A Critical Review of Assumptions About the Prairie Dog as a Keystone Species

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A Critical Review of Assumptions About the Prairie Dog as a Keystone Species

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ABSTRACT / Prairie dogs (*Cynomys* spp.) have been labeled as keystone species because of their influence on biological diversity and ecosystem function. However, the validity of several assumptions used to support keystone status is questionable. We review the strength of the evidence and the magnitude of the prairie dog's effects on ecosystem structure and function. We use this review to reevaluate the keystone role for prairie dogs. Our goal is to encourage sound management of the prairie dog ecosystem by improving the ecological foundation of their keystone status.

Our review confirms that prairie dogs affect a number of ecosystem-level functions but that their influence on prairie vertebrates may be less than previously suggested. Species richness and abundance patterns were variable among plants, mammals, and birds and were not consistently higher on prairie dog colonies compared to uncolonized areas. In addition, only nine of the 208 species listed in the literature as observed on or near prairie dogs colonies had quantitative evidence of dependence on prairie dogs. Abundance data indicated opportunistic use of colonies for an additional 20 species. A total of 117 species may have some relationship with prairie dogs, but we lacked sufficient data to evaluate the strength of this relationship. The remaining 62 species may be accidental or alien to the system.

Despite our conclusion that some prairie dog functions may be smaller than previously assumed, collectively these functions are quite large compared to other herbivores in the system. We suggest that prairie dogs also provide some unique functions not duplicated by any other species and that continued decline of prairie dogs may lead to a substantial erosion of biological diversity and landscape heterogeneity across prairie and shrub-steppe landscapes. Thus, we concur that keystone status for prairie dogs is appropriate and may aid conservation efforts that help protect species dependent on prairie dogs and support other important ecosystem functions.

The much maligned prairie dog has been the target of widespread eradication campaigns over the past century, largely as a consequence of their reputation as range and agricultural pests (Clark 1989). Sylvatic plague and habitat loss have also contributed to the estimated 98% population decline in prairie dog numbers (Marsh 1984, Anderson and others 1986, Miller and others 1990, Cully 1993). Particularly severe reductions of the Utah prairie dog (*Cynomys parvidens*) have prompted its listing as a federally threatened species.

Where prairie dogs still persist, they conspicuously alter prairie landscapes and provide foraging, shelter, and nesting habitat for a diverse array of species. Prairie dogs serve as prey for a number of predators including black-footed ferrets and prairie rattlesnakes (see Appendix 1 for scientific names). Their burrows provide nest sites and shelter for vertebrates such as tiger salamanders and burrowing owls, as well as for invertebrates. Prairie dogs alter plant species composition and vegetation structure (Whicker and Detling 1988), creating open habitats. They also can affect ecosystem processes such as disturbance and nutrient cycling rates (Whicker and Detling 1988).

Prairie dogs have been labeled a keystone species based on the assumption that they have a pronounced effect on biological diversity in prairie systems (Reading and others 1989, Miller and others 1994, Benedict and others 1996, Roemer and Forrest 1996, Weltzin and others 1997a, Wuerthner 1997). It has been argued that if we save prairie dogs, we save a key component of the prairie ecosystem that includes declining grassland species considered dependent upon prairie dog colonies for survival (Miller and others 1990, 1994). Thus, prairie dogs have been targeted as a conservation

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priority. Indeed, the black-tailed prairie dog (*C. ludovicianus*) was recently petitioned to receive candidate species status under the Endangered Species Act, based in part on its role in supporting numerous dependent species (Biodiversity Legal Foundation and Sharps 1994). This petition was denied, in part, because the petitioners' conclusions about the purported keystone role of prairie dogs in the prairie system were deemed equivocal (Gill 1995).

Prairie dogs clearly have an important role in grassland systems. It is our premise, however, that the magnitude of the prairie dog's role has been overstated in the literature. Here we review the evidence supporting the following assumptions that have been cited as evidence of their keystone role: (1) prairie dogs regulate ecosystems (Hansen and Gold 1977, O'Meilia and others 1982, Agnew and others 1986, Miller and others 1990); (2) passerine, small mammal, and predator abundance is higher at colonies (O'Meilia and others 1982, Clark and others 1982, Agnew and others 1986, Krueger 1986, Sharps and Uresk 1990, Reading and others 1989, Miller and others 1990, 1994); (3) species richness and diversity is higher at colonies (Hansen and Gold 1977, O'Meilia and others 1982, Agnew and other 1986, Clark and others 1982, Reading and others 1989, Sharps and Uresk 1990, Miller and others 1990, 1994); and (4) over 200 vertebrate species are associated with prairie dog colonies (Campbell and Clark 1981, Clark and others 1982, Reading and others 1989, Sharps and Uresk 1990, Biodiversity Legal Foundation and Sharps 1994, Miller and others 1990, 1994). We reviewed over 200 references on prairie dogs and associated taxa dating back as early as 1902. We focus on black-tailed prairie dogs because they are the most extensively studied and the most widely distributed of the prairie dog species, but also include evidence for Mexican prairie dog (*C. mexicanus*), white-tailed prairie dog (*C. leucurus*), Utah prairie dog, and Gunnison's prairie dog (*C. gunnisoni*).

Based on the strength of existing evidence, we then reevaluate whether prairie dogs function as a keystone species. We use Paine's (1969) original definition of keystone species, which reflects species whose activities greatly influence the composition, integrity, and functioning of communities. We also use a more recent definition proposed by Power and others (1996), who define a keystone species as one whose overall impact on a community is large, as well as disproportionately large relative to its abundance. We conclude that although some aspects of their role have been overstated in the literature, the available evidence clearly indicates that prairie dogs function as a keystone species. We also suggest that only well-documented ecological functions of prairie dogs should be the basis for management decisions.

Review of the Prairie Dog's Role

Ecosystem Regulation

The disturbance caused by grazing and burrowing activities of prairie dogs affects a number of ecosystem-level processes (Whicker and Detling 1988). Prairie dog grazing affects vegetation structure by decreasing vegetation height and cover and altering plant species composition (Coppock and others 1983a, Brizuela and others 1986, Cid and others 1989, Cincotta and others 1989, Weltzin and others 1997a,b). Prairie dog burrowing and grazing can also affect the rates of nitrogen cycling and lead to increased nitrogen uptake by plants (Holland and Detling 1990), which may account for the preferential grazing of prairie dog colonies by pronghorn, elk and bison (Coppock and others 1983b, Krueger 1986, Wydeven and Dahlgren 1985). Below ground, prairie dogs increase soil mixing and affect rates of energy and material flows (Ingham and Detling 1984). Across the landscape, variation in colony density and duration of occupancy can lead to a shifting mosaic of patches that differ in vegetation structure, composition, and quality (e.g., nutrient availability) within and among patches (Bonham and Lerwick 1976, Archer and others 1987). Cumulatively, prairie dog activities influence patch dynamics and contribute to overall landscape heterogeneity.

Superimposed over the disturbance caused by prairie dogs are the impacts of fire and climatic variability. These processes generally operate at spatial scales much greater than the scale of individual prairie dog colonies, although human activities have decreased the scale of both fire and prairie dog disturbance regimes. The patch-level disturbance created by prairie dogs interacts with these large-scale disturbances, altering their effects on landscape structure and dynamics (Coppock and Detling 1986, Weltzin and others 1997a). For example, prairie dog colonies may serve as fire breaks and may also magnify the effects of cyclical and seasonal drought. Higher than average rainfall may either enhance or diminish the effects of prairie dog disturbance. Historically, bison were also an important agent of disturbance across the Great Plains and may have influenced the dispersal and distribution of prairie dogs and may have selectively grazed prairie dog colonies (Coppock and others 1983b, Krueger 1986, Wydeven and Dahlgren 1985).

Collectively, these direct and indirect impacts of prairie dog grazing and burrowing have a pronounced effect on ecosystem processes and patterns, even though prairie dog numbers are only a fraction of historic levels. Considering that the historic range of prairie dogs may well have covered over 40 million ha (Anderson and others 1986), their impact on landscape structure and dynamics must have been dramatic.

Abundance Patterns

It is frequently cited that the overall abundance of birds, small mammals, and terrestrial predators is higher on colonies (O'Meilia and others 1981, Clark and others 1982, Agnew and others 1986, Reading and others 1989, Miller and others 1990, 1994, Sharps and Uresk 1990). However, several details have been omitted that bear on the interpretation of these patterns. The higher abundance (total individuals) of small mammals and passerines on colonies relative to adjacent areas (O'Meilia and others 1982, Agnew and others 1986, Mellink and Madrigal 1993, Barko 1996) can be accounted for solely by the abundance patterns of deer mice, grasshopper mice, and horned larks. Higher terrestrial predator abundance is based on the statement that ''dog towns had 5.7 times the frequency of predators (coyotes and badgers) as off-town areas'' (Krueger 1986); however, the validity and generality of this pattern cannot be evaluated because no information on methods and analysis were provided in this paper.

Species Richness Patterns

Keystone species commonly affect community structure by increasing species richness (Mills and others 1993). Although it is widely stated that prairie dogs can increase species richness (Hansen and Gold 1977, Clark and others 1982, O'Meilia and others 1982, Reading and others 1989, Miller and others 1990, 1994), prairie dogs do not appear to consistently increase species richness and may sometimes decrease richness at the scale of individual colonies. Agnew and others (1986) found that out of a total of 39 bird species, 36 species occurred on colonies compared to 29 species off colonies, a pattern frequently used to assert the keystone role of prairie dogs (Reading and others 1989, Miller and others 1990, 1994). Although the entire list of 36 species observed on colonies was not provided, their results indicate that at least seven of these species were from a species pool that included exotics (rock dove, European starling, house sparrow) or waterbirds (mallard, northern pintail, blue-winged teal, sora, yellow-headed blackbird). It is unlikely these species evolved a strong relationship with prairie dogs. In a similar study, 30 species were found on colonies compared to 27 species in adjacent uncolonized areas (Barko 1996). Thus, the available evidence indicates that there may be only a minimal contribution to colony-scale biological diversity accounted for by an increase in avian species richness on colonies.

For small mammals, species richness may actually be lower on colonies compared to nearby uncolonized areas (O'Meilia and others 1982, Agnew and others 1986, Mellink and Madrigal 1993). In addition, several species of rodents observed in uncolonized areas are completely absent from colonies (O'Meilia and others 1982, Agnew and others 1986, Mellink and Madrigal 1993). This pattern often has been overlooked in summaries of the prairie dog's role.

Plant species richness is probably related to the degree of prairie dog disturbance. Intermediate disturbance levels have the greatest floral species richness, although this pattern varies somewhat among forbs, grasses, and shrubs (Whicker and Detling 1988). Plant species richness can also vary within colonies as a function of colony age (Whicker and Detling 1988). In addition, species richness patterns may vary across seasons, vegetation types (e.g., shortgrass prairie vs shrub-steppe), and prairie dog species (Weltzin and others 1997b).

This confusing array of richness patterns indicates that using these patterns to characterize the role of prairie dogs is problematic. Species richness at the scale of colonies provides little information about how prairie dogs influence the integrity of the community. This is better addressed by comparing species composition, which can differ among areas with and without prairie dogs. Many plant and animal species reach their highest densities on colonies. For example, the reduction of little bluestem (*Andropogon scoparius*) on black-tailed colonies may allow annual forbs, such as prairie dogweed (*Dyssodia papposa*) to increase in abundance relative to undisturbed prairie, where they are quite rare (Coppock and others 1983a). In mesquite grasslands, historic populations of black-tailed prairie dogs, in conjunction with other herbivores associated with colonies, may have prevented woody species such as mesquite (*Prosopis* spp.) from attaining dominance (Weltzin and others 1997a). Thus, changes in species composition resulting from prairie dogs can increase species richness, but at scales much larger than previously studied.

Dependence of Vertebrates on Prairie Dog Colonies

Criteria for establishing dependence. Another way to evaluate the influence of prairie dogs on the integrity of the system is to quantify the degree to which species depend on prairie dogs. We defined dependent species as those species whose fitness is increased by the

Table 1. Strength of dependence/association of 208 vertebrate species found in proximity to prairie dog towns

Strength of association	Definition	If prairie dogs go extinct	Possible examples
Dependent species			
Obligate	Almost totally dependent upon prairie dogs for survival	Species goes extinct	Black-footed ferret
Facultative			
Strong	Use one or more features of prairie dog towns that have limited availability off towns	Decrease in local and regional abundance	Burrowing owl, mountain plover
Weak	Use features of prairie dog towns that are also abundant off towns, or use of towns varies in space or time	Abundance may decrease locally if alternative habitats limiting	Ferruginous hawk, horned lark
Associated species			
Opportunistic	Species more generally associated with prairie grasslands; occur on prairie dog towns, but tend to be more abundant off towns	Little or no change in abundance; may increase if undisturbed habitat preferred	Western diamondback rattlesnake, western meadowlark, pronghorn
Accidental	Do not use features of towns, but are seen on, or near, towns due to habitat features that occur in proximity to towns	No change likely	Yellow warbler, white pelican, ladder-backed woodpecker
Alien	Exotic or domestic animals	No change likely	Domestic cattle, house sparrow, Norway rat

presence of prairie dogs, which included both obligate (require prairie dogs for survival) and facultative species (use features of prairie dog colonies that have limited availability elsewhere; Table 1). We compiled a list of 208 vertebrate species that have been cited as associated with prairie dogs (Appendix 1; references in Table 2). Prairie dog associates have been minimally defined as those species seen on, near, or flying over prairie dog colonies and does not reflect use of prairie dog colonies. Consequently, this list includes species that range in association from obligate species to species associated with habitat features (e.g., wetlands, reservoirs, trees) located on or near colonies that are not a consequence of prairie dog activities (Table 1). We developed four criteria to determine which of the 208 species listed as prairie dog associates are truly dependent upon prairie dogs:

1. *Abundance of species is higher on prairie dog colonies than comparable areas without prairie dogs.* In general, a greater disparity in abundance indicates a greater degree of dependence. However, because this criterion is based on correlational patterns, it provides only weak evidence of dependence.

2. *Species use features of prairie dog towns, which are a direct consequence of prairie dog activities or presence, at greater frequencies than similar features off colonies.* This criterion helps to quantify the degree of specialization on features of prairie dog colonies. For instance, burrowing owls may use prairie dog burrows at a greater frequency than the burrows of other species.

3. *Survivorship or reproductive success is lower off prairie dog colonies than on colonies.* Thus, colonies may serve as sources of recruitment, whereas alternative habitats may constitute ecological sinks that require continued immigration to maintain populations. For example, although mountain plovers and horned larks sometimes nest on agricultural land, agricultural practices may reduce nest success (Hurley and Franks 1976, Knopf and Rupert 1998).

4. *Populations of dependent species decline if prairie dog populations decline.* Declines in strongly dependent species should occur both locally and regionally if prairie dogs are extirpated. Species only marginally dependent on colonies might decline locally, but not regionally, if availability of alternative habitats is sufficient to support populations elsewhere across their range. For example, in several areas in Colorado and New Mexico, wintering and migrating ferruginous hawk numbers declined locally following a crash in prairie dog populations as a result of a sylvatic plague (*Yersinisia pestis*) epizootic (Jones 1989, Cully 1991). Evidence of meeting this criterion, particularly in combination with decreased fitness off colonies, is the most compelling support for dependence.

Documenting dependence on prairie dogs is rather difficult. Because dependence can vary in space and time, scale of analysis is crucial. For example, horned larks may be more abundant on colonies compared to nearby undisturbed areas (Agnew and others 1986, Barko 1996), but may reach numbers comparable to

Table 2. Review of studies providing lists of species associated with prairie dog colonies

Authors	Location	No. of colonies	Prairie dog species[a]	On / off colonies	Quantified methods	Results[b]	No. spp / taxa Herps	Birds	Mammals
Koford 1958	ND, SD, WY, CO	>4	BT	On	No	SL	2	6	14
Tyler 1968	OK	280	BT	On	No	SL,[c] SA, HU, LR	17	56	16
Agnew and others 1986	MT	3	BT	On / off	Yes[d,e]	SL,[f] SR, SA[f]		36	4
Campbell and Clark 1981	WY	46	BT	On	No	SL	9	33	22
Clark and others 1982	NM, CO, WY	47	BT, WT, GU	On	Yes[g]	SL	26	51	30
O'Meilia and others 1982	OK	6	BT	On / off[h]	Yes[e]	SL, SR, SA			6
Mellink and Madrigal 1993	Mexico	1	MX	On / off[i]	Yes[e]	SL, SR, SA			5
Reading and others 1989	MT	16	BT	On	Yes[g]	SL, LR	1	70	12
Sharps and Uresk 1990	SD	?	BT	On	No	SL, LR	10	88	36
Barko 1996	OK	5	BT	On / off	Yes[d,g]	SL,[c] SR, SA		32	

[a]BT = black-tailed, WT = white-tailed, GU = Gunnison's, MX = Mexican.

[b]SL = species lists, SR = compared species richness on and off colonies, SA = species abundance, HU = information on habitat use, LR = lists includes additional species from literature review.

[c]Excluded species observed that did not use colony features.

[d]Number of visits / colony unclear.

[e]Statistical analysis of abundance patterns provided.

[f]Only partial lists of bird species provided.

[g]Sampling effort variable per colony.

[h]Experimental release of prairie dogs.

[i]Compared occupied to abandoned.

that found on colonies on otherwise disturbed prairie habitat or outside the prairie dogs' range (Hurley and Franks 1976). Taken individually, each criterion cannot sufficiently rule out alternative explanations for correlational patterns consistent with dependence. For example, secretive species may appear more abundant on colonies than in adjacent taller vegetation merely because of detection differences. In addition, failure to meet a specific criterion could result from lack of data, because not all criteria are required for dependence, or because a species is truly not dependent on prairie dogs. Thus, nondependent species may sometimes appear to meet a single criterion or dependent species may not satisfy every criteria. Convincing evidence of dependence on prairie dogs will generally require meeting more than one criterion but not necessarily all four.

Results of dependence analysis. We found that few of these criteria were met by most presumed prairie dog associates. Only nine vertebrate species had data documenting at least one of the four criteria (Table 3). Furthermore, data addressing fitness (criterion 3) was available for only two species. Other vertebrate species (e.g., badger, tiger salamander, prairie rattlesnake) are often assumed to be dependent on prairie dogs, but there are currently no published data to support this. Further work is clearly needed to confirm, or rule out, dependence for many of these candidate dependent species and to determine if other species meet any of the four dependence criteria.

Species ranged in their degree of association from obligate to opportunistic use of colonies (Table 1). Only one species, the black-footed ferret, is truly an obligate. This species is near extinction primarily due to a range-wide decimation of the prairie dog ecosystem, in conjunction with secondary poisonings and susceptibility to distemper and plague (Clark 1989). Mountain plovers and burrowing owls may be strongly facultative species because they apparently have suffered population declines within the prairie dog's range following declines in prairie dogs. These three species had the strongest evidence for dependence.

The remaining six candidate dependent species had weaker evidence of dependence and each met only one

Table 3. Species listed as prairie dog associates that meet one or more criteria for dependence

Species	Black-footed ferret[a]	Burrowing owl[b]	Mountain plover[c]	Ferruginous hawk[d]	Golden eagle[e]	Swift fox[f]	Horned lark[g]	Deer mouse[g]	Grasshopper mouse[h]
Criterion 1 Abundance higher on colonies	*[i]	*	*				*	*	*
Criterion 2 Greater use of colonies	*	*	*						
Criterion 3 Fitness higher on colonies	*		*						
Criterion 4 Population declines with prairie dog decline	*	*	*	*	*	*			

[a]Anderson and others 1986, Biggins and Godbey 1995, Biggins and others 1985, 1993, Clark and others 1985, Forrest and others 1985, Hilman and Linder 1973, Sheets and others 1972.

[b]Agnew and others 1986, Barko 1996, Butts and Lewis 1982, Desmond and Savidge 1996, Hughes 1993, Martin 1973, Zarn 1974.

[c]Barko 1996, Graul and Webster 1976, Knopf 1996, Knopf and Rupert 1998, Knowles and Knowles 1984, Knowles and others 1982, Olson 1985, Olson and Edge 1985, Olson-Edge and Edge 1987.

[d]Blair and Schitoskey 1982, Cully 1991, Gilmer and Stewart 1983, Houston and Bechard 1984, Howard and Wolfe 1976, Jones 1989, Lokemoen and Duebbert 1976, MacLaren and others 1988, Steenhoff and Kochert 1985, Wakely 1978, Woffinden and Murphy 1977, 1989.

[e]Cully 1991, Jones 1989.

[f]Hilman and Sharps 1978, Hines and Case 1991, Sharps 1989, Uresk and Sharps 1986, Zumbaugh and Choate 1985.

[g]Agnew and others 1986, Barko 1996, Cutter 1958, Kilgore 1969.

[h]Agnew and others 1986, O'Meilia and others 1982.

[i]Denotes criteria supported by data.

of the four criteria (Table 3). These species would probably decline locally following a decline in prairie dogs if alternative prey or habitat were unavailable (i.e., weakly facultative; Table 1). Examples include ferruginous hawks, golden eagles, and swift foxes, which are generalist predators that likely feed on prairie dogs in an opportunistic manner, but may specialize locally on prairie dogs when alternative prey sources are scarce. Evidence of dependence by ferruginous hawks and golden eagles is indicated by local declines during migration and on wintering grounds in New Mexico and Colorado following prairie dog population declines (Jones 1989, Cully 1991). In addition, wintering ferruginous hawks in Colorado typically have higher abundances on prairie dog colonies than areas without prairie dogs (Kotliar, unpublished data). A decline in swift foxes in South Dakota was also observed following declines in prairie dogs (Sharps 1989). South Dakota is the only area where data indicate that prairie dogs comprise a sizable proportion of the swift fox diet (Hillman and Sharps 1978, Uresk and Sharps 1986), which is otherwise usually dominated by nocturnal rodents (Kilgore 1969). The other three weakly facultative species (horned lark, deer mouse, and grasshopper mouse) are generalists that use open areas created by prairie dog activities. Horned lark abundance was one to two orders of magnitude higher on prairie dog colonies compared with uncolonized grasslands (Agnew and others 1986). Deer mice and grasshopper mice, although relatively abundant off colonies, were observed at densities three to four times higher on prairie dog colonies compared to uncolonized grassland (O'Meilia and others 1982, Agnew and others 1986). The degree to which any of these species would actually decline or simply move elsewhere if prairie dogs decline, however, is unclear and depends on whether prey, burrows, or open habitat is limiting. However, the limited data suggest that prairie dogs may influence the distribution patterns of these six species across the landscape.

What about the remaining 199 associated species? Abundance data for criterion 1 were only available for 20 species: five species reached slightly higher abundance levels on colonies, five species had similar abundance levels on and off colonies or had mixed patterns, and ten species had higher abundance levels off colonies (Appendix 1). This indicates that these 20 species at least occasionally occur on colonies, but probably do not prefer colonies, and may even prefer undisturbed grasslands (e.g., grasshopper sparrow).

An additional 117 species lacked abundance data on and off colonies, but their life history information indicated they could potentially use colony attributes. This included species that are often presumed to be prairie dog dependents (e.g., tiger salamander, prairie rattlesnake, badger), but which lack data to document dependence. It also included species such as western harvest mice that may actually prefer undisturbed grasslands. Fifteen species use ephemeral pools that sometimes develop on colonies. Prairie dogs may not be responsible for the rare occurrence of these shallow ponds, but their activities keep them relatively free of vegetation, a condition that may be preferred by amphibians and shorebirds that use these pools.

Of the remaining 62 species, 10 are domestic and exotic species (Table 1). Most of the remaining 52 species are waterbirds, more commonly associated with deep water (e.g., waterfowl, pelicans), that may have been observed flying over, or near, a prairie dog colony, but not actually using the colony. Although we cannot rule out the possibility that these species were using the colonies, we suggest that based on habitat affinities, many, if not most, of these 52 species were probably accidental. Because lists of species associated with prairie dog colonies have been used to justify conservation of prairie dogs, caution should be used when including potentially accidental and exotic species in lists of prairie dog associates.

Our evaluation of dependence highlights the considerable range in strength of association with prairie dogs for the 208 species. Life history information and expert review of species lists suggests that many purported associated species have a weak relationship to prairie dogs at best. We also stress that for most species, relationships to prairie dogs cannot be determined from available data. Even in studies in which data were available, sample sizes and geographic coverage were often small (Table 2). Considering that association with prairie dogs probably varies across habitats and species of prairie dog, extrapolation outside the geographic coverage of one particular study is tenuous. Further research is clearly needed to clarify the relationship of most of the 208 species to prairie dogs.

In summary, our review of both species richness patterns and assessment of strength of association suggests that the prairie dog's influence on vertebrate species richness may be lower than frequently asserted. Nevertheless, prairie dogs substantially contribute to biological diversity across their range because prairie dog colonies support a different composition of species than uncolonized areas (O'Meilia and others 1982, Agnew and others 1986, Mellink and Madrigal 1993). In addition, potentially dependent species such as black-footed ferrets, mountain plovers, burrowing owls, ferruginous hawks, and swift foxes have suffered population declines, and many either have, or are under consideration for, special protection under the Endangered Species Act (Samson and Knopf 1994). Because the long-term viability of declining dependent species may be compromised should prairie dogs continue to decline, management for prairie dogs will clearly benefit these species that are at risk.

Are Prairie Dogs a Keystone Species?

Paine's Keystone Species

To reevaluate the keystone role of prairie dogs, we first assess whether our revised prairie dog role is consistent with Paine's original concept of a keystone species whose ''activities greatly modified species composition and physical appearance'' and determined ''the integrity of the community and its unaltered persistence'' (Paine 1969). Our review indicates that nine vertebrate species may decline or disappear at a local scale, and in several cases at a landscape scale, if prairie dogs are eliminated. The black-footed ferret is apparently so specialized on prairie dogs that it does not persist where prairie dogs are eliminated. In addition, the continued reduction of prairie dog populations could hasten the demise of mountain plovers and burrowing owls, or decrease the abundance and distribution of the ferruginous hawk, golden eagle, swift fox, horned lark, grasshopper mouse, and deer mouse, diminishing biological diversity across prairie landscapes. Thus, it is not necessary to believe that prairie dogs have 208 associated species to conclude that they affect community integrity.

The disturbance activities of prairie dogs are akin to the disturbance role of the starfish (*Pisaster*) in the rocky intertidal that Paine used as a model of a keystone predator (Paine 1966, 1969). This disturbance role affects both species composition and ecosystem functions. Prairie dogs are not the only agents of disturbance in the Great Plains, but the scale at which they operate is unique. Prairie dogs aggregate into colonies that are sometimes quite dense and large, often persisting at a site over several decades. Their sedentary and colonial behavior tends to concentrate disturbance to a greater degree than the more dispersed and shorter duration disturbances caused by the actions of other

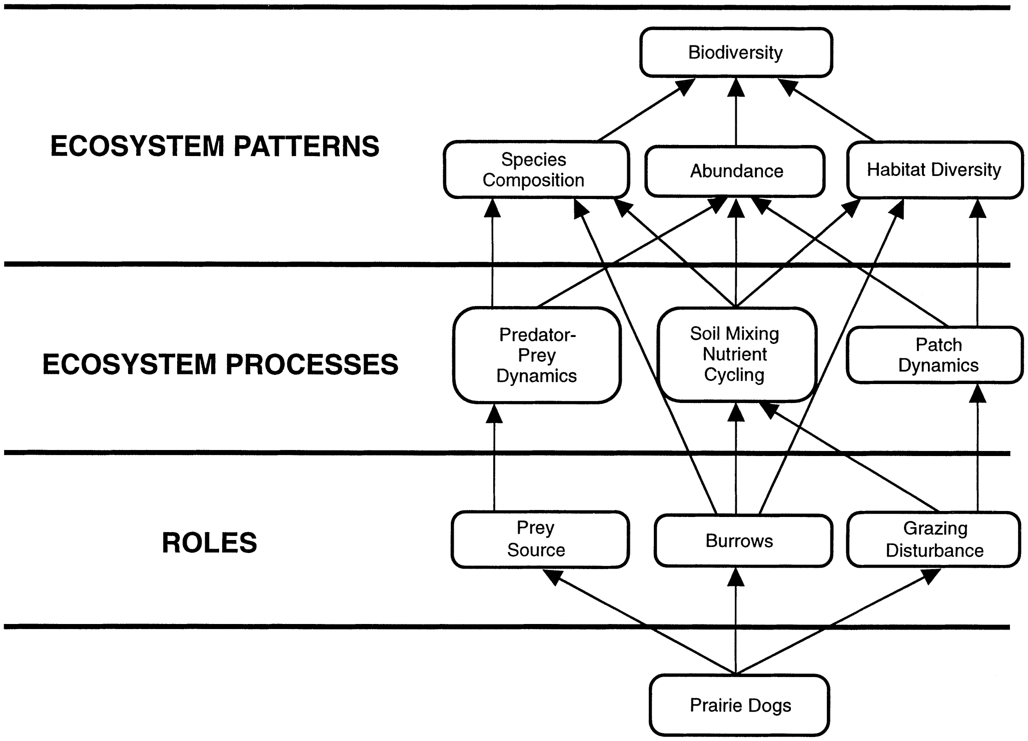

Figure 1. Dominant pathways by which prairie dogs affect ecosystem structure and function.

fossorial mammals, as well as more nomadic ungulates. The disturbance function of prairie dogs becomes even more critical in highly altered prairies that have lost natural disturbance regimes created by fire and large ungulate herds. Consequently, we conclude that prairie dog activities are important to ecosystem integrity and persistence. Thus, even though we found the magnitude of the prairie dog's role was sometimes overstated in the literature, it does meet Paine's qualitative definition of a keystone species.

Power's Keystone Species

Since Paine's original concept was developed, the term keystone has become rather loosely applied and its use in setting conservation priorities has been questioned (Mills and others 1993), leading to an attempt to clarify its definition (Power and others 1996). This new definition has two components: (1) a keystone species has a large overall effect on community or ecosystem structure or function, and (2) this effect is disproportionately large relative to its abundance (Power and others 1996). In addition, Power and others (1996) developed an equation for evaluating per capita effects that provides a quantitative framework for evaluating keystone status. In light of the new keystone definition, we evaluated whether the influence of prairie dogs on ecosystem processes and diversity patterns constitutes large overall effects and whether these effects are large relative to other species in prairie systems.

We begin by assessing whether prairie dogs have a large overall effect on ecosystem structure and function. Although prairie dogs do not consistently increase vertebrate and plant species richness at small scales, they do locally alter species composition and increase landscape-scale diversity by affecting the abundance and distribution of dependent species. In addition, they affect a number of ecosystem-level processes that, in turn, affect landscape heterogeneity and diversity. Individually, none of these functions is particularly large, but collectively they do have a pronounced effect on ecosystem structure and function (Figure 1).

To assess whether these effects can be considered large, we compare the overall impact of prairie dogs to other native herbivores in prairie systems. Prairies are also grazed by ground squirrels and historically were grazed by bison (Benedict and others 1996). Ground squirrels and pocket gophers provide burrows and also serve as prey, although their spatial distribution is typically more dispersed than prairie dogs. The magnitude of the impact of each prairie dog function probably matches or exceeds that of other Great Plains herbivores, but we suggest that none of the other species matches the diverse number of ways prairie dogs influence the system. Furthermore, keystone species

Table 4. Primary consumption of selected herbivores at Badlands National Park

Species	Range area (ha)	Density (per ha)	Mean weight (kg)	Mean daily energy intake (kJ)	Mean daily forage intake (kg-dry wt)	Estimated energy consumption[a] (per kg)	Estimated daily energy consumption (kJ/ha)[b]	Estimated daily dry weight forage consumption (kg/ha)[c]
Black-tailed prairie dog[d]	1300	37.5	1	620	0.053	620	23,250	1.9
Bison[e]	9700	0.04	636	74,250	20.0	117	3,062	0.8
Mule deer[e]	9700	0.023	90	10,766	2	120	244	0.05
Pronghorn[e]	9700	0.021	46	8,618	1.4	187	177	0.03

[a]Mean daily energy intake / mean body weight.
[b]Consumption / kg * density / ha.
[c]Mean daily forage intake * density / ha.
[d]Beckstead 1977; Hansen and Cavender 1973.
[e]Belovsky 1986.

typically function as either predators, prey, mutualists, or habitat modifiers (Mills and others 1993, Power and others 1996). Thus, prairie dogs differ from most conventional keystone species because they fulfill more than one function, acting as prey and modifying the habitat structure and dynamics in several ways. Therefore, we conclude that prairie dogs do indeed have a large overall impact in prairie systems.

To evaluate the second criterion (large effects relative to abundance), we evaluated per capita effects on an ecosystem trait. Operationally, calculation of per capita impacts has a number of difficulties (Power and others 1996). As is the case with most keystone species, experimental data are not available for prairie dogs. Despite this challenge, we conducted a preliminary comparison of per capita disturbance effects using data from Badlands National Park in South Dakota (Beckstead 1977). Black-tailed prairie dogs occupy approximately 12% of the park's 11,000-ha Badlands Wilderness Area, which also supports an intact guild of native ungulate herbivores (bison, mule deer, and pronghorn). Population levels of these species probably reflect historic levels. We estimated per capita primary consumption, standardized by biomass, for each of these four herbivores (Table 4). We also compared primary consumption per hectare. Due to higher basal metabolic rates, primary consumption per kilogram of body weight was greatest for prairie dogs. In addition, the sedentary and colonial behavior of prairie dogs concentrated their activities relative to the more nomadic ungulates; at observed densities, daily consumption per hectare by prairie dogs was at least an order of magnitude higher than any ungulate species. Even if the bison herd size were doubled, prairie dog consumption would still exceed cumulative ungulate consumption. These results indicate that standardized per capita effects of prairie dogs on ecosystem function may meet or exceed the impacts of other herbivores in the Great Plains. We conclude that existing data also meet the criteria of Power and others for keystone species.

Management Implications of Keystone Status for Prairie Dogs

We agree with previous conclusions that prairie dogs are a keystone species that should be targeted for conservation efforts. Prairie dogs have long been controlled on federal, tribal, state, and private lands, primarily at government expense, without any regard for their inherent values (Miller and others 1990). Because keystone status indicates that management for prairie dogs will benefit other species, it provides an important evaluation criterion for balancing two dominant and opposing management themes, prairie dog eradication and conservation. Indeed, keystone status has led public land managers to reevaluate widespread prairie dog eradication programs (Miller and others 1994). It also provides leverage for managers to protect prairie dog habitat when weighing management decisions among multiple uses of public lands and may help to offset the negative view of prairie dogs held by much of the general public.

Even though we agree that prairie dogs have important functions, we caution conservation proponents against overstating the role of prairie dogs. Protective measures for prairie dogs can be justified by existing data that clearly show the disproportionately large effects prairie dogs have on the health and functioning of prairie and shrub-steppe systems. Although dependent, and possibly opportunistic species, can benefit from prairie dog conservation, an inflated list of associated vertebrate species could mislead managers into the belief that management actions on behalf of prairie dogs will provide a safety net for most prairie species. Such misleading assumptions weaken the scientific credibility of biologists and ultimately could hamper conservation efforts (Bury and Corn 1995). Furthermore, although managers must rely heavily on litmus tests like the keystone species concept to set conservation priorities, caution must be used to avoid misplaced emphasis on a single index of ecological integrity (Landres and others 1988).

Limitations not withstanding, there is sufficient evidence that prairie dogs are crucial to the structure and function of native prairie systems. In addition to their keystone role, prairie dogs have inherent value, and because of severe population declines, deserve protection in their own right (Wuerthner 1997). We believe that future control of prairie dogs, at least on public lands, should be weighed against potential loss of biological diversity and degradation of ecosystem integrity, as well as the loss of a unique part of our North American prairie heritage.

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Appendix 1. Vertebrate species cited as associated with prairie dogs and evidence of dependence[a]

Species	Features of colonies used[b]	Citation[c]
a. Data support at least one criterion for dependence		
Black-footed ferret *Mustela nigripes*	PD,BU	1, 8
Mountain plover *Charadrius montanus*	OV	2, 3, 7
Burrowing owl *Athene cunicularia*	BU	2, 3, 4, 6, 7, 8
Golden eagle *Aquila chrysaetos*	PD,OP	1, 2, 3, 7, 8
Ferruginous hawk *Buteo regalis*	PD,OP	2, 3, 4, 6, 7, 8
Horned lark *Eremophila alpestris*	OV	2, 3, 4, 6, 7, 8, 10
Deer mouse *Peromyscus maniculatus*	PV	1, 2, 3, 6, 8
Northern grasshopper mouse *Onychomys leucogaster*	PV	1, 3, 6, 8
Swift fox *Vulpes velox*	PD,OP	2, 8
b. Abundance slightly higher on colonies compared to adjacent undisturbed grassland		
Killdeer *Charadrius vociferus*	OV	2, 3, 6, 7, 8, 10
Mourning dove *Zenaida macroura*	OV	2, 3, 4, 6, 7, 8
Barn swallow *Hirundo rustica*	PV	2, 3, 6, 7, 8, 10
White-footed mouse *Peromyscus leucopus*	PV	5
Onychomys arenarius	PV	9
c. Abundance not significantly different between colonies and undisturbed grassland or abundance patterns mixed		
Western meadowlark *Sturnella neglecta*	PV	2, 3, 4, 6, 7, 8, 10
Common grackle *Quiscalus quiscula*	PV	6, 10
Thirteen-lined ground squirrel *Spermophilus tridecemlineatus*	PV	1, 2, 3, 4, 6, 8
Hispid pocket mouse *Perognathus hispidus*	PV	6, 8
Western harvest mouse *Reithrodontomys megalotis*	PV	6, 8
d. Abundance higher on undisturbed grassland compared to colonies		
Upland sandpiper *Bartramia longicauda*	PV	2, 6, 7, 8
Common nighthawk *Chordeiles minor*	PV	2, 3, 7, 10
Grasshopper sparrow *Ammodramus savannarum*	PV	6, 7, 8
Lark bunting *Calamospiza melanocorys*	PV	2, 3, 6, 7, 10
Red-winged blackbird *Agelaius phoeniceus*		2, 6, 7, 8, 10
Desert cottontail *Sylvilagus audubonii*	PV	1, 2, 3, 4, 8, 9
Black-tailed jackrabbit *Lepus californicus*	PV	1, 2, 4, 8, 9
Ord's kangaroo rat *Dipodomys ordi*	PV	1, 2, 4, 8, 9
Plains harvest mouse *Reithrodontomys montanus*	PV	8
Prairie vole *Microtus ochrogaster*	PV	6, 8

Appendix 1. (Continued)

Species	Features of colonies used[b]	Citation[c]
e. No published comparative abundance data		
Tiger salamander *Ambystoma tigrinum*	BU, TP	2, 3
Plains spadefoot toad *Scaphiopus bombifrons*	TP	2
Couch's spadefoot toad *Scaphiopus couchi*	TP	2
Green toad *Bufo debilis*	TP	2
Texas toad *Bufo speciosus*	TP	2
Woodhouse's toad *Bufo woodhousei*	TP	2
Great plains toad *Bufo cognatus*	TP	8
Chorus frog *Pseudacris triseriata*	TP	3, 8
Great plains narrow-mouthed frog *Gastrophryne olivacea*	BU, TP	2
Yellow mud turtle *Kinosternon flavescens*	TP	2
Ornate box turtle *Terrapene ornata*	PV	2, 4
Prairie rattlesnake *Crotalus viridis*	PD, OP,BU	
Western diamondback rattler *Crotalus atrox*	PD, OP,BU	1, 2
Mohave rattlesnake *Crotalus scutulatus*	PD, OP,BU	9
Lesser earless lizard *Holbrookia maculata*	PV	2, 4
Eastern fence lizard *Sceloporus undulatus*	BU	2
Texas horned lizard *Phrynosoma cornutum*	BU, PV	2, 4
Short-horned lizard *Phrynosoma douglassi*	PV	3
Texas spotted whiptail *Cnemidophorus qularis*	BU, PV	2
Little striped whiptail *Cnemidophorus inornatus*	BU, PV	4
Racerunner *Cnemidophorus sexlineatus*	BU, PV	2
Gopher snake *Pituophis melanoleucus*	BU, PV	2, 3
American avocet *Recurvirostra americana*	TP	7
Lesser golden plover *Pluvialis dominica*	OV, TP	2
Marbled godwit *Limosa fedoa*	TP	7
Long-billed curlew *Numenius americanus*	SV, TP	2, 6, 7, 8, 10
Willet *Catoptrophorus semipalmatus*	TP	7
Greater yellowlegs *Tringa melanoleuca*	TP	7
Lesser yellowlegs *Tringa flavipes*	TP	7
Wilson's phalarope *Phalaropus tricolor*	TP	7, 8
Long-billed dowitcher *Limnodromus scolopaceus*	TP	8
Baird's sandpiper *Calidris bairdii*	OV, TP	2
Buff-breasted sandpiper *Tryngites subruficollis*	OV, TP	2
Turkey vulture *Cathartes aura*	PD, OP	2, 6, 8, 10
Bald eagle *Haliaeetus leucocephalus*	PD, OP	2, 8
Mississippi kite *Ictinia mississippiensis*	OP	2, 10
Northern harrier *Circus cyaneus*	OP	1, 2, 3, 6, 7, 8
Prairie falcon *Falco mexicanus*	OP	1, 2, 3, 6, 7, 8
Sharp-shinned hawk *Accipiter striatus*	OP	7
Red-tailed hawk *Buteo jamaicensis*	PD, OP	1, 2, 3, 6, 8, 9
Swainson's hawk *Buteo swainsoni*	PD, OP	2, 3, 4, 6, 7, 8, 9, 10
Rough-legged hawk *Buteo lagopus*	PD, OP	1, 2, 8
Crested caracara *Polyborus plancus*	PD, OP	9
American kestrel *Falco sparverius*	OP	2, 3, 4, 6, 7, 8, 9, 10
Merlin *Falco columbarius*	OP	7, 8, 10
Lesser prairie chicken *Tympanuchus pallidicinctus*	OV	2
Sharp-tailed grouse *Tympanuchus phasianellus*	OV	1, 6, 7, 8
Sage grouse *Centrocerus urophasianus*	OV	3, 7
Northern bobwhite *Colinus virginianus*	PV	2
Scaled quail *Callipepla squamata*	PV	2, 10
Great horned owl *Bubo virginianus*	OP	3, 6
Snowy owl *Nyctea scandiaca*	PD, OP	8
Northern flicker *Colaptes auratus*	PV	2, 7, 8
Eastern kingbird *Tyrannus tyrannus*	PV	2, 6, 7, 8, 10
Western kingbird *Tyrannus verticalis*	PV	2, 3, 6, 7, 8, 10
Cassin's kingbird *Tyrannus vociferans*	PV	10
Scissor-tailed flycatcher *Tyrannus forficatus*	PV	2
Say's phoebe *Sayornis saya*	PV	6, 8

Appendix 1. (Continued)

Species	Features of colonies used[b]	Citation[c]
Violet-green swallow *Tachycineta thalassina*	PV	8
N. rough-winged swallow *Stelgidopteryx serripennis*	PV	6, 8
Cliff swallow *Hirundo pyrrhonota*	PV	2, 3, 7, 8, 10
Black-billed magpie *Pica pica*	PV	3, 7, 8
Chihuahuan raven *Corvus cryptoleucus*	PV	2, 10
American crow *Corvus brachyrhynchos*	OP	2, 6, 8, 10
Common raven *Corvus corax*	OP	8
American robin *Turdus migratorius*	PV	7, 8
Northern shrike *Lanius excubitor*	OP	8
Loggerhead shrike *Lanius ludovicianus*	OP	2, 3, 6, 7, 8, 10
Northern mockingbird *Mimus polyglottos*	PV	2, 8, 10
Sage thrasher *Oreoscoptes montanus*	PV	7
Curved-billed thrasher *Toxostoma curvirostre*	PV	4, 10
Water pipit *Anthus spinoletta*	PV	8
Sprague's pipit *Anthus spragueii*	PV	2
Rufous-sided towhee *Pipilo erythrophthalmus*	PV	8
Baird's sparrow *Ammodramus bairdii*	PV	7
Vesper sparrow *Pooecetes gramineus*	PV	2, 3, 7, 8, 10
Savannah sparrow *Passerculus sandwichensis*	PV	2, 3, 7
Lark sparrow *Chondestes grammacus*	PV	2, 4, 7, 8, 10
Cassin's sparrow *Aimophila cassinii*	PV	10
Chipping sparrow *Spizella passerina*	PV	8
Brewer's sparrow *Spizella breweri*	PV	7
Slate-colored junco *Junco hyemalis*	PV	8
White-crowned sparrow *Zonotrichia leucophrys*	PV	8
Chestnut-collared longspur *Calcarius ornatus*	OV	2, 3, 6, 7, 8
McCown's longspur *Calcarius mccownii*	OV	2, 3, 7, 8
Lapland longspur *Calcarius lapponicus*	PV	2
Snow bunting *Plectrophenax nimalis*	PV	3
Dickcissel *Spiza americana*	PV	8
Bobolink *Dolichonyx oryzivorus*	PV	8
Eastern meadowlark *Sturnella magna*	PV	2
Brewer's blackbird *Euphagus cyanocephalus*	PV	2, 7, 8
Brown-headed cowbird *Molothrus ater*	PV	2, 3, 7, 8
Boat-tailed grackle *Quiscalus major*	PV	2
Pine siskin *Carduelis pinus*	PV	8
American goldfinch *Carduelis tristis*	PV	8
Eastern mole *Scalopus aquaticus*	PV	2
Eastern cottontail *Sylvilagus floridanus*	PV	8
White-tailed jackrabbit *Lepus townsendii*	PV	1, 3, 7, 8
Least chipmunk *Eutamias minimus*	PV	3
Spotted ground squirrel *Spermophilus spilosoma*	PV	2
Northern pocket gopher *Thomomys talpoides*	PV	8
Plains pocket gopher *Geomys bursarius*	PV	2, 4, 8
Olive-backed pocket mouse *Perognathus fasciatus*	PV	3, 8
Silky pocket mouse *Perognathus flavus*	PV	9
Southern plains woodrat *Neotoma micropus*	PV	2, 4
Coyote *Canis latrans*	PD,OP	1, 2, 3, 4, 7, 8
Red fox *Vulpes fulva*	OP	3, 7, 8
Long-tailed weasel *Mustela frenata*	PD,OP	3, 4, 8
Badger *Taxidea taxus*	PD,OP	1, 2, 3, 4, 7, 8
Spotted skunk *Spilogale putorius*	OP	8
Striped skunk *Mephitis mephitis*	OP	2, 3, 8
Bobcat *Lynx rufus*	PD,OP	1, 2, 8
Elk *Cervus elaphus*	PV	7
Mule deer *Odocoileus hemionus*	PV	3, 7, 8
White-tailed deer *Odocoileus virginianus*	PV	8
Pronghorn *Antilocapra americana*	PV	1, 3, 4, 7, 8
Bison *Bison bison*	PV	1, 2, 8

Appendix 1. (Continued)

Species	Features of colonies used[b]	Citation[c]
f. Life history information indicates accidental species		
Northern leopard frog *Rana pipiens*		3
Western toad *Bufo boreas*		3
Bullfrog *Rana catesbeiana*		8
Sagebrush lizard *Sceloporus graciosus*		3, 4
Chihuahua spotted whiptail *Cnemidophorus exsanguis*		4
Plains garter snake *Thamnophis radix*		8
Smooth green snake *Opheodrys vernalis*		8
Common garter snake *Thamnophis sirtalis*		3
Eared grebe *Podiceps nigricollis*		7
Pied-billed grebe *Podilymbus podiceps*		7
White pelican *Pelecanus erythrorhynchos*		7
Double-crested cormorant *Phalacrocorax auritus*		7
Black-crowned night heron *Nycticorax nycticorax*		7
Great blue heron *Ardea herodias*		7, 8
Trumpeter swan *Cyngus buccinator*		8
Snow goose *Chen caerulescens*		2
Canada goose *Branta canadensis*		7, 8
Mallard *Anas platyrhynchos*		6, 7, 8
Gadwall *Anas strepera*		7, 8
Ruddy duck *Oxyura jamaicensis*		7
Green-winged teal *Anas crecca*		3, 7
American wigeon *Anas americana*		7
Northern pintail *Anas acuta*		6, 7, 8
Northern shoveler *Anas clypeata*		8
Blue-winged teal *Anas discors*		6, 7, 8
Canvasback *Aythya valisineria*		8
Redhead *Aythya americana*		7
Lesser scaup *Aythya affinis*		7
Sora *Porzuna carolina*		6, 8
American coot *Fulica americana*		7
Ring-billed gull *Larus delawarensis*		7, 8
Herring gull *Larus argentatus*		7
California gull *Larus californicus*		7
Belted kingfisher *Ceryle alcyon*		8
Red-headed woodpecker *Melanerpes erythrocephalus*		8
Downy woodpecker *Picoides pubescens*		8
Ladder-backed woodpecker *Picoides scalaris*		2
Blue Jay *Cyanocitta cristata*		8
Eastern bluebird *Sialia sialis*		8
Mountain bluebird *Sialia currucoides*		7, 8
Gray catbird *Dumetella carolinensis*		8
Yellow warbler *Dendroica petechia*		8
Common yellowthroat *Geothlypis trichas*		8
Yellow-breasted chat *Icteria virens*		8
Yellow-headed blackbird *Xanthocephalus xanthocephalus*		6, 7, 8
Bullock's oriole *Icterus bullockii*		2
Western tanager *Piranga ludoviciana*		8
Common redpoll *Carduelis flammea*		8
Richardson's ground squirrel *Spermophilus richardsonii*		7
Porcupine *Erethizon dorsatum*		8
Raccoon *Procyon lotor*		2, 3, 8
Mink *Mustela vison*		3, 8
g. Domestic or introduced species		
Gray partridge *Perdix perdix*		7
Ring-necked pheasant *Phasianus colchicus*		8
Rock dove *Columbia livia*		2, 6, 8, 10
European starling *Sturnus vulgaris*		2, 6, 7, 8

Appendix 1. (Continued)

Species	Features of colonies used[b]	Citation[c]
House sparrow *Passer domesticus*		2, 6, 8
Norway rat *Rattus norvegicus*		8
House mouse *Mus musculus*		6, 8
Domestic horse *Equus caballus*		3, 7
Domestic cattle *Bos taurus*		3, 7
Domestic sheep *Ovis aries*		3, 7

[a]See Table 1 for definitions.

[b]PD = prairie dogs as prey or carrion, OP = other vertebrate prey or carrion found on colonies, BU = burrows for nesting/shelter, OV = open vegetation or bare ground for nesting/foraging, PV = prairie vegetation for nesting/foraging, TP = temporary pools for breeding/foraging.

[c]1, Koford 1958; 2, Tyler 1968; 3, Campbell and Clark 1981; 4, Clark and others 1982; 5, O'Meilia and others 1982; 6, Agnew and others 1986; 7, Reading and others 1989; 8, Sharps and Uresk 1990; 9, Mellink and Madrigal 1993; 10, Barko 1996.

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