

Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico

Gerardo Ceballos*, Jesús Pacheco & Rurik List

Instituto de Ecología, UNAM, Ap. Postal 70-275, 04510, México, D.F.

Prairie dogs are considered to be both a keystone species and an ecosystem engineer in grasslands. To partially test these hypotheses we evaluated burrow densities, soil removal, and mammal (i.e. rodents and carnivores) species composition, richness, diversity, and abundance in grasslands with and without prairie dogs (*Cynomys ludovicianus*) in north-western Mexico. We measured habitat heterogeneity as a function of burrow density. As predicted, density of burrows was much higher in areas with prairie dogs. Soil mix was also much higher in prairie dog colonies. Grasslands with and without prairie dogs differed in small mammal species composition, richness, density, and diversity; four species were exclusively found in areas with prairie dogs. Interestingly, carnivore communities were similar in areas with and without prairie dogs. Our results support the hypothesis that prairie dogs and their activities enhance regional species diversity, and thus are an important component of the grassland ecosystem

© 1999 Academic Press

Keywords: burrows; carnivores; diversity; ecosystem engineer; habitat heterogeneity; keystone species; mammals; prairie dogs; small mammals

Introduction

Prairie dogs are an important species in North American grasslands. They have profound impacts on abiotic and biotic features of their ecosystems. They can influence environmental heterogeneity, plant succession, hydrology, nutrient cycling, biodiversity, and landscape architecture (Koford, 1958; Uresk, 1985; Archer *et al.*, 1987; Whicker & Detling, 1988; Cid *et al.*, 1991; Coppock *et al.*, 1993 *a, b*; Weltzin *et al.*, 1997 *a*). Because of their role in the structure and function of many grasslands they are considered a 'keystone species' (e.g. Miller *et al.*, 1994) and an 'ecosystem engineer' (*sensu* Jones *et al.*, 1994; Weltzin *et al.*, 1997 *a*).

Prairie dogs and their activities can affect vegetation characteristics such as species

^{*} Corresponding author (E-mail: gceballo@miranda.ecologia.unam.mx).

composition, diversity, height, structure, biomass, and productivity (Bonham & Lerwick, 1976; Coppock *et al.*, 1983 *a*; Archer *et al.*, 1987; Whiker & Detling, 1988; Miller *et al.*, 1994). Recently, an elegant series of studies have shown that prairie dogs and associated fauna can be an over-riding factor suppressing the establishment of mesquite (*Prosopis*) communities, and thus preventing the disappearance of grasslands and the spread of desertification (Weltzin *et al.*, 1997 *a, b*).

Prairie dog colonies are also an important factor in determining the composition and diversity of invertebrates and vertebrates. They form colonies or towns that can hold thousands or millions of individuals, where they and their associated fauna are preyed upon by numerous mammalian, avian, and reptilian predators (e.g. Koford, 1958; Sharps & Uresk, 1990; Ceballos *et al.*, 1993; Mellink & Madrigal, 1993; Cotera-Correa, 1996; List, 1997). They live in complex burrow systems that are used for refuge by many mammals, birds, reptiles, amphibians, and arthropods (Campbell & Clark, 1981; Sharps & Uresk, 1990). Several studies have shown changes in vertebrate species composition and a decline in biomass, species richness, and abundance in areas where prairie dogs have been eradicated (O'Meilia *et al.*, 1982; Agnew *et al.*, 1986; Knopf, 1994).

In historic times, prairie dogs occupied millions of hectares of land that have since been severely reduced and fragmented (Marsh, 1984; Ceballos et al., 1993; Miller et al., 1994). What are the ecological consequences of the prairie dogs' disappearance? There is evidence that grasslands occupied by prairie dogs have been negatively impacted, from the landscape level to the species level. Unfortunately the reduced abundance and range of prairie dogs makes it difficult to assess the role of these animals on grassland ecosystems. Most of the remnant colonies are small and the documented effects of prairie dogs on ecosystem processes and biodiversity have not been conclusive. In this study we evaluated the effect of prairie dogs on habitat heterogeneity and species diversity of small mammals and carnivores. We used burrow density as an indicator of habitat heterogeneity. We evaluated the hypotheses that burrow density and diversity of small mammals and carnivores increase in grasslands occupied by black-tailed prairie dogs (Cynomys ludovicianus) town's. Our study site was located in north-western Mexico, in the Janos-Nuevo Casas Grandes complex, which is probably the largest continuous prairie dog complex left in North America (Ceballos et al., 1993). This complex offers a unique opportunity to carry out studies to evaluate the role of prairie dogs on their ecosystem because it is of similar size to their former colonies.

Materials and methods

This study was carried out from 1992 to 1996 in the Janos-Nuevo Casas Grandes (JNCG) prairie dog complex (Ceballos *et al.*, 1993). The complex is located on the grasslands and scrublands south-east of the Sierra Madre Occidental, in the state of Chihuahua (around 30°50′ N, 108°25′ W), approximately 50 km south of the Mexico–U.S. border. The grasslands merge to the west and north into arid scrub typical of the Chihuahuan Desert and into pinyon and oak forests to the south and east in the foothills of the Sierra Madre Occidental. Hot summers and cold winters characterize the arid climate. Mean annual precipitation is 307 mm, with most precipitation concentrated in July and August; scattered showers occur during the winter (Rzedowski, 1981). The mean temperature is 15·7°C (García, 1973), ranging from –15°C in winter to 50°C during the summer. Grasslands are characterized by grasses and annual herbs, including *Bouteloa gracilis*, *B. curtipendula*, *B. hirsuta*, *Aristida hamulosa*, *Fouqueria splendens*, *Prosopis laevigata*, *Festuca imbricata*, and *Hilaria*

mutica. There are isolated patches of cholla (*Opuntia* spp.), yucca (*Yucca* spp.), ephedra (*Ephedra trifurca*), and mesquite (*Prosopis* spp.) scrub within the grasslands.

Hereafter, we refer to grasslands without prairie dogs also as grasslands, and grasslands with prairie dogs also as colonies.

Burrow density and soil removal

Total and active prairie dog (*Cynomys ludovicianus*) burrow densities were determined by running 1 km \times 3 m wide parallel transects (0·3 ha) systematically through grasslands and prairie dog colonies, using Rolatape distance-measuring wheels. Transects were oriented toward the prairie dog town. When the outer edge of the town was reached, transects were turned 90 degrees toward the unsampled section of the town. After 40 m, transects were again turned 90 degrees, creating a transect parallel to the previous one, but in the opposite direction. All transects were separated by 40 m. Because of the overwhelming differences in burrow densities, only 20 km of transects were carried out in grasslands without prairie dogs and 385 km in grasslands with prairie dogs.

To calculate the amount of soil removed and mixed by prairie we used the figures provided by Sheets *et al.* (1971). A typical prairie dog burrow system has two entrances, 1 to 3 m deep, 15 m long, and 10 to 13 cm in diameter. Whicker & Detling (1993) calculated that prairie dogs mix around 200 to 225 kg of soil per burrow system. We used these figures for both areas with and without prairie dogs. This method overestimates the amount of soil removed in areas without prairie dogs, because there were also burrows made by kangaroo rats or carnivores. However, the lack of data on specific soil removal for other species precluded us from making a more precise analysis.

Small mammal surveys

Small mammals were live-trapped in two grassland sites with prairie dogs, and in one grassland site without prairie dogs, the only site with no evidence of prairie dog activity. Three 0.56 ha grids separated by at least 300 m were set in each grassland. Information was collected for three consecutive nights during the new moon period, in trapping sessions carried out in August and October 1992, and February 1993. On each plot, 72 Sherman traps $(23 \times 8 \times 9 \text{ cm})$ were set at permanent stakes, 9 m apart, arranged in a 9×8 grid. Traps were baited with a mixture of rolled oats, peanut butter, and vanilla extract. Captured individuals were marked with an ear-tag or toe clipping. For every animal captured we recorded the species, individual number, sex, weight, age, reproductive condition, ear and foot length, and place of capture. To estimate population density we considered an area of 0.9 ha for each quadrat, to account for the edge effect. To calculate the edge effect we added an area around the border of the plot, similar to the average displacement (20 m) between trapping sessions that rodents displayed in a previous study in the area (Pacheco, 1998).

Carnivore surveys

Carnivore diversity was determined from 1994 to 1996, using scent-stations and spotlighting transects. In 1994, 410 scent stations, which consisted of 1 m² of fine dust baited with canned sardine, were set up in a stratified design in grasslands with (230 stations) and without (180 stations) prairie dogs. Scent stations were 500 m apart

		Total burrow number	Burrow density (b ha ⁻¹)	
Colony	Km sampled		Total	Active
El Alto	90	1143	42.3	26.9
El Cuervo I	49	723	48.9	32.1
El Cuervo 2	86	1279	49.5	29.7
Salto de Ojo	62	1563	84.3	53.2
Pancho Viľla	24	449	$62 \cdot 3$	30.7
Tierras Prietas	74	1914	86.5	$55 \cdot 6$
Total	385	7071	61.2	38.0

Table 1. Total and active burrow density (per ha) in six prairie dog towns in the Janos-Nuevo Casas Grandes Complex, Chihuahua, Mexico

located on 5 km transects separated by a minimum distance of 2 km. Each transect was sampled on only one night. Between 1994 and 1995 carnivores were sampled every month by conducting 1234 km of spotlighting transects by car; a stratified design was used where 787 and 446 km of the transects were located in grasslands with and without prairie dogs, respectively. Transects covered a total area of 740 km 2 (472-4 and 268-1 km 2 in areas with and without prairie dogs, respectively). Each transect was conducted only once each season/month.

