987) that when physical apportionment in three-dimensional space, through time, was more fully considered, this translated into only 5% direct dietary competition during a full year. Among other factors, prairie dogs can most easily reach what cattle cannot, and vice versa.

Meanwhile, statistically significant increases in silicon concentrations have been found in grasses growing on prairie dog colonies, as opposed to those growing beyond their boundaries Brizuela et al. (1986). That increase did not, however, appear to result in digestibility problems for livestock, in contrast to what was suggested in unrelated studies about possible results of higher silicon levels in plants consumed by grazers.

This relates to an important set of issues that are routinely sidestepped in evaluations of grazing comparisons. Animal weight gain, measured per animal and per unit of land, when summed over the entire season, are the parameters of greatest economic importance. The return to ranchers is defined from them, quite obviously for calves and stockers, and little less directly for cows or bulls. Percentage utilization of vegetation is the primary environmental measure of pressure, being careful to specify utilization of exactly what, and when measured. Nevertheless, stocking rate (usually expressed as Animal Unit Months) is the most common actual measurement for grazing activity, even though it is merely a marker for the other, more directly useful parameters. The relationship between animal gain per individual and per unit of land is a complex one, both economically and ecologically, as they are to some extent inversely proportional, while their practical values will fluctuate with the relative worth of animals and the land. Nevertheless, weight gains over larger areas is both of the highest importance economically and the one element that most completely integrates all other grazing considerations: plant species distribution and time availability, potential nutritional quality, digestibility, and any negative factors, such as toxicity.

The balance of nutritional possibilities from yet unconnected work with prairie dogs makes it seem literally tragic that a series of in-the-field, integrative studies of relative weight gains for livestock have not been followed up from a fully scientific perspective, especially since weighing large animals has become so much easier with recent advances in equipment. The sole peer-reviewed and published study (O'Meilia et al. 1982) is in immediate contrast to the most pervasively held theory, i.e., that prairie dogs are highly detrimental to cattle. They found that cattle weight gains did *not* decline, at least to a statistically significant degree, when on-prairie-dog-town versus off-town grazing trials were conducted near Woodward, Oklahoma. These authors did point out slight reductions in the rate of gain, which might have been of economic concern. However, those declines must be seen in the context of the extremely heavy (80 to 95% utilization) stocking rates for cattle within that study. Such a high intensity rarely has been optimal for either rate of gain or ecosystem response (Caldwell 1984). More recent, unpublished data from rancher-conducted experiments on Nebraska National Forest grazing leases has indicated that where trial plots included prairie dog towns, a smaller number of livestock produced more pounds of gain per land unit than was derived by standard stocking on otherwise comparable areas where there were no prairie dogs (Uresk 1992).

Maximum Populations

Another key shibboleth around the livestock industry is that prairie dog populations will explode if left unchecked, so that they will dominate and denude entire grazinglands, which could be referred to as the “Stephen King scenario”. Part of this perception stems, once again, from Merriam (1902) and comparable observations that were made after many years of widespread, profound abuse by excessively heavy concentrations of livestock, when uninterrupted prairie dog town dimensions indeed could be measured in square kilometers. A dilemma occurs for most rational discussions on this point, since the earliest quantitative observations were made well after the arrival of domesticated grazers, in great numbers, on the scene, so that there are, for all practical purposes, no undisturbed comparisons. The issue remains controversial (e.g., Vermeire et al. 2004 vs. Forrest 2005).

“Long-term research with marked individuals shows that black-tailed, Gunnison’s, and Utah prairie dogs (Sciuridae: *Cynomys ludovicianus*, *C. gunnisoni*, and *C. parvidens*) all reproduce slowly, despite claims of ranchers and early naturalists” (Hoogland 2002). Current active populations and inactive colonized areas in the northern Great Plains were estimated by aerial surveys to occupy less than 250,000 ha (Sidle et al. 2001). In another study at the southeastern edge of the anticipated geographic range for prairie dogs, populations occupied <1% of available land, and were declining (Lomolino and Smith 2001).

