Landscape and Community Characteristics of Black-tailed Prairie Dog Colonies

Whitney C. Johnson
B.S. University of Colorado at Boulder, 1995

A thesis submitted to the
Faculty of the Graduate School
of the University of Colorado in partial
fulfillment of the requirements for a
Master of Arts degree
Department of Environmental, Population, and Organismic Biology
2002

CONTENTS

TABLES

FIGURES

Johnson, Whitney Charles (Master of Arts, Environmental, Population, and Organismic Biology)

Landscape and Community Characteristics of Black-tailed Prairie Dog Colonies

Thesis directed by Assistant Professor Sharon K. Collinge

Black-tailed prairie dogs (*Cynomys ludovicianus*) significantly affect the distribution and abundance of many grassland species. Small mammal communities on black-tailed prairie dog colonies may serve as reservoirs for sylvatic plague (*Yersinia pestis*) by harboring infected fleas. I compared small mammal communities on and off six black-tailed prairie dog colonies to determine which small mammal species are possible plague hosts. Rodent communities on prairie dog colonies were dominated by deer mice (*Peromyscus maniculatus*), and were less diverse than those off prairie dog colonies. Hispid pocket mice (*Chaeotdipus hispidus*) were more abundant on grasslands without prairie dogs, and western harvest mice (*Reithrodontomys megalotis*) were observed only in grasslands without prairie dogs. In the Boulder, Colorado, black-tailed prairie dog colonies have lower small mammal species diversity, but do not affect the density of small mammals. To properly conserve native biodiversity in mixed-grass prairies, managers should balance the preservation needs of prairie dog colonies and their associated small mammal communities with the preservation needs of the species not found on prairie dog colonies.

I also studied prairie dog density and the density of active burrow entrances (burrow density) within a colony relative to the amount of urbanization, roads, and other prairie dog colonies at 200-, 1000- and 2000-m from the perimeter of 22 colonies. I used burrow density as a proxy for prairie dog density. Burrow density within a colony increased as the amount of urbanization and roads increased in the landscape at all spatial scales. However, burrow density was not correlated with the amount of other prairie dog colonies in the landscape. Using Akaike's Information Criterion (AIC), I determined the best, most parsimonious models that predicted burrow density. Three variables: boundedness, the density of roads at the 2000-m scale, and the percentage of the landscape covered with other prairie dog colonies at the 200-m scale best predicted prairie dog active burrow entrance density. My results indicate that anthropogenic landscape features immediately surrounding prairie dog colonies and up to 2-km away were both positively related to the density of black-tailed prairie dogs, whereas nearby prairie dog colonies may slightly lower prairie dog density within colonies.

Introduction

Prairie dogs (*Cynomys* spp.) create major ecological disturbances in the grassland ecosystems they occupy (Coppock et al. 1983). They significantly reduce vegetation height, species richness and cover, and excavate burrows that offer shelter for other grassland species (Coppock et al. 1983; Whicker & Detling 1988; Kotliar et al. 1999). These open habitats contrast with the surrounding grassland thereby contributing to local and regional landscape heterogeneity (Whicker & Detling 1988; Kotliar et al. 1999). The associated localized disturbance brought on by the presence of prairie dog colonies is thought to beneficially affect grassland biodiversity at broader spatial scales. It has been claimed that over 200 species rely on prairie dogs and their colonies for persistence (Clark et al. 1982; Sharps & Uresk 1990; Kotliar et al. 1999). For these reasons, prairie dogs are considered to be a keystone species (sensu Paine 1969) and ecosystem engineer (sensu Jones et al. 1994) of short- and mixed-grass prairie ecosystems in western North America. Keystone species are defined as those that have a disproportionate effect on the structure and function of an ecosystem relative to their abundance, and performing a role unlike any other species in the community (Paine 1969; Power et al. 1996; Kotliar et al. 2000). It is believed that if prairie dogs were to go extinct, or even be locally extirpated, many species that rely on prairie dogs and their colonies would also disappear (Miller et al. 1990, 1994).

Whether prairie dogs actually are keystone species has come under recent debate (Miller et al. 1994; Stapp 1998; Kotliar et al. 1999). There have been few published ecological studies documenting actual dependence of other species on prairie dog colonies (Stapp 1998; Kotliar et al. 1999). Only nine out of a cited 208 species have been found to depend on prairie dogs for food, shelter, or at least one of the associated changes prairie dogs make to the prairie ecosystem (Kotliar et al. 1999). Black-footed ferrets (*Mustela nigripes*), mountain plovers (*Charadrius montanus*), and burrowing owls (*Athene cunicularia*) in particular have been shown to have strong links to grasslands with prairie dog colonies. The critically endangered black-footed ferrets primary diet is the prairie dog and ferret's are also dependent on prairie dog burrows for shelter; ferrets will not survive without large prairie dog colony complexes (Minta & Clark 1989; Miller et al. 1990, 1994; Kotliar et al. 1999). Burrowing owls use prairie dog burrows for shelter (Miller et al. 1994; Desmond & Savidge 1996; Kotliar et al. 1999). Prairie dogs were found twice as often in badgers (*Taxidea taxus*) stomachs and scat than other prey items (Goodrich and Buskirk 1998). Horned larks (*Eremophila alpestris*) are found in higher abundances on prairie dog colonies than in grasslands without prairie dogs (Agnew et al. 1986).

The numerous other species claimed to rely on prairie dog colonies were sighted on prairie dog colonies but no dependent relationship could be concluded from the reviewed papers (Kotliar et al. 1999). Although fewer species depend on prairie dog colonies in grassland ecosystems than once believed, the black-tailed prairie dog is still considered a keystone species because of its ability to drastically change the nutrient dynamics and species composition of short- and mixed-grass prairie ecosystems (Kotliar et al. 1999, 2000).

Black-tailed prairie dogs (*Cynomys ludovicianus*) have been reduced to less than 2% of their historical abundance due to disease, competition with cattle ranching operations, agriculture, and most recently urban and suburban development (Miller et al. 1990, 1994; American Society of Mammalogists 1998). Sylvatic plague (*Yersinia pestis*) kills up to 99% of prairie dogs in affected colonies (Cully et al. 1997; Cully & Williams 2001; Biggins & Kosoy 2001). Furthermore, prairie dogs are increasingly coming into conflict with humans for available habitat along the Colorado Front Range (Colorado Department of Natural Resources 2000). There have been few published studies on the effects of urbanization on prairie dog demography (but see Dawson 1991), probably because prairie dog conflict with urban development is a relatively recent occurrence. In the near future, the terms "urban" and "rural" prairie dogs (Dawson 1991) will be commonplace in prairie dog ecology.

In Chapter I of this study, I report on the effects of prairie dog colonies on small mammal community composition in the mixed-grass prairie of Boulder County, Colorado. It is important to determine what species are present on prairie dog colonies in order to make predictions about possible alternate hosts of plague and about overall disease dynamics in this system. Previous studies of small mammals on and off prairie dog colonies have resulted in conflicting data, and no studies have been completed in the Colorado Piedmont.

In Chapter II, I report on the effects of landscape context on prairie dog density. Most studies on prairie dogs have been completed in non-urbanized areas (Hoogland 1995). However, in Boulder County, Colorado, urbanization is perforating once continuous native grassland and embedding prairie dogs in urban and suburban landscapes. It is poorly understood whether the amount a colony is bounded by unsuitable habitat affects prairie dog density. If colonies surrounded by higher or lower amounts of unsuitable habitat have different prairie dog densities, then prairie dog demography may be different in these areas (Rayor 1985; Dawson 1991). Moreover, higher densities of prairie dogs may increase spread of disease; plague transmission rates increase with higher prairie dog density (Biggins & Kosoy 2001; Cully & Williams 2001). In this study, I determined the effects of increased urbanization and road density on prairie dog density at three spatial scales, and how the area of prairie dog colonies in the surrounding landscape affected prairie dog density. I predicted that the above variables would not affect prairie dog density at any of the three spatial scales.

Literature Cited

Agnew, W., D. W. Uresk, and R. M. Hansen. 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.

American Society of Mammalogists. 1998. American Society of Mammalogists' resolution on the decline of prairie dogs and the grassland ecosystem in North America. Journal of Mammalogy 79:1447-1448.

Biggins, D. E., and M. Y. Kosoy. 2001. Influences of introduced plague on North American mammals: implications from ecology of plague in Asia. Journal of Mammalogy 82:906-916.

Colorado Department of Natural Resources. 2000. Black-tailed prairie dog study of eastern Colorado. Prepared by EDAW, Inc. Fort Collins, CO. 49 pp.

Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983. Plant-herbivore interactions 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

Clark, T. W., T. M. Campbell III, D. G. Socha, and D. E. Casey. 1982. Prairie dog colony attributes and associated vertebrate species. Great Basin Naturalist 42(4):572-582.

Cully, J.F., Jr., A.M. Barnes, T.J. Quan and G. Maupin. 1997. Dynamics of plague in a Gunnison's prairie dog colony complex from New Mexico. Journal of Wildlife Diseases 33:706-719.

Cully, J. F. Jr., and E. S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy 82(4):894-905.

Dawson, R. E. 1991. Comparison of body mass and demography between urban and rural populations of black-tailed prairie dogs (*Cynomys ludovicianus*). Masters Thesis, University of Colorado at Boulder. 71pp.

Desmond, M. J., and J. A. Savidge. 1996. Factors influencing burrowing owl (*Speotyto cunicularia*) nest densities and numbers in western Nebraska. American Midland Naturalist 136:143-148.

Goodrich, J. M., and S. W. Buskirk. 1998. Spacing and ecology of North American badgers (*Taxidea taxus*) in a prairie-dog *(Cynomys leucurus)* complex. Journal of Mammalogy 79(1):171-179.

Hoogland, J.L. 1995. The Black-Tailed Prairie Dog, Social life of a Burrowing Mammal. The University of Chicago Press, Chicago, IL.

Kotliar, N. B. 2000. Application of the new keystone species concept to prairie dogs: how well does it work? Conservation Biology 14(6):1715-1721.

Kotliar, N. B., B. W. Baker, A. D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24(2):177-192.

Miller, B., C. Wemmer, D. Biggins, and R. Reading. 1990. A proposal to conserve black-footed ferrets and the prairie dog ecosystem. Environmental Management 14:763-769.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology 8(3):667-681.

Minta, S. C., and T. W. Clark. 1989. Habitat suitability analysis of potential translocation sites for black-footed ferrets in northcentral Montana. Pp. 29-45 in: The prairie dog ecosystem: managing for biological diversity. Eds. T.W. Clark, D. Hinkley, T. Rich. Montana BLM Wildlife Technical Bulletin No.2.

Paine, R.T. 1969. A note on trophic complexity and community stability. American Naturalist 103:91-93.

Powers, ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, and Paine RT. 1996. Challenges in the quest for keystones. BioScience 46: (8) 609-620.

Rayor, L. S. 1985. Effects of habitat quality on growth, age of first reproduction, and dispersal in Gunnison's prairie dogs (*Cynomys gunnisoni*). Canadian Journal of Zoology 63:2835-2840.

Sharps, J. C., and D. W. Uresk. 1990. Ecological review of black-tailed prairie dogs and associated species in western South Dakota. Great Basin Naturalist 50(4):339-345.

Stapp, P. 1998. A reevaluation of the role of prairie dogs in Great Plains grasslands. Conservation Biology 12(6):1253-1259.

Whicker, A. D., and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances: prairie dogs alter grassland patch structure, nutrient cycling, and feeding-site selection by other herbivores. BioScience 38(11):778-785.

Chapter I: A comparison of small mammal communities on grasslands with and without black-tailed prairie dogs in Boulder County, Colorado

Abstract: Black-tailed prairie dogs (*Cynomys ludovicianus*) significantly affect the distribution and abundