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Prairie Dog Overpopulation: Value Judgement or Ecological Reality?

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Abstract.--The subject of prairie dog (Cynomys ludovicianus) overpopulation is complex, and judgements of overpopulation may not be based on prairie dog population size or density. Caughley's (1981) model of animal overpopulation is applied here to prairie dogs to clarify the basis for a judgement of overpopulation in each of several cases. There are ecological components to all such cases, but a purely ecological judgement of overpopulation requires much more information than is currently available. However, defensible management of prairie dog systems is a goal, and time-honored but flawed assumptions are never an adequate substitute for results derived from thorough, scientific studies of prairie dog systems as a basis for management actions.

INTRODUCTION

A general model delineating four classes of overpopulation was proposed by Caughley (1981) to clarify the ecological and nonecological values upon which judgements of overpopulation are based. In this paper I use Caughley's model as a framework for a discussion of prairie dog (Cynomys ludovicianus) overpopulation, within which I evaluate the reasons for such judgements in each of several cases. A purely ecological (class 4) judgement of overpopulation applies where prairie dogs cause a change in the typical dynamics and interactions of the plant-animal-soil system, and its structural and functional properties, to the extent that the system approaches or exceeds its boundaries, and is significantly altered from its initial condition. While all classes of overpopulation involve some ecological components, the three remaining classes subsume conflicts where the primary values (e.g., social and economic values) responsible for a judgement of overpopulation are nonecological.

CONFLICTS WITH HUMAN INTERESTS: CLASS 1 OVERPOPULATION

Socio-economic values associated with human interests, such as the maintenance of public

health or healthy rangelands, dominate the public attitude toward prairie dog management. The two most frequently cited problems, plague (Yersinia pestis) transmission and competition with livestock for forage, have questionable significance based on available data. The human cases resulting from plague are so few as to be of no direct ecological consequence. [For example, 3.8% of 105 human plague cases in the United States, 1974-1980, were associated epidemiologically with C. gunnisoni and none with C. ludovicianus (Barnes 1982).] Prairie dogs are extremely susceptible to plague, and outbreaks among them are self-limiting (Barnes 1982). Prairie dog mortality typically exceeds 99% during plague epizootics (Cully 1986, Barnes 1982), after which the disease recedes or moves on, and normally does not regenerate for several years (Barnes 1982).

Recent evidence (Barnes 1982, Quan 1981) indicates that humans must go out of their way to contract plague from prairie dogs. Humans are thought to be incidental to the rodent-to-flea plague cycle because "ample exposure" to the disease during large-scale outbreaks among rodents in 1976 in Colorado produced no human cases (Quan 1981). Plague acquired from prairie dog sources normally results from direct contact with an infected animal rather than the bite of a prairie dog plague flea (Opisocrostis spp.), since the fleas rarely bite humans (Barnes 1982). In addition, the Plague Division of the Center for Disease Control currently has no evidence of prairie dog transmission of plague to livestock (Quan, pers. commun.).

Despite this evidence, the social value of a plague-free human population is undeniable, and prairie dogs are viewed as a threat in the

western and southwestern states, where plague is endemic. However, judgements of overpopulation that are tied to this social value have no ecological basis, and prairie dog population sizes or densities may be largely irrelevant.

On rangelands, economic values seem to be the basis of overpopulation judgements because prairie dogs are viewed as competitors of livestock for forage. While this competition claim (Merriam 1902) is almost as old as ecology itself, it is unsupported by the empirical evidence. Recent examinations of the assumptions, methods, and results of animal competition studies have discredited conclusions asserting the presence and importance of competition in nature (Wiens 1977; Connell 1980, 1983; Strong 1983). These developments have important implications for the prairie dog-livestock conflict. Evidence such as simple prairie dog diet studies (see Fagerstone 1982) or studies of diet similarity or ecological overlap between prairie dogs and livestock (e.g., Hansen and Gold 1977) is now regarded as inadequate to demonstrate competition. More rigorous data are required. For example, a fundamental question where competition is suspected is whether or not the particular plant-animal-soil system shows stable population dynamics or whether unpredictable fluctuations are characteristic. Competition is expected more often under stable, equilibrial conditions where populations fluctuate in a density-dependent manner and where the food resource, in this case, is limiting. In such a system a negative interaction must be demonstrated among putative competitors. In addition, data must be obtained on spatio-temporal scales appropriate to the system and the question. Even when all these conditions are satisfied, competition may act only intermittently due to natural fluctuations in both biotic and abiotic components of the system. Thus, it is no simple matter to gather adequate data to convincingly demonstrate competition.

No such data exist for any prairie dog-livestock system, but O'Meilia et al. (1982) and Uresk and Bjugstad (1983) have addressed the interaction question with controlled field experiments. Their results suggest that prairie dog-livestock competition did not occur during their studies. For example, Uresk and Bjugstad (1983) reported higher peak standing crop on prairie dog-only than cattle-only treatments, and also that cattle plus prairie dog treatments had a higher peak standing crop than cattle-only treatments. This indicated that prairie dogs were not responsible for limiting cattle food supplies. Furthermore, O'Meilia et al. (1982) reported no significant differences in steer weight gain in pastures with and without prairie dog grazing, despite reduced herbage availability in pastures containing prairie dogs.

In fact, field experiments (Krueger 1986) and simulation modeling (Vanderhye 1985) have shown mutualistic interactions between prairie dogs and another large ruminant [bison (<u>Bison bison</u>)] and suggest the potential for a positive relationship between prairie dogs and cattle under certain spatio-temporal and habitat conditions.

Clearly, the direct and indirect effects of prairie dogs on livestock are not uniformly negative and could be positive in some situations. However, the potential for competitive interactions cannot be dismissed because previous results have been inconclusive, and may be especially great where livestock are maintained at unstably high densities for protracted periods, under spatially restricted conditions.

From the evidence reviewed above, judgements of overpopulation in cases of prairie dog-livestock conflicts do not appear to be examples of actual or potential class 4 ecological problems. Here, prairie dogs are assumed to be responsible for decreased revenues, but the assumption is unsupported. Although O'Meilia et al. (1982) indicated that the market value of steers grown on pastures with prairie dogs was somewhat less than that of steers grown on pastures without prairie dogs in their study, this conclusion stems from a logical flaw in their analysis. Their major result of no significant differences in weight gains between steers on pastures with and without prairie dogs showed differences in steer weights between the two groups to be statistically indistinguishable. Consequently, it is inappropriate to discuss the two groups as distinct, in market value or other comparisons. The unsupported assumption that prairie dogs are responsible for decreased revenues is itself based on prior unsupported ecological assumptions related to competition, although the potential for economic losses due to competition is certainly real, and the potential for competition sometimes high. As in the case of prairie dogs and plague, prairie dog population sizes or densities may be unrelated to economically motivated but ecologically unsupported judgements of overpopulation in prairie dog-livestock interactions, based on current evidence.

REDUCTION OF PREFERRED SPECIES:
CLASS 2 OVERPOPULATION

Class 2 overpopulation applies where prairie dogs reduce densities of their plant and animal associates preferred by man, especially livestock forage species. Although this is an example of an indirect class 1 problem, it is directly a class 2 concern and therefore addressed here.

Recent studies have reported significant declines in the number of perennial species on prairie dog towns (Lerwidk 1974) and in the grass:forb ratio on portions of dog towns (Bonham and Lerwick 1976, Coppock et al. 1983, Krueger 1986), under combined ungulate-prairie dog grazing. Uresk and Bjugstad (1983) reported a slight (6%) decline in grass production on a prairie dog versus cattle grazing treatment. In

addition, Agnew et al. (1986) found fewer small rodent species on prairie dog towns than on undisturbed mixed-grass prairie, and concluded that prairie dog activities negatively affect rodents associated with the dense vegetation of uncolonized mixed-grass prairie.

In contrast, a number of studies have reported enhancement of prairie dog associates, including increases in plant cover, density (Uresk and Bjugstad 1983, Koford 1958, Bonham and Lerwick 1976), species diversity (Coppock et al. 1983, Bonham and Lerwick 1976), forage nitrogen concentration (Coppock et al. 1983, Krueger 1986) and digestibility (Coppock et al. 1983). Some animal species also show a positive response to prairie dogs. For example, Agnew et al. (1986) found increased densities of deer mice (Peromyscus maniculatus), grasshopper mice (Onychomys leucogaster), and bird densities and diversities on prairie dog towns. O'Meilia et al. (1982) reported increased small mammal and arthropod biomass on dog towns. Clark et al. (1982), Hansen and Gold (1977), and Uresk and Bjugstad (1983) found that prairie dogs improved habitat for any animals that are benefited by holes or short or sparse vegetation, such as burrowing owls (Athene cunicularia) and other birds, desert cottontails (Sylvilagus audubonii), rattlesnakes (Crotalis viridis), and other prairie dog predators.