Perhaps the best approach to the unrestrained expansion question (given that the availability of a time machine remains unlikely) is to examine reclaimed reference areas, where larger animal grazing has been moderated, but active prairie dog poisoning has been withheld. On Wind Cave National Park in western South Dakota, approximately 10,000 hectares of bison range have had no timber cover through the last 50 years, so therefore have been accessible to prairie dogs (Rice 1993). That grassland has been occupied by an average of 1 bison per 20 hectares, on a year-round basis. Chemical control of prairie dogs was confined to the park and monument boundaries, and then only as necessary to keep prairie dogs from emigrating to adjacent private land. At Wind Cave during this extended period, prairie dog populations have varied to cover between just 3 to 8 percent of their available rangeland. However, even there, argument has existed over the extent and need for prairie dog control, with Hoogland et al. (1987) expressing that the town that they had observed for 14 years had not changed its boundaries, but Klukas (1987) arguing in the same publication that active control needed to become frequent.

On Badlands National Park in South Dakota, 400 to 800 bison (with a preferred maximum of 500) graze 17,000 hectares of the park, essentially all of which is available to prairie dogs (John Donaldson, Chief Ranger, 1993, personal communication). Counts of prairie dogs from 1929 to the present indicate that they have stabilized, over the long term, at an average landscape coverage of 10 percent.

These long-term in-practice experiments underline the observation that prairie dog towns are limited either to short-grass prairies created by natural soil and climatic conditions, or to where heavy grazing by larger animals has shortened other species of vegetation (e.g., on mixed prairies) (Whicker and Detling 1988a). It is heavy grazing by other species within or at the perimeter of prairie dog towns that creates the conditions (e.g., suppression of cover favoring predators) that can allow those towns to expand more widely, especially

during drought years (Osborn and Allen 1949; Uresk et al. 1981; Uresk and Bjugstad 1983). These expansions can be reversible if livestock reductions are sustained (Snell 1985), as the experience on the parks cited above suggests.

A significant relationship has been established for area of perturbation by burrowing animals and the longevity of the consequent patches in the landscape, with an exponent close to the allometric scaling factor for mammalian processes related to body size (Whitford and Kay 1999). Thus, the bigger colonies are not only more visible at the time they are most active, but likely to be for longer afterwards. However, the nutrient cycling, buried seeds, water collection, and soil structural changes from burrower activity can all be beneficial for general productivity both at the time of activity and later (Whitford and Kay 1999). Human impatience and observational oversimplification can become inappropriate factors during evaluations.

Potential limits on expansion of prairie dog populations also are tied to the presence of their natural predators, and not just to restraints on the stocking of larger grazers on the same land area (Koford 1958). Both of these conditions generally exist in the self-limiting populations cited above, with predators typically given freer rein on public than private land, although several naturally-adapted predators (e.g., black footed ferrets and wolves) are currently still generally absent. Hunting, pet collection, and other direct human utilization of prairie dogs may substitute for some natural predation, but it would require quite intensive management for people to match the growth-checking efficiency of these potentially prolific breeders' co-evolved enemies.

Wider-Reaching Considerations

As long as plants remain where they grow, the nutrients they remove from the soil are for the most part returned there when they die. Grazing, however, can have an impact on soil fertility, if the plant-withdrawn nitrogen is removed from the growing site and taken to further distances by the grazers (or their predators, including humans). This generalized loss may be balanced by an increased local nitrogen return if those animals concentrate on dog towns, because excreted nitrogen tends to be deposited in proportion to the time spent in any particular location. Although experimental data have failed thus far to prove this logically-likely possibility, they have also failed to disprove it (Woodmansee 1981). What has been shown clearly is that the lower standing cover on prairie dog towns increases soil temperatures by roughly 2.5° C, which should increase nitrogen mineralization rates. This, in turn, should speed this nutrient's availability to plants, which also would assist in what has already been proven to be their increased aboveground nitrogen production (Holland and Detling 1990).

