The Role of Prairie Dogs as a Keystone Species: Response to Stapp

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Introduction

Stapp (1998) recently argued that it was premature to characterize prairie dogs (*Cynomys* spp.) as keystone species. In particular, Stapp directed much of his criticism at a paper some of us wrote (Miller et al. 1994). He mistakenly interprets the main objective of our paper as providing evidence that prairie dogs are keystone species. Rather, the purpose of that paper was to outline an integrated strategy for conserving prairie dogs, and the theme was legal protection, habitat preservation, education, and economic incentives. It was presented in the context of prairie dog management policies having reduced grassland diversity. A discussion of the effect of prairie dogs on the ecosystem was, therefore, limited largely to an introductory paragraph. In this comment we address levels of knowledge about prairie dogs and prairie dogs as a keystone species.

Levels of Knowledge about Prairie Dogs

Deciding when data are sufficient for action can be contentious because personal values play a large role. For example, biologists evaluate the validity of experiments by quantifying statistical probabilities of error. Yet agency managers often need to act when data do not yet meet the standards for publication in scientific journals. Recognizing that lost resources are often irreplaceable, we advocate erring on the side of nature until experiments resolve the uncertainty (Noss & Cooperrider 1994). This is an important point when management actions such as poisoning of prairie dogs are being considered.

At the start of this century there were an estimated 40,000,000 ha of prairie dog habitat; by 1960, that had been reduced to 600,000 ha (Marsh 1984), a decline of 98.5% in 60 years. The factors involved in that decline are still in force (Biodiversity Legal Fund et al. 1998; National Wildlife Federation 1998). When threats of plague and poisoning are assessed, the individual prairie dog is not the independent unit because it is likely that those factors act on the entire colony, which increases the potential for disaster.

So we should not let uncertainty paralyze action. It is always easy to call for more data, but after a certain point this can stonewall efforts. We argue that we must act in the face of uncertainty, using the best information available while striving to increase knowledge and understanding. In our opinion, we already know enough to improve prairie dog management practices, which still include poisoning, unrestricted shooting, and a single-species focus.

But science is not the only factor that influences policy. Any practical application of knowledge to decisions involves personalities, politics, economics, attitudes of managers and stakeholders, fear of conflict, resistance to changes in policy, bureaucratic culture, prevailing myths, administrative procedures, and more (Clark 1997). We should not fall into the trap of thinking that more knowledge will automat-

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(Coppock et al. 1983; Detling & Whicker 1988; Whicker & Detling 1988, 1993; Detling 1998). Stapp (1998) did not contest this and stated that "Numerous studies have demonstrated that prairie dogs can have large and significant effects on plant productivity, community dynamics, and nutrient cycling (Whicker & Detling 1988), and in this regard alone, one could argue that prairie dogs play important if not keystone roles in many prairie ecosystems."

Of note is a recent paper documenting that mesquite (*Prosopis* spp.) spread from 27% of the ground cover to 61% of the cover in the first 23 years after prairie dogs were removed from an area in Texas (Weltzin et al. 1997). Similarly, List (1997) documented that mesquite advanced 1450 m from the edge of a poisoned prairie dog colony in Chihuahua, Mexico, covering 14% (683 ha) of the former colony during an 8-year period.

In addition, aboveground prairie dog grazing facilitates belowground herbivory, and on the prairie much of the energy flow occurs belowground (Ingham & Detling 1984). To this end, prairie dog colonies support higher numbers of nematodes and higher levels of soil nitrogen (Ingham & Detling 1984). This gives plants a higher nutritional content, higher digestibility, and a greater ratio of live plants to dead plants, and those changes play a role in creating favorable feeding habitat for other herbivores (Whicker & Detling 1993).

Prairie dogs remove roughly 225 kg of soil per burrow system and, because burrow densities often range from 20–40 ha, that contributes greatly to soil turnover (Whicker & Detling 1993). Both the burrow and mound change soil chemistry, increase macroporosity of soil to allow deep penetration of precipitation, and increase the incorporation of organic materials into the soil (Munn 1993; Outwater 1996). The burrow system also provides a third dimension of available habitat structure in an otherwise two dimensional grassland.

The mosaic of vegetation structure, burrow system, higher and more stable prey abundance for predators (Goodrich & Buskirk 1998), and altered ecological processes (increased nitrogen content, succulence, and productivity) affect the patterns of species diversity for prairie plants and animals. For example, species like black-footed ferrets (*Mustela nigripes*), mountain plovers (*Charadrius montanus*), ferruginous hawks (*Buteo regalis*), deer mice (*Peromyscous maniculatus*), and forbs profit from prairie dog activities (Whicker & Detling 1993; Kotlier et al. 1999). On the other hand, species like mesquite and vertebrates associated with tall vegetation are limited by prairie dogs (Weltzin et al. 1997; Kotlier et al. 1999). This is an example of how prairie dogs can increase overall diversity across a landscape (sensu Paine 1966)

Number of Species Associated with Prairie Dogs

We have stated (Miller et al. 1994) that, based on published species lists, nearly 170 species rely on prairie dog colonies at some level for survival. In our effort to be brief, we chose our words poorly. This, however, was a minor point in the 1994 article, which was written to propose a management plan for prairie dogs. Indeed, the primary reference (Reading et al. 1989) explicitly recognized that some species were undoubtedly casual associates of prairie dog colonies and repeatedly stated the need to investigate their level of dependency.