While the depression or enhancement of preferred prairie dog associates can involve complex ecological interactions, these changes have not been shown to constitute class 4 problems. Nor are the changes uniformly negative. Judgements of class 2 overpopulation seem motivated by conflicts of economic values with putative monetary losses presumed due to prairie dog preemption of livestock forage. Like prairie dog-livestock competition, there is still no direct evidence to verify the assumption that where prairie dogs reduce the densities of livestock forage species, these reductions negatively affect lifestock or cause decreased revenues. The potential for negative ecological and economic effects from prairie dog reductions of livestock forage species is certainly real, and especially large where pasture size is limited and livestock densities maintained at high levels over protracted periods. However, without the necessary ecological evidence, class 2 economic judgements will continue to be based on unsupported economic and ecological assumptions. Prairie dog densities or numbers may again be largely irrelevant.

"FOR THEIR OWN GOOD": CLASS 3 OVERPOPULATION

No examples of the class 3 argument, that prairie dogs harm themselves by being too numerous or densely populated for their own good, have been reported. A class 3 argument would likely be invoked only where prairie dogs enjoy "protected" status, as in a national park or privately owned nature preserve.

In the absence of sufficient scientific study, and where population levels were presumed high, density-dependent effects such as rodent stress syndrome (Vaughan 1978) could be invoked to support the argument that individual prairie dogs were suffering from overpopulation. It is unknown whether prairie dogs are susceptible to stress syndrome, but considerable evidence suggests that some rodent species possess population self-regulatory mechanisms involving density-tolerant aggressive genotypes and density-intolerant dispersing genotypes (Vaughan 1978). In theory, prairie dog populations with these genotypes would be capable of density self-regulation and could potentially avoid the negative effects of rodent stress syndrome. Another argument, that of high ectoparasite load per individual (Hoogland 1979, 1981), could also be invoked to support a class 3 claim, but its ecological correlate, namely decreased predation risk per individual, compensates for negative effects of ectoparasites in prairie dogs (Hoogland 1981).

Thus, there is no current evidence to show that prairie dogs suffer as a direct result of high numbers or densities of conspecifics. Further study is needed to determine whether and when class 3 overpopulation applies to prairie dogs.

POTENTIAL ECOLOGICAL CRISIS: CLASS 4 OVERPOPULATION

A case of class 4 overpopulation will likely have socio-economic and political ramifications, but the judgement itself is based on purely ecological considerations. A class 4 judgement applies where prairie dog numbers or densities cause a change in the typical dynamics and interactions, and the structural and functional properties of the system, to the extent that the system approaches or exceeds its boundaries and is significantly altered from its initial condition. The information needed to define cases of class 4 overpopulation thus includes a knowledge of typical population dynamics and interactions of system components and how they vary, the location and character of system boundaries, and their relation to increases in prairie dog numbers and densities. None of this information is currently available for any prairie dog system.

Nonetheless, some theoretical possibilities exist. First, prairie dog populations may exhibit point or oscillatory equilibrial dynamics, at one or more stable levels, or their population densities might fluctuate in a stochastic manner (fig. 1) (Caughley 1981, Noy-Meir 1975, May and Beddington 1981, Sinclair 1981). Interactions among system components, such as plants and herbivores, may be tightly coupled and stable (fig. 2), unstable, or loosely coupled
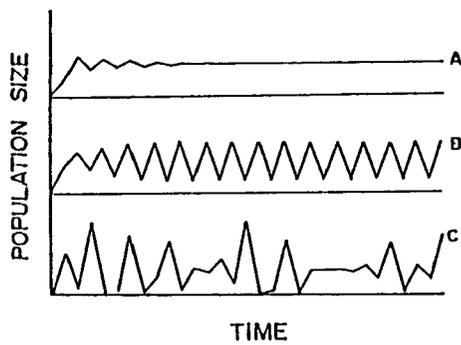
Figure 1.-- Types of population dynamics: (A) stable point equilibrium, (B) stable cycle; (C) chaotic flux (adapted from May 1981).