Small mammals often aid in seed and spore dispersal, especially of the mycorrhizal fungi that can be critical to mature plant nutrient uptake rates, heightened success in seedling establishment, and the consequent diversity of plant stands (Sieg 1987). Even the 'wasted' material cut, but not consumed, by prairie dogs for protection from predators may be beneficial to soil fertility because this material moved to the soil surface deteriorates faster, and thus cycles available nutrients, than the portions that are left standing. Reduction in particle size by chewing activity even more sharply augments plant decomposition rates.

In addition, small mammal mounds can have lower soil bulk density, with its consequent increased permeability, and thereby serve to store more water below ground, away from evaporative or runoff losses, and thus available for later use by neighboring plants (Mollison 1991).

It is commonly assumed that rodent mounds should be detrimental to soil stability. However, no direct evidence has been found that, at least in natural situations, burrowing or grazing activity by small mammals added measurably to more general soil erosion rates (Koford 1958). Localized increases in runoff from the bare portions of mounds may be compensated for by increased soil-nutrient absorption within plant growth which occurs in rings around those mounds (Uresk 1992). That local augmentation, in turn, seems likely to be sustained by fertilization from washed-down fecal material that prairie carry dogs out of their burrows onto the mound surface, together with the increased water availability created by runoff from the mounds.

Prairie dog towns have been confirmed to favor the presence of insectivorous rodent species (i.e., mice and voles), which may reduce outbreaks of such insect groups as beetles, grasshoppers, flies, moths, millipedes, centipedes, and mites (Agnew et al. 1987). An enhanced presence of insect consumers on prairie dog areas has not commonly received comment, but, especially in a diversity context (Fig. 1), this factor needs specific attention, since insects can be greater competitors for forage for livestock (and crops) than any other animal form. The latter point can become especially important because serious insect outbreaks tend to be correlated with system-wide stresses, such as below average precipitation, which already limit the forage available to larger grazers, and make nearby agricultural crops particularly vulnerable.

Among the many possibly unexpected consumers of insects, whose additive effects could be quite considerable, swift fox (*Vulpes velox*) diets have been observed to include more than 25% insects by weight (Uresk and Sharps 1986). Another group, burrowing owls (*Speotyto cunicularia*), which live in prairie dog-built tunnels, also primarily consumed insects (MacCracken et al. 1985). As active hunters, these predators should selectively destroy the larger insect consumers of plants. Similarly, burrows serve as a source of cover for rodent consumers such as owls, weasels, ferrets, and snakes (Clark et al. 1982). These could be expected to reduce excessive small mammal populations in the less-protected adjacent ecosystem(s), including particularly susceptible agriculture.

From such considerations as these, it may become more apparent why, even in the short term, prairie dogs' indirect alterations to ecosystem-level productive capacity might begin to compensate for any direct competitive effects they may have with livestock (Fig. 1). Over longer periods, the prairie dogs' nutrient cycling and soil structure activities bring deeper materials up during their burrowing, and mix soil of all levels, which few, if any, other species can do as effectively (Koford 1958). Their burrowing and clipping also allow additional plant and animal species to flourish (each with its own role in both in macro- and micronutrient availability), a consequence that may have virtues which are important to the eventual growth patterns of the most desirable grasses and forbs for livestock and for such large native grazers as bison and pronghorn.

Biodiversity And Other Longer-Term Functions

The question of whether or not there are “keystone” species among ecosystems lies amidst the more general issue of the importance of biological variety across the landscape. Many logical indicators point towards the beneficial effects of an increase in species diversity, including raising primary and secondary production across varying physical conditions. These augmentations can stem from differing general adaptations and/or positive feedbacks during the processing and transfer of resources (Fig. 1). A single species could well become central in reaching the highest levels of localized efficiency by the same extrapolation, albeit for a limited, though possibly recurrent, period in a world of ever-shifting environmental conditions. Without that species, one would still find a functioning system, but not one operating with the throughput and damping stability that could exist with it present.