A recent review of 206 vertebrate species seen on prairie dog colonies produced quantitative data indicating that 9 of the species depended on prairie dogs (Kotlier et al. 1999). Abundance data for an additional 20 species indicated the opportunistic use of prairie dog colonies, and abundance data for another 117 species was lacking on or off colonies, but their life history indicated that they could potentially benefit from prairie dog activities (Kotlier et al. 1999). We recognize the difficulty in assembling such a list, and we contend that it will be a useful tool to stimulate research. Over time the list will change as researchers uncover new information. For example, see a recent paper by Ceballos et al. (1999) for new information on small rodents that preferentially use prairie dog colonies in Mexico.

Conclusion

The prairie dog fits the definition of a keystone species by significantly affecting ecosystem structure, function, and composition, and the impact of prairie dogs is not wholly duplicated by any other species (Kotlier et al. 1999; see also resolutions from the Society for Conservation Biology [1994] and the American Society of Mammalogists [1998]). Stapp (1998) suggested that it is enough to protect the prairie dog for its own intrinsic value. We disagree. Although their intrinsic value is important, so is their effect on other species. As one example, it would be possible to protect viable numbers of prairie dogs without conserving sufficient prairie dog area to maintain a viable population of black-footed ferrets. A 1000-ha prairie dog complex could hold between 5,000 and 20,000 prairie dogs, yet a prairie dog complex of that size would hold only about 20 black-footed ferrets (Forrest et al. 1988). That is why the ecosystem effects are important.

In 1994 we proposed that by managing prairie dogs we could take a large step toward managing a system, because a keystone species has such a significant effect on the structure, function, and processes of an ecosystem. Although the effects of prairie dogs may vary across their geographic range, they still exist in a form that makes the 1994 statement logical. We hope that increased awareness and attention of the prairie dog's role will stimulate the financial and political support necessary for coordinated ecosystem research at dedicated plots across its range and permit them to survive long enough in ecologically meaningful populations for biologists to obtain these data.

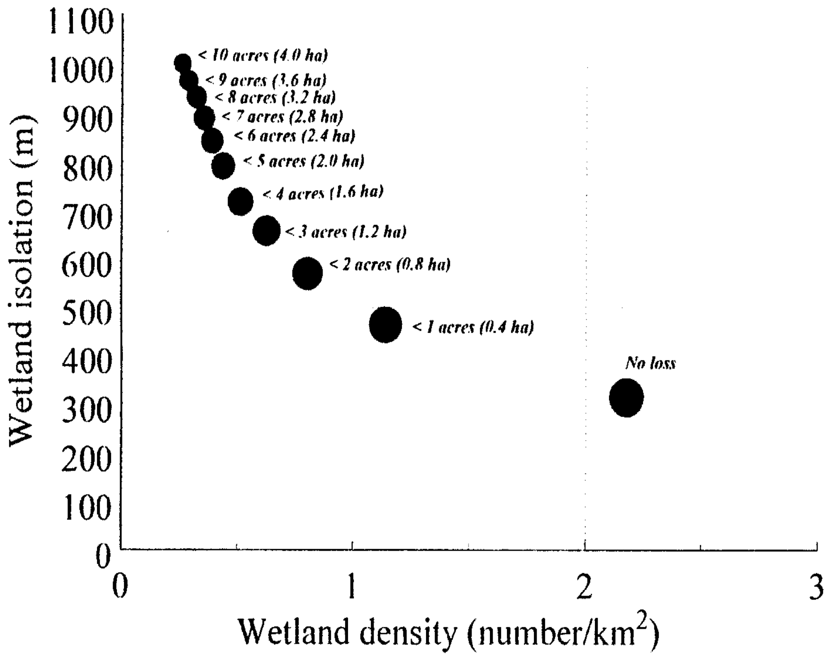

Figure 2. Changes in wetland density and isolation in relation to simulated, size-structured loss of wetlands in undisturbed landscapes in Maine. Points represent the metrics of wetland mosaics averaged across all landscapes sampled (n = 25), with sequentially larger size classes of wetlands removed (≤1, ≤2, ≤3, . . . ≤10 acres). Aggregate wetland area (percentage of landscape in wetland) is indicated by symbol size (smallest, 6%; largest, 7.5%).

NWI data reveal that substantial numbers of wetlands were overlooked by the interpreters of the aerial photographs used to delineate and map wetland mosaics (Stolt & Baker 1995). The problem is acute for small, forested wetlands, whereas larger and nonforested wetlands were detected reliably. Correction for this mapping bias, however, would likely accentuate rather diminish the differences observed between the scenario of complete wetland protection versus predicted losses of smaller wetlands (Fig. 2), whereas the remainder of the patterns detected would remain largely unchanged. Thus, the spatial analysis of wetland distributions I report indicates that wetland mosaics can absorb only modest losses and still retain wetland densities minimally sufficient to sustain the wetland biota. If conservation of wetland biodiversity is a goal of wetland protection programs, regulations used in nationwide wetlands permitting should be redesigned accordingly.

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ically improve policy. Indeed, one reason so many conservationists become frustrated with their work lies in the limited influence that reputable science actually plays in the policy process (Clark et al. 1994).

The Prairie Dog as a Keystone Species

A detailed analysis of whether prairie dogs are a keystone species should include a definition of the term Keystone, which Stapp (1998) did not provide. Without a guiding definition, the boundaries of any critic's statements are removed.

Keystone species influence ecosystem structure, composition, and function in a unique and significant manner through their activities, and the effect is disproportionate to their numerical abundance (Paine 1980; Mills et al. 1993; Power et al. 1996; Kotlier et al. 1997, 1999). In short, to be a keystone species prairie dogs must exert an effect, the effect must be larger than predicted by their abundance, and the effects should be unique (Kotlier et al. 1997, 1999).

Equivocal Results

In his essay, Stapp (1998) correctly noted that many prairie dog studies had produced equivocal results. We agree, but a number of methodological factors can influence such comparisons. First, in addition to experiments having been conducted in different grassland habitats (mentioned by Stapp [1998]), there are also ecological differences among the five species of prairie dog. Stapp, however, states that our (Miller et al. 1994) "argument for federal protection implicitly suggests that prairie dogs play similar roles in all grasslands in which they occur." We implied no such thing. We did suggest that prairie dogs have an effect across their range, but the quality and quantity of that effect varies from site to site. Federal protection does not mean cookbook ecological interpretations that are applied uniformly across the range.

Second, humans have caused great damage to the prairie dog ecosystem. Early in the century, when that ecosystem was relatively intact, there was little emphasis on understanding ecological effects. Instead, research focused on prairie dog eradication (Bell 1918, 1921). As a result of poisoning and an introduced plague bacterium (*Yersinia pestis*), the landscape mosaic of prairie dog colonies and off-colony grasslands has been destroyed, and we are left with only small and isolated colonies of prairie dogs.

Thus, recent research on prairie dogs has been limited to studying artifacts of what once existed. It is no surprise that different scales would influence results. It makes intuitive sense that a small and isolated prairie dog colony would have a different ecological effect than a series of large prairie dog complexes existing as a shifting mosaic within a landscape. One would expect a small and isolated colony to have a species composition more similar to that of the surrounding landscape simply because it would be overwhelmed by that landscape. Finally, looking at studies individually, as did Stapp (1998), does not reveal much about how prairie dogs affect biological integrity across the landscape (Kotlier et al. 1999).

To look at the ecosystem effects of prairie dogs experimentally requires establishing experimental plots across the range, dedicating the plots for a long period of time, coordinating methods and effort among sites, and procuring significant political and financial backing (Carpenter et al. 1995). These things have not yet been done; studies to date have not been coordinated for methodology or season.

Two studies from Mexico demonstrate how size of colony and location of plot can produce equivocal results. Manzano (1996) found higher avian species richness on prairie dog colonies than on grasslands (17 species to 11 species). In summer the larger prairie dog colonies showed a higher species richness of birds just inside the edge of a colony than in the center, whereas small colonies showed no difference between the edge and center (Manzano 1996). Similarly, a study of small mammals showed increasing richness, density, and diversity along a gradient from the center of large colonies to their periphery, and those measures peaked 200 m outside the colony boundary (Ceballos & Pacheco 1997; Pacheco 1999). The richness, density, and diversity of small mammals associated with prairie dog colonies (whether in the colony center, inside the edge, or within the first 200 m outside the border) were higher than on grasslands unoccupied by prairie dogs.

Location of plot is therefore an important source of variation. In particular, some plots that researchers had considered off-colony may have been affected by the proximity of the colony. For example, Agnew et al. (1988) placed their off-colony plots 200–1000 m from the colony, and O'Meilia et al. (1982) used 12 pastures (6 with prairie dogs and 6 control) that were each 2.5 ha in size and located within a 30-ha area.

Finally, research concentrated in one season can mask the temporal importance of a resource (Van Horne 1983). For example, avian species richness did not change seasonally on colony edges (Manzano 1996). In winter, however, grassland migrants arrived and species richness increased in colony centers (Manzano 1996).

Effects of Prairie Dogs on Ecosystem Composition, Structure, and Processes

The activities of prairie dogs substantially alter the grassland system they inhabit. The effects on associated species can be positive or negative, but together they create a landscape mosaic that promotes overall prairie diversity (Paine 1966).

For example, prairie dogs affect vegetation structure, productivity, nutrient cycling and ecosystem processes

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