(Caughley 1981, May and Beddington 1981, Noy-Meir 1981, Sinclair 1981). Populations of plants and animals may fluctuate stably within system boundaries (fig. 3a) or above (fig. 3b) or below these thresholds (Noy-Meir 1981, Sinclair 1981). An upswing in prairie dog population densities or numbers may push the system to a breakpoint (May 1977) [perhaps a common occurrence in vegetation-herbivore systems (Noy-Meir 1981) and especially anticipated if prairie dogs were an ecological keystone species], beyond which the system either cannot return to its ground state (May and Beddington 1981, Walker 1981), or can return only with significant external input. If the system bounds are not exceeded, the components of the system would be expected to recede over time to equilibrium levels or to levels of stochastic flux within the original system boundaries. Alternatively, if the system bounds are exceeded due to a prairie dog population upswing, the structural and functional components of the original system are expected to shift to a condition that no longer constitutes the ground state. Rather, some alternate state is assumed. The system itself may contain several alternate states (fig. 4) (May and Beddington 1981,
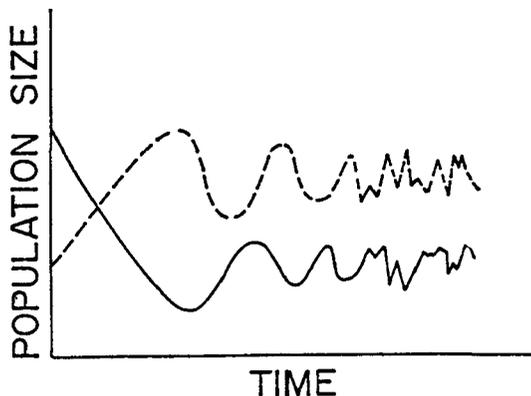

Figure 2.--Tightly coupled stable interaction between plant community (- - -) and herbivore population (———) (adapted from Sinclair 1981).
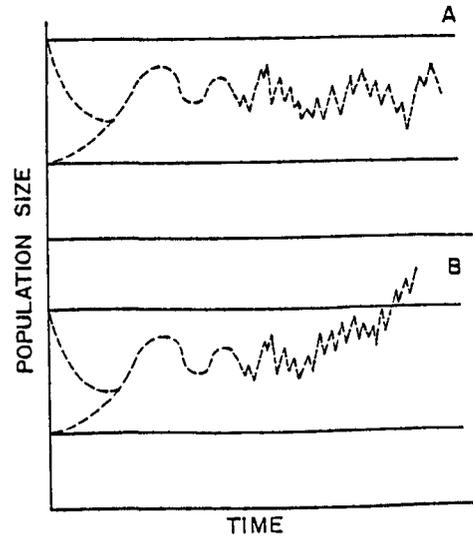

Figure 3.--(A) Region within which an herbivore population will return to the same equilibrium position; (B) herbivore population flux above upper threshold of system (adapted from Sinclair 1981).

Sinclair 1981) into which the shift may occur. Or the shift might be to a state outside the original system (fig. 5). Theorists speculate that these shifts will probably be deleterious, leaving the new system potentially irreversibly degraded (Noy-Meir 1981, May and Beddington 1981). Obviously, massive research efforts will have to be undertaken before class 4 overpopulation is understood for even one prairie dog system.

MANAGEMENT OF PRAIRIE DOG OVERPOPULATION

Although management of overpopulation will vary in each case according to the land-use goals and predominant values that have defined the type of overpopulation, the incorporation of ecologically defensible actions in management plans
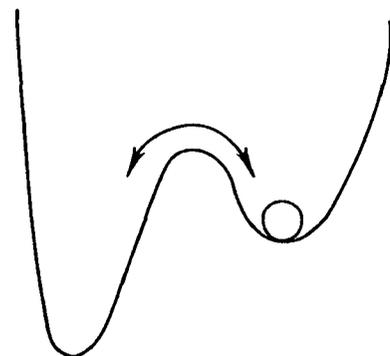

Figure 4.--Theoretical system containing two alternate states (after Noy-Meir 1975).
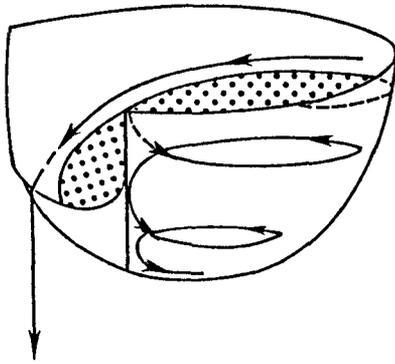
Figure 5.--Theoretical system undergoing shift to
   state outside original system, indicated by
   arrow leaving system domain (dish) (adpated
   from Holling 1973).

could enhance their success and facilitate the
achievement of land-use goals.

For example, in cases of class 1 and 2
overpopulation, where prairie dogs appear to be
in conflict with economic land-use goals, man-
agers need to determine whether prairie dogs are
actually causing economic problems by first
studying the relevant ecological interactions
closely. There is a critical need for correctly
executed and interpreted studies of putative
competition. Replicated field experiments at the
appropriate local scale (Wiens 1986) represent
the best way to demonstrate prairie dog-livestock
competition. Experimental results can then be
used to demonstrate related economic effects.
Where prairie dogs are not implicated in economic
and ecological declines, managers must suspect
livestock as major contributors to such declines
(Schenbeck 1986). Livestock densities are often
held at unstably high levels (Noy-Meir 1981),
which put the system at risk of long-term deteri-
orations, fluctuations or even state shifts.
Prairie dogs may simply amplify a preexisting
livestock-generated problem. Efforts to control
prairie dogs where livestock are the primary
offenders will not solve ecological problems and
may increase rather than ease the land user's
economic (Collins et al. 1984) and ecological
burdens. However, where prairie dogs or prairie
dogs and livestock are definitely responsible for
depressed yield and income or are pushing the
system toward its boundaries, prairie dogs must
be reduced in a cost-effective manner and live-
stock densities concurrently reduced as well
(Schenbeck 1986; see also Uresk et al. 1982,
Snell and Hlavachick 1980, Snell 1985). In this
way, long-term deteriorations or violent fluctua-
tions in the system are avoided, and economic and
ecological stability are promoted (Noy-Meir
1981).

In class 1 cases where plague is a concern,
the self-limiting nature and transmission charac-
teristics of the disease (Barnes 1982, Quan 1981)
support a hands-off management policy. Because

plague will come and go unpredictably through
prairie dog populations, and because prairie dog
populations themselves may have unpredictable
dynamics, the most ecologically and economically
sensible approach seems to be simply avoiding
contact with plague-infested populations and
plague-killed carcasses, rather than launching
expensive eradication campaigns against prairie
dogs or plague, since these campaigns normally
have limited, short-term success (e.g., Barnes et
al. 1972). However, where large human popula-
tions are in constant contact with plague-
infested prairie dogs, continuous plague eradica-
tion campaigns may be the only viable management
option given prevailing social values and
concerns.

In cases of class 2 overpopulation, managers
must first recognize that the inherently dynamic
nature of ecological systems will inevitably
result in some changes in the abundance of plant
and animal associates of prairie dogs. Local
extinction of some of these species might even
occur as a normal event (Sinclair 1981). In
general, reduction of a few plant species in an
array of food types does not constitute grounds
for a declaration of overabundance (Sinclair
1981). Furthermore, a "play-safe" policy that is
too conservative in its estimates of permissible
abundance for prairie dogs and their plant or
animal associates may encourage the loss of
resistant and resilient genotypes (Noy-Meir 1981)
among these species, as well as declines in
overall system resistance (Walker 1981). Where
prairie dog reduction of preferred species is
suspected, efforts similar to those required to
demonstrate competition will be needed to demon-
strate the role of prairie dogs in any such
reductions, and whether there are any significant
associated economic effects. As long as the
changes in densities of prairie dog associate
populations do not constitute prairie dog-induced
class 4 overpopulation, or have proven economic
significance, a management program that encour-
ages maintenance of resistant and resilient
genotypes and maintenance of system resistance is
preferable to economically (Collins et al. 1984)
and ecologically indefensible programs that
potentially endanger the system and bankrupt the
land owner over a period of years.

If class 3 overpopulation were demonstrated,
managers necessarily would have to reduce prairie
dog densities or numbers in accord with the
prevailing (social) value behind this type of
judgement, namely, the prevention of suffering
among prairie dogs.

Examples of class 4 overpopulation are
currently theoretical but have abundant socio-
economic and political implications for any cases
empirically demonstrated in the future. The
ecological consequences of a state shift caused
by class 4 overpopulation are manifold and poten-
tially long-lived, deleterious, and irreversible.
Management of class 4 cases will likely be
directed toward avoiding the potentially devas-
tating consequences of a state shift into an

irretrievably degraded system and may be accomplished by reductions of densities or overall numbers of prairie dogs or other species responsible for pushing the system toward its limits. The fact that some class 1 and class 2 cases exhibit elements of class 4 overpopulation emphasizes the need for research on prairie dog population dynamics, the interactive dynamics of the components of prairie dog systems, and the location of system-specific boundaries in relation to these dynamics and interactions. These results would help managers recognize whether and when an ecological crisis might actually be at hand and help distinguish class 4 situations from the more prevalent but less critical class 1 and class 2 cases.

Clearly, socio-economic values and assumptions that are disconnected from the ecological realities of prairie dog systems can be the basis for flawed and indefensible judgements of overpopulation, as well as costly errors in management. In management plans, long-accepted assumptions are not adequate substitutes for results from thorough studies of prairie dog systems. Managers must use the knowledge gained from such studies to simultaneously promote socio-economic and ecological values and defensible prairie dog management over the long run so that land-use goals can be achieved.

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