In the context of implications of diversity, dividing plants and animals into species is inherently an intellectual construct. These human-imposed subdivisions do not necessarily consider functional adaptations. These can be of extreme importance to a system’s response to external pressures, e.g., consistently shorter stature by a localized grass variant to allow evading grazing pressure from a dominant herbivore. Speciation, as contemporary science assigns it, is based on structural, molecular, and reproductive characteristics. These do not always tie to drought or insect resistance, responses to light or disease, or many of the other functionally critical internal attributes of organisms. Also important at the ecosystem level are the mutualistic character of activities, which may be behavioral as well as physiological, e.g., animal pollination of flowers and active burial of seed stocks.

Therefore, using species numbers alone as a measurement basis, as most biodiversity analyses do, can lead to a serious underestimation of useful complexity. Of course, species collection in almost all studies only considers those convenient to collect, e.g., larger and aboveground plants and animals. Others, from bacteria to microscopic fungi, as well as larger ones, all can be vital to ecosystem function.

The value of these factors, and others, in the system may not become evident for generations, eras, or even millennia. A pertinent example is the deep mixing of soil nutrients, and the soil aeration, which are a by-product of prairie dog burrowing, and whose effects widen as dog towns drift spatially over many years. Seen additively, these and similar supra-species and/or within-species characteristics are likely to add values to the overall system’s function that will extend well beyond those that might be expected simply from species numbers alone. What role these additional species, and their difficult-to-quantify adaptations, play in long-term productivity and stability could be the subject of interminable study by itself. At the least, however, they will facilitate energy, nutrient, and information flows by adding many parallel and interacting paths (Fig. 1).

The net influence of prairie dogs, as they function together with larger grazers, is to create and maintain islands of short grasses and forbs that have especially high rates of nutrient turnover and consequent availability in the midst of otherwise more homogeneous, taller, grass-dominated stands. In South Dakota, this has had the practical result of concentrating at least 40% of all current wildlife species in and around prairie dog towns (Reading et al. 1989; Sharps and Benzon 1984). Colonies can be seen to act as “food stores and shopping malls” (Sharps 1994) for predators, because of the number of small mammals, birds, and

invertebrates that have been attracted to the especially productive conditions extant there (Clark et al. 1982; Agnew et al. 1986; Agnew et al. 1987). Among these are a longer effective growing season for most herbage consumed by prey species, an extended sight-line (as a result of prairie dog clipping activity), sheltering burrows, and, not negligibly, the year-round availability of the prairie dogs themselves as a food resource. In recent years, the most dramatic resident for the public eye has been the prairie dogs' obligate predator, the black-footed ferret (*Mustela nigripes*). A much longer list of semi-obligates e.g. swift fox, burrowing owl, mountain plover (*Eupoda montana*) and associate species (a variety of hawks, owls, eagles, ungulates, furbearers, reptiles, amphibians, and invertebrates) was provided by Sharps (1994).

An Example of a Possible Mechanism Yet To Be Studied

Most measurement patterns for the potential utility of biodiversity are such that their users have difficulty grasping how adding another consumer or consumers (e.g., prairie dogs and their ancillaries) to a seemingly already well-utilized system could possibly be an advantage, or be neutral in their effect. Changes in protein efficiency ratios may provide insight into the mechanism of how a reduction in the by-weight-measured availability of forage can still result in equivalent or superior growth in larger grazing animals. For this, the more-simply-measured total nitrogen levels in forages are part, but not all, of the nutrient intake-value story.

Essential amino acids must be present among nitrogen-containing molecules above a discrete minimum level, and in quite precise proportions to allow protein synthesis for animal tissue maintenance or growth. Unavoidably, if there is an individual chemical absence or imbalance among these amino acids at the exact time of protein assembly from its constituent nutrients, all related chain building within animal cells stops. Any partially finished proteins can then only be used for energy, or just discarded by the body, and their relatively nutrient-energy-intensive information and structural content will be lost.

Both overall digestibility and internal amino acid balance influence the practical availability of nitrogenous compounds for this critical chain building. As forage plants age during each year's growth cycle, first their useful amino acid balance and digestibility, then also their total nitrogen content, successively falls below the grazing animals' growth and maintenance requirements (Hughes et al. 1962). As a general principle, the newer the plant material, the more closely it approaches the amino acid balance requirements for animal tissue synthesis (Yorks 1976). Accordingly, when prairie dog activity maintains plants in a earlier growth stage, it should be providing both improved essential amino acid availability, and more appropriate ratios, at the point of use by grazing animals. The increased conversion efficiency of plant nutrients into muscle tissue that consequently should result from this would allow fewer pounds of this kind of forage to produce greater rates of gain among the animals that consume it.

Recently, it has been confirmed that mammals can sense these amino acid balances, and seek out more appropriate mixes (Hao et al. 2005). Unfortunately, studies that monitor grazing selectivity tend to not to extend to more nutritionally stressed seasons (e.g., Guenther and Detling 2003).

This potential change in efficiency would be especially important to livestock in the late summer and fall, and to year round grazers whenever temperatures were appropriate directly or below snow. Prairie dogs continually keep plants in younger growth phases, or shifted to species with a higher nitrogen content, and therefore may provide a balancing nutrient availability during the period when off-dog-town forages would have matured past the point of adequate protein availability for their most effective dietary utilization. Not only should this earlier-growth-stage, late-season forage eaten by livestock in places where prairie dogs are active be more constructive for herbivore growth, but it could also increase the value of lower-nitrogen forage consumed within a few hours on neighboring areas by mixing it during the digestion process with the higher-quality dog-town material. It would thereby serve a similar, and likely superior, function as artificially-supplied protein supplements that are utilized, at considerable expense, in other ranching situations. The experimental measures of animal activity and growth that were cited previously may result, in part, from these possibilities.

Through mechanisms such as protein efficiency, Buckminster Fuller's often-cited adage of doing more with less can apply to diversity in ecosystem function, and to the consequent economic utility of such diversity. Testing by weighing cattle as they are put onto and off ranges, more effectively tracking nutritional quality and its probable advantages, would be a considerable step forward in making grazing assessments from simply multiplying the number of animals by the time they spend on the range, as is now most commonly done. Paralleling those field tests with analyses of amino acid presence could tell yet more.

Integrative Production

Related to the potential advantages created by prairie dogs, however, is a cautionary and stringent need to keep livestock stocking rates well below the traditional "take half, leave half" consumption pattern. Additional amino acids produced through a longer effective growing season, especially by more complicated or thorough animal use patterns, may well augment plant stress levels. However, suggesting reduced stocking rates to balance potential pressures on plant survival margins was not a grazing management strategy deduced for the needs of multiple use alone.

Friedman and Elberse (1976) and Caldwell (1984) argue that the rate of removal of plant leaves during drought years may be the most important factor in the ability of plants to compete within a community [drought in this context is defined as either a year whose precipitation is 25% or more below the long-term mean, or two years in a row with less than average moisture]. Malechek (1984) underlines the importance of threshold effects, where system-level collapses can occur unpredictably as a result of stress, while Box (1984) found that when drought (and arrival timing) is fully considered, long-term peak sustainable use will occur at a lower average utilization rate than that which in the past was considered most appropriate for average or better precipitation years. Holechek (1991) established from a 20 year study in New Mexico that a maximum of 30% utilization of plant material by livestock gave more satisfactory overall returns than did higher rates of use.

There are, of course, many other factors involved in effective livestock management, including seasonal timing and precise location of use. However, especially when considering the reality of ranch management, where herd sizes and stocking densities may not be quickly

changed in response to conditions, and seasonal weather is not predictable in advance, it is not surprising that the Bureau of Indian Affairs (1994), from historical experience in prairie dog country concluded that when livestock use rates have exceed 25% of the long-term average forage production, range deterioration has resulted.

Within appropriate constraints on total use, balancing grazing pressure among larger animals with differing preferences should logically result in a more stable long-term system, since no single use pattern will be pursued consistently. The caveat is that excessive pressure by multiple species can do more serious damage than any one species alone. A single user will find at least one type of plant distasteful, which can then, even when there is serious abuse, retain some soil holding capability. However, when the many preferences of a diverse group of grazers are left unrestrained, they can indeed truly denude, for nothing may be spared (J.D. Rodgers 1987, University of Wyoming, personal communication).

Nevertheless, the necessarily increased supervision needed for multiple grazing species situations can be repaid by the economic advantage gained by having additional plant and animal types, beyond cattle or sheep and a few grasses, present on a given piece of rangeland. Centrally, as dominant species are more closely adapted to local climate and plant distributions, their requisite management costs tend to fall accordingly (Yorks 1989). Not wholly coincidentally, there are aesthetic, as well as ecological, advantages to such a more complex system.

North America's larger native ungulates are coming to have a particularly high value to landowners, through both hunting leases and other uses (Hudson et al. 1989; White 1987). In the present context, these potential values can be more readily realized when coupled with the attractiveness of the balance provided by prairie dog towns among available plant growth forms for such species as elk, antelope, and bison. Additionally, the fur from carefully limited harvests of predators such as coyote and badger, whose presence is essential to successful prairie dog control, and the feathers of others, could contribute substantially to the profits of a thoughtfully managed ranch operation. It has often seemed counterintuitive, but carefully restrained harvests of species, including predators, whose ranges are now limited, can allow increased numbers of them to exist. In other words, population losses from hunts can be more than balanced by the encouragement for these animals, especially in the form of habitat availability and watchfulness for poachers) that is derived from the economic returns from those limited harvests. Given our world's limited land area, and the intense, increasing competition for its use, animals whose value is seen as higher by owners will always displace other, apparently less profitable species (Yorks and Capels 1988). Thus, bison are now returning on private land on America's prairies, and other native life-forms may follow them.

The direct benefits of shared-species land use may be augmented dramatically if value-added, employment-generating practices such as final processing of resident animals into meat, fur, and art (e.g., from antlers and bone) are also considered, especially when these activities are carried out nearby, with adequate visitor housing. Among other things, fewer people will pay to see a cow than a prairie dog or an antelope, especially in the latter's substantially native environment. These related, auxiliary use possibilities have special importance for the areas where prairie dogs are adapted, both because of their isolated, rural, plains landscape character, and the otherwise presently limited economic chances for

the human residents there. This is particularly true for localities on many Native American reservations, which have such historically high rates of unemployment.

In Conclusion

Figure 1 summarizes some of the general considerations that might be most useful in interpreting what prairie dogs mean for ever-changing ecological and human interest perspectives, which will be different for every location according to the considerations partially expressed in Figure 2. The imaginary slider on the right side of Figure 1 indicates direction, the colors, human and ecological value, while the arrows pick up some primary active vectors, which are at least partially under human control, but except for the central pair, mediated by prairie dogs. Figure 5 suggests how scientists and others might look more objectively at the various and necessarily selective studies that have been or might be conducted. All such characteristics will vary with scale, a point too seldom appreciated, and problems that might be concluded for smaller areas may balance out for larger ones.

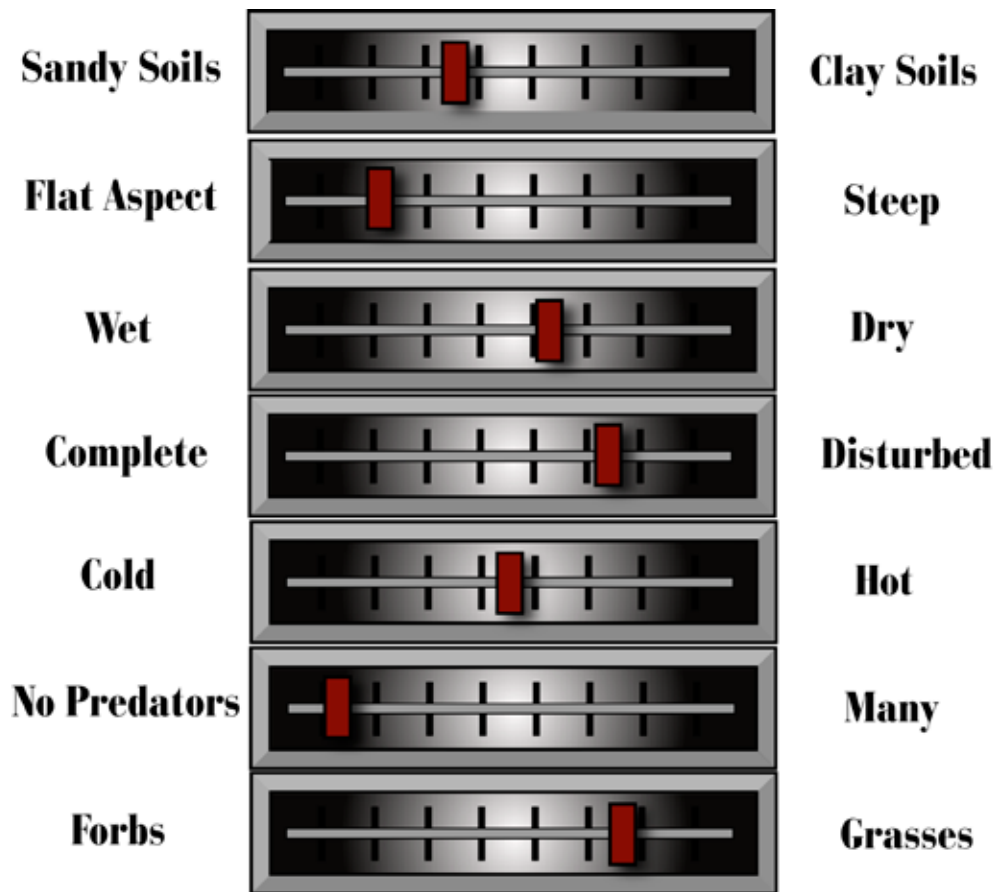


Figure 5. Visualizing possible controls on the likelihood of prairie dog community size and growth. This suggestion, based on a sound recording equalizer and set a possible optimum, represents only a few of the possibilities, but lends a way to approach relationships and evaluate how studies past and present may be better appreciated and designed.

Useful net productivity may be defined differently for ecosystems and for humans, who

typically wish to export nutrients away from fields and ranches. For the latter, it seems most unwise to overlook either the mechanisms or the specifics of profit opportunities in a time of heavy economic pressure on agriculturally related enterprises. For land managers, practical and profitable acceptance of carefully limited multiple-species land use and harvests, which seem likely to be more easily compatible with prairie dogs, would seem a splendid place to seek augmentation. From both the urban perspective and that of ranchers, maintaining and/or enhancing positive feedback links in a complex chain, and emphasizing the values in each, should be eminently satisfying at all levels of analysis.

Prairie dogs have been considered a scourge on the prairie by many, if not most, landowners during the past hundred years. When re-examined within a context of moderation of other land use pressures, and especially in combination with creativity in multiple species growth, harvests, and value-added processing, they may instead reflect their long-term benefit for soil development in more short-term, year-to-year returns from rangelands. With proper restraint in larger grazing animal stocking rates, prairie dog activity could be adding to, rather than reducing, red meat production and other outputs of economic value, while maintaining a vital wildlife and plant function reservoir.

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