Results

Burrow density and soil removal

The number of burrows per unit area was higher in areas with prairie dogs. The average number of burrows per hectare (b h $^{-1}$) was 52·7, with a relatively high spatial variation, i.e. among colonies, where range values were 42·3 and 86·5 b h $^{-1}$ (Table 1). Of these, 51% were active. Assuming a similar average density throughout all the 55,000 ha of prairie dog colonies, the total number of burrows in the Janos-Nuevo Cases Grandes Complex would be 2,898,500, including 1,478,235 active and 1,420,265 inactive burrows. The number of burrows in grasslands without prairie dogs was, on average, 6·3 ha $^{-1}$, ranging from 3·3 to 16·6. This includes the burrows of carnivores and kangaroo rats (*Dipodomys spectabilis*).

The amount of soil removed in prairie dog colonies and grasslands was very different. Values for prairie dog towns varied from 4759 to 9731 kg ha⁻¹ with an average of 5930 kg ha⁻¹. In contrast, values for grasslands varied from 371 to 1867 kg ha⁻¹ with an average of 708 kg ha⁻¹. Altogether, prairie dogs could remove 326,000 tons of soil in the Janos-Nuevo Casas Grandes complex.

Small mammal diversity

Small mammal diversity was higher in grasslands with prairie dogs (Table 2). Ten species of small mammals representing three families (Sciuridae, 1 spp; Heteromyidae, 4 spp; Muridae, 5 spp) were collected. Species recorded were granivorous (*Perognathus flavus, Chaetodipus hispidus, Dipodomys merriami, Dipodomys spectabilis, Peromyscus leucopus*, and *Reithrodontomys megalotis*), herbivorous (*Spermophilus spilosoma, Sigmodon fulviventer*, and *Neotoma albigula*), or insectivorous (*Onychomys torridus*). Sizes varied from 7 to 200 g.

There were important differences in species composition, richness, diversity, and density in grasslands with and without prairie dogs (Table 2; Fig. 1). All species found

Table 2. Small mammal composition and diversity in grasslands with prairie dogs (Cynomys					
ludovicianus) (El Cuervo, San Pedro) and without prairie dogs (La Loma) in the					
Janos-Nuevo Casas Grandes, Chihuahua, Mexico					

Locality	Species richness	Diversity H'	Evenness J'		Species	Density (individuals ha^{-1})
El Cuervo	10	0.881	0.881	47.0	C.h.	14.1
					P.f.	$7 \cdot 4$
					O.t.	$5 \cdot 2$
					P.l.	$5 \cdot 2$
					D.s.	$4 \cdot 4$
					D.m.	4.1
					R.m.	3.0
				S.f.	$1 \cdot 4$	
					N.a.	1.4
					S.s.	0.7
San Pedro	4	0.562	0.933	$24 \cdot 1$	O.t.	8.6
					P.f.	8.1
					C.h.	14.1
					D.s.	$2 \cdot 6$
La Loma	6	0.666	0.856	13.3	O.t.	3.7
					D.m.	3.7
					C.h.	1.1
					P.l.	0.7
					D.s.	0.3

Statistical comparisons:

Diversity: Hutcheson test (Zar, 1984).

in grasslands were found in prairie dogs colonies. Interestingly, four species occurred only in the grasslands (*S. spilosoma*, *P. flavus*, *S. fulviventer*, and *N. albigula*). Three of these species were herbivorous and one granivorous. Species richness varied from four to ten species in grasslands with prairie dogs (El Cuervo and San Pedro, respectively) and was six in the grassland without prairie dogs (La Loma).

Trends of species diversity were variable, with grasslands without prairie dogs having an intermediate diversity (Table 2). El Cuervo had statistically higher species richness. Species diversity was similar in San Pedro and La Loma. The three localities had a relatively similar homogeneity or evenness, indicating that the abundance of species was similar.

Total small mammal densities were statistically higher in prairie dog colonies when compared with grasslands (two-way ANOVA, df. = 29, p > 0.01). Species density was almost four times higher (El Cuervo) and two times higher (San Pedro) than in La Loma. Species density varied from > 1 to 14 individuals ha⁻¹. Only four species reached densities higher than 7 individuals ha⁻¹. *Chaetodipus hispidus* occurred at highest densities in El Cuervo, and *Dipodomys spectabilis* (0·3 individuals ha⁻¹) had the lowest densities in La Loma. The densities of species found in the three sites showed a similar trend, being consistently higher in grasslands with prairie dogs (Table 2). This was the case for *Perognathus flavus* and *Onychomys torridus* (densities in San Pedro > El Cuervo > La Loma).

⁽¹⁾ San Pedro-El Cuervo: $t \cdot 0.05$ (2) 87.22 = 1.987, $t \cdot 0.05 = -4.435$, p < 0.001.

⁽²⁾ San Pedro-La Loma: $t \cdot 0.05$ (2) 128.86 = 1.978, $t \cdot 0.05 = -1.31$, p > 0.05.

⁽³⁾ El Cuervo-La Loma: $t \cdot 0.05$ (2) 66.52 = 1.997, $t \cdot 0.05 = 4.27$, p < 0.001.

C.h. = Chaetodipus hispidus; P.f. = Perognathus flavus; O.t. = Onychomys torridus; P.l. = Perognathus leucopus; D.s. = Dipodomys spectabilis; D.m. = Dipodomys merriami; R.m. = Reithrodontomys megalotis; S.f. = Sigmodon fulviventer; N.a. = Neotoma albigula; S.s. = Spermophilus spilosoma.

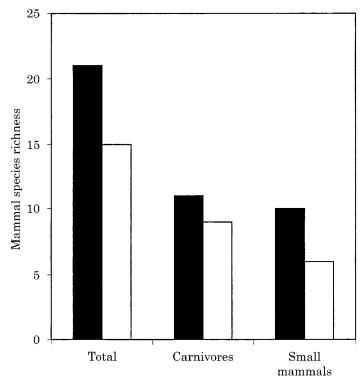


Figure 1. Comparisons of total species richness, small mammals, and carnivores in grasslands with and without black-tailed prairie dogs (*Cynomys ludovicuianus*) in north-western Mexico.

Carnivore diversity

Contrary to our expectations, there were practically no differences in carnivore diversity in areas with and without prairie dogs (Tables 3 & 4). We recorded 11 species that represented four families (Canidae, *Canis latrans, Vulpes macrotis*; Felidae, *Lynx rufus*;

Table 3. Carnivore composition and diversity based on scent stations and spotlighting in grasslands with and without prairie dogs (Cynomys ludovicianus) in the Janos-Nuevo Casas Grandes. Chihuahua. Mexico

Method	Species richness	Diversity <i>H</i> ′	Evenness J'	Occurrence
Scent station				
With prairie dogs Without prairie dogs	7 8	0·5504 0·6527	0·6513 0·7228	51 48
Spotlighting				
With prairie dogs Without prairie dogs	7 6	0·5262 0·5660	0.6227 0.7274	237 119
Total				
With prairie dogs Without prairie dogs	11 9			

Table 4. Relative abundance (in average number of individuals seen per 10 km of transect) of carnivores in grasslands with and without prairie dogs in the Janos-Nuevo Grandes complex. Data obtained in spotlighting transects. Basariscus astutus and Lynx rufus are excluded from this table because they were only recorded in scent stations

	With prairie dogs	Without prairie dogs	
Canis latrans	1.145	0.655	
Vulpes macrotis	1.366	0.923	
Mustela frenata	0.002	0.0	
Taxidea taxus	0.01	0.008	
Conepatus mesoleucus	0.002	0.0	
<i>Mephitis</i> spp.	0.155	0.940	
Spilogale putorius	0.001	0.0	
Procyon lotor	0.0	0.004	

Mustelidae, *Mustela frenata, Taxidea taxus, Conepatus mesoleucus, Mephitis macroura, Mephitis mephitis, Spilogale putorius*; Procyonidae, *Procyon lotor, Bassariscus astutus*). Because of similar tracks and physical appearance, *Mephitis macroura* and *M. mephitis* were analysed by genus in all analyses except species richness. The composition, richness, and abundance of carnivore species in prairie dog colonies and grasslands were similar (Tables 3 & 4). The most abundant species were kit foxes and coyotes, followed by Mephitis skunks and badgers (*Taxidea taxus*). Other species were recorded at low numbers. *Lynx rufus* was only recorded in prairie dog colonies. Mephitis skunks were more abundant in grasslands ($0.9 \ vs \ 0.15 \ individuals \ per 10 \ km transect, respectively; <math>t = 6.04, \ p < 0.005$).

Discussion

Prairie dogs as ecosystem engineers

Our results support the hypothesis that prairie dogs and their activities have profound impacts on grassland ecosystems by increasing habitat heterogeneity, modifying ecosystem processes, and enhancing regional biodiversity. Prairie dogs can be considered to be ecosystem engineers (*sensu* Jones *et al.*, 1994) because they influence the abiotic and biotic characteristics of their habitat, landscape architecture, and ecosystem structure and function (Fig. 2). Prairie dogs and their burrowing activities alter soil properties, and modify chemical and physical characteristics, soil mix, turnover rates, microclimate, and patchiness (e.g. Sheets *et al.*, 1971; Munn, 1993; Whicker & Detling, 1993). For example, we estimated that rodents at our study site removed several hundred thousand tons of soil.

Burrow systems also alter the surface topography, runoff, and water infiltration (Koford, 1958, Munn, 1993). Prairie dogs modify vegetation structure, plant composition, plant communities, biomass production, below/above-ground biomass, and nutrient cycling (see Archer *et al.*, 1987; Weltzin *et al.*, 1997*a*; Whicker & Detling, 1993 for summaries). The combined result of all these effects is the maintenance of grasslands and their biodiversity and the prevention of desertification in the American South-west (Weltzin *et al.*, 1997*a*).

Prairie dogs as keystone species

Our work and many other studies indicate that prairie dogs are a keystone species

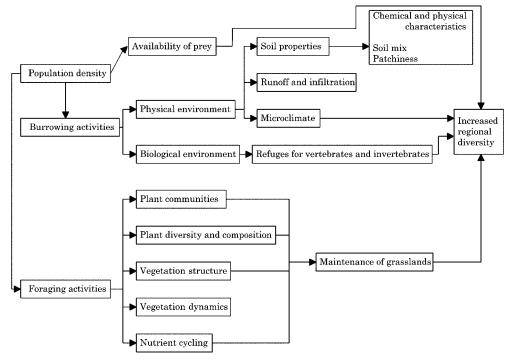


Figure 2. Simplified diagram of the impacts of prairie dogs and their activities in ecosystem function and biological diversity.

(Koford, 1958; Uresk, 1985; Archer et al., 1987; Whicker & Detling, 1988; Cid et al., 1991; Coppock et al., 1983 a, b; List, 1997; Wetzin et al., 1997 a; Pacheco, 1998). There is no doubt that they have a strong influence on the structural and functional characteristics of their habitat, which enhance regional biodiversity. However, recently, there have been strong criticisms about the role of prairie dogs as keystone species. Stapp (1998) indicated that the 'effects of prairie dogs on other animals may be more limited and equivocal' than previously suggested. Such criticisms are difficult to justify because they ignore at least four basic issues.

First, natural variability on the effect of prairie dogs and their activities in grasslands along the huge latitudinal gradient where the species is found should be expected. Very likely, in a similar way to other ecological phenomena, additional studies will show that prairie dogs and their activities influence ecosystem function and promote biological diversity in most but not all grasslands where they occur. It would be simplistic to expect a similar role throughout their geographic range, without taking into account the variability in physical and biotic conditions of these grassland ecosystems. Second, historically, prairie dogs occupied millions of hectares and typical colonies had hundreds of thousands to millions of individuals. Presently, most colonies are extremely small, fragmented and isolated. Under these 'unnatural' conditions it is likely that the effects of prairie dogs are underestimated. Third, many studies have evaluated the relationship of prairie dogs on vertebrate diversity by comparing adjacent grasslands that, in biological terms, form a continuum for vertebrate species. A more realistic scenario is to select areas that are properly separated to constitute different habitats.

More importantly, there are rigorous studies that have shown profound effects of prairie dogs and their activities on individual species and communities of mammals and

birds. We are not aware of similar studies on reptiles and amphibians. Prairie dogs can influence the diversity of vertebrates through their presence (as prey), and through foraging and burrowing activities. For example, in the flat landscape of the Janos-Nuevo Casas Grandes grasslands, trees and surface rocks are lacking or are very scarce. In these areas, underground burrows are sites of refuge for many vertebrates and invertebrates. In fact, of 21 species of vertebrates that we have observed to den in the prairie dog burrows of the area (Appendix), 11 depend on available shelters for their survival, while the remaining 10 are capable of digging their own burrows. Digging through the hard ground of the prairie is a difficult task at which prairie dogs are proficient (Hoogland, 1995); therefore, all these species benefit from the fossorial activities of the prairie dogs by having available 10 times as many burrows to use than in grasslands without prairie dogs. Furthermore, kit foxes are preyed upon by coyotes, which are their main source of mortality in some areas (Ralls & White, 1995). Kit foxes can escape more easily from coyote predation in areas with more burrows. This is probably a major cause for the increased survival of the kit foxes in our study area compared to other parts of their range (List, 1997).

Several studies have shown that birds such as the burrowing owl (*Speotyto cunicularia*) depend on prairie dog burrows for shelter (Butts & Lewis, 1982; Desmond *et al.*, 1995; Desmond & Savidge, 1996). Grasslands birds (Agnew *et al.*, 1986; Manzano *et al.*, in press), raptors (Cully, 1991), and other species such as mountain plovers (*Charadrius montanus*, Knowles *et al.*, 1982) are also more abundant in prairie dog towns than in adjacent grasslands.

Our study showed a differential response by small mammals and carnivores to the presence of prairie dogs. As shown by other studies (e.g. O'Meilia *et al.*, 1982; Agnew *et al.*, 1986), we found that small mammal species richness, diversity, and density (or abundance) were higher in areas with prairie dogs when compared with grasslands without prairie dogs. At our study site (List & McDonald, in press), and in other sites (Dano, 1952, cited in Stapp, 1998), cottontail rabbits (*Sylvilagus* spp.) were more abundant in prairie dog towns.

In contrast, our results showed that carnivore species richness, diversity, and density did not strongly differ in grasslands with and without prairie dogs. There are several possible explanations for these results. Individuals of medium size, and larger mammals with high vagility, may use large areas that include adjacent prairie dogs towns, grasslands, and other habitats. That is indeed the case in our study site for coyotes and kit foxes, where average home range size was 90 and 11.5 km², respectively, and included grasslands, prairie dog towns, and mesquite scrubs (List, 1997). On the other hand, prairie dogs can positively influence carnivores in subtle ways. For example, the local distribution and activity of badgers (Taxidea taxus) depends on fossorial prey, such as the prairie dog (Clark et al., 1982; Messick, 1987). In our study site prairie dogs were the main prey for coyotes and kit foxes, even for individuals that had their dens far away from the prairie dog towns (List, 1997). We suggest that the density of carnivores would decrease if prairie dogs were absent. The magnitude of carnivore decrease would depend on the degree to which a species depended on prairie dogs for food or for shelter (see also Miller et al., 1994). The best example of such an effect is the black-footed ferret (Mustela nigripes) which almost became extinct as a result of the reduction of the prairie dog ecosystem (Miller et al., 1994).

Implications for conservation

Miller *et al.* (1994) discussed the basic data for considering prairie dogs to be a keystone species, and its implications for conservation and policy-making. We have

presented further evidence supporting the concept of prairie dogs as keystone species. We strongly disagree with Stapp (1998) who argues that more data are needed to justify the protection of prairie dogs in grassland ecosystems. We feel that additional data will only confirm what we already know. With less than 5% of their original range remaining, it would be a historical mistake to wait further. Protecting prairie dogs offers a unique opportunity to maintain the grasslands and their biodiversity in North America. This is a case were a single-species approach to conservation is amply justified.

Finally, we would like to emphasize the importance of the Janos-Nuevo Casas Grandes complex to protect the prairie dog ecosystem and to understand the role of prairie dogs in ecosystem function and biodiversity. This very large complex offers a unique opportunity to evaluate the role of prairie dogs on their ecosystem because it resembles the former magnitude of prairie dog colonies.

We would like to express our gratitude to Fenton R. Kay for his encouragement. B. Kotler and an anonymous reviewer made suggestions that improved the final manuscript. Our field work in the Janos region has been kindly supported by the National University of Mexico (UNAM), the National Council of Science and Technology (CONACyT), the Ministry of the Environment (SEMARNAP), the AID program (US) and The People's Trust for Endangered Species (PTES).

References

- Agnew, W., Uresk, D.W. & Hansen, R.M. (1986). Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed grass prairie in western South Dakota. *Journal of Range Management*, 39: 135–139.
- Archer, S.R., Garret, M.G. & Detling, J.K. (1987). Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. *Vegetario*, 72: 159–166.
- Bonham, C.D. & Lerwick, A. (1976). Vegetation changes induced by prairie dogs on shortgrass range. *Journal of Range Management*, 29: 221–225.
- Butts, K.O. and Lewis, J.C. (1982). The importance of prairie dog towns to burrowing owls in Oklahoma. *Proceedings of the Oklahoma Academy of Science*, 62: 46–52.
- Campbell, T.T., III and Clark, T.W. (1981). Colony characteristics and vertebrate associates of white-tailed and black-tailed prairie dogs in Wyoming. *American Midland Naturalist*, 105: 269–276.
- Ceballos, G., Mellink, E. & Hanebury, L. (1993). Distribution and conservation status of prairie dogs (*Cynomys mexicanus* and *C. ludovicianus*) in Mexico. *Biological Conservation*, 63: 105–112.
- Cid, M.S., Detling, J.K., Whicker, A.D. & Brizuela, M.A. (1991). Vegetational responses of a mixed-grass prairie site following exclusion of prairie dog and bison. *Journal of Range Management*, 44: 100–105.
- Clark, T.W., Campbel, T.M., III, Socha, D.G. & Casey, D.E. (1982). Prairie dog colony attributes and associated vertebrate species. *Great Basin Naturalist*, 24: 572–582.
- Coppock, D.L., Detling, J.K., Ellis, J.E. & Dyer, M.I. (1983*a*). Plant–herbivore interaction in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia*, 56: 1–9.
- Coppock, D.L., Ellis, J.E., Detling, J.K. & Dyer, M.I. (1983b). Plant–herbivore interaction in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. *Oecologia*, 56: 10–15.
- Cotera-Correa, M. (1996). Untersuchungen zur ökologischen Anpassung des Wüstenfuchses Vulpes macrotis zinseri B. in Nuevo León, Mexiko. Ph.D. thesis, Ludwig-Maximilians-Universität München. 105 pp.
- Cully, J.F., Jr. (1991). Response of raptors to reduction of a Gunnison's prairie dog population by plague. *American Midland Naturalist*, 125: 140–149.
- Desmond, M.J. & Savidge, J.A. (1996). Factors influencing burrowing owl (*Speotyto cunicularia*) nest densities and numbers in western Nebraska. *American Midland Naturalist*, 136: 143–148.

- Desmond, M.J., Savidge, J.A. & Seibert, T.F. (1995). Spatial patterns of burrowing owl (*Speotyto cunicularia*) nests within black-tailed prairie dog (*Cynomys ludovicianus*) towns. *Canadian Journal of Zoology*, 73: 1375–1379.
- García, E. (1973). *Modificaciones al sistema de clasificación climática de Köeppen* (2a Ed). México D.F.: Instituto de Geografía. Universidad Nacional Autónoma de México, 220 pp.
- Hoogland, J.L. (1995). The Black-tailed Prairie Dog. Chicago: The University of Chicago Press, 557 pp.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1994). Organisms as ecosystems engineers. Oikos, 69: 373–386.
- Knopf, F.L. (1994). Avian assemblages on altered grasslands. Studies in Avian Biology, 15: 247–257.
- Knowles, C.J., Stoner, C.J. & Gieb, S.P. (1982). Selective use of black-tailed prairie dog towns by mountain plovers. *Condor*, 84: 71–74.
- Koford, C.B. (1958). Prairie dogs, whitefaces, and blue grama. Wildlife Monographs, 3: 6-78.
- List, R. (1997). Ecology of kit fox (*Vulpes macrotis*) and coyote (*Canis latrans*) and the conservation of the prairie ecosystem in northern Mexico. Unpublished Ph.D. thesis, University of Oxford, Oxford. 189 pp.
- List, R. & Macdonald, D.W. (in press). Species inventory and abundance of carnivores in the Janos-Nuevo Casas Grandes prairie dog Complex. *Revista Mexicana de Mastozoología*.
- Manzano, P., List, R. & Ceballos, G. (in press). Avian diversity in grasslands from Northwestern Mexico. *Journal of Field Ornithology*.
- Marsh, R.E. (1984). Ground squirrels, prairie dogs and marmots as pest on rangeland. In: *Proceedings of the conference for organization and practice of vertebrate pest control*, August 30, September 3, 1982, Hampshire, England. pp. 195–208. Fernherst, Inglaterra: ICI Plant Protection Division.
- Mellink, E. & Madrigal, H. (1993). Ecology of Mexican prairie dogs, *Cynomys mexicanus*, in El Manantial, northeastern Mexico. *Journal of Mammalogy*, 74: 631–635.
- Messick, J.P. (1987). North American badger. In: Novak, M., Baker, G.A., Obbard, M.E. & Malloch, B. (Eds), Wild Furbearer Management and Conservation in North America, pp. 587–597. Ontario, Canada: Ontario Trappers Association, Ministry of Natural Resources. 1168 pp.
- Miller, B., Ceballos, G. & Reading, R. (1994). The prairie dog and biotic diversity. *Conservation Biology*, 8: 677–681.
- Munn, L.C. (1993). Effects of prairie dogs on physical and chemical properties of soils. In: Oldemeyer, J.L., Biggins, D.E., Miller, B. & Crete, R. (Eds), *Proceedings of the Symposium on the Management of prairie dog complexes for the reintroduction of the black-footed ferret*, pp. 11–17. Washington DC: Fish and Wildlife Service, Dept. of Interior. 96 pp.
- O'Meilia, M.F., Knopf, F.L. & Lewis, J.C. (1982). Some consequences of competition between prairie dogs and beef cattle. *Journal of Range Management*, 35: 580–585.
- Pacheco, J. (1998). Relación entre los perros de la pradera y el mantenimiento de la biodiversidad en el noroeste de Chihuahua. Tesis de Maestría, Facultad de Ciencias, Universidad Nacional Autónoma de México, México D.F.
- Ralls, K. & White, P.J. (1995). Predation of San Joaquin kit foxes by larger canids. *Journal of Mammalogy*, 76: 723-729.
- Rzedowski, J. (1981). Vegetación de México. México, D.F.: Limusa.
- Sharp, J.C. & Uresk, D.W. (1990). Ecological review of Black-tailed prairie dogs and associated species in Western South Dakota. *Great Basin Naturalist*, 50: 339–345.
- Sheets, R.G., Linder, R.L. & Dahlgren, R.B. (1971). Burrow systems of prairie dogs in South Dakota. *Journal of Mammalogy*, 52: 451–453.
- Stapp, P. (1998). A re-evaluation of the role of prairie dogs in Great Plains grasslands. *Conservation Biology*, 12: 1253–1259.
- Uresk, D.W. (1985). Effects of controlling black-tailed prairie dogs on plant production. *Journal of Range Management*, 38: 466–468.
- Weltzin, J.F., Archer, S. & Heitschmidt, R.K. (1997*a*). Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology*, 78: 751–763.
- Weltzin, J.F., Dowhower, L. & Heitschmidt, R.K. (1997b). Prairie dog effects on plant community structure in southern mixed-grass prairie. *Southwestern Naturalist*, 42: 251–258.
- Whicker, A.D. & Detling, J.K. (1988). Ecological consequences of prairie dog disturbances. *Bioscience*, 38: 778–785.

Whicker, A.D. & Detling, J.K. (1993). Control of grassland ecosystem processes by prairie dogs. In: Oldemeyer, J.L., Biggins, D.E., Miller, B. & Crete, R. (Eds), Proceedings of the Symposium on the Management of prairie dog complexes for the reintroduction of the black-footed ferret, pp. 18–27. Washington DC: Fish and Wildlife Service, Dept. of Interior. 96 pp.

Zar, J. H. (1984). Biostatistical Analysis (2nd Edn). Englewood Cliffs, NJ: Prentice-Hall. 718 pp.

Appendix 1. Vertebrate species observed to use prairie dog burrows on the Janos-Nuevo Casas Grandes prairie dog complex in north-western Chihuahua, Mexico

Class	Order	Family	Genus and species	Common name
Reptilia	Sauria			
	Sugriu	Prynosomatidae		
		T)	Phrynosoma cornutum Phrynosoma douglasi Sceloporus undulatus Holbrookia maculata	horned lizard horned lizard spiny lizard
	Serpentes	Teiidae	Cnemidophorus exsanguis Cnemidophorus uniparens	whiptail lizard whiptail lizard
	Serpentes	Colubridae		
			Pituophis melanoleucus Thamnophis eques	
	N	Viperidae	Crotalus molossus Crotalus viridis	rattle snake rattle snake
	Testudines	Emydidae	Terrapene ornata	box terrapin
		Kinosternidae	Kinosternon flavescens	mud turtle
Aves	Strigiformes	g		
		Strigidae	Speotyto cunicularia	burrowing owl
Mammalia	Lagomorpha		Sylvilagus audubonii	desert cottontail
	Rodentia		Sylvilagus audubbilli	desert cottonian
		Sciuridae	Spermophilus spilosoma	ground squirrel
	Carnivora	Canidae		
			Canis latrans Vulpes macrotis	coyote kit fox
		Procyonidae	v агрез тастонs	AIL IUA
		v	Bassariscus astutus	ringtail
		Mustelidae	Mustela frenata Taxidea taxus Mephitis mephitis	long-tailed wease badger striped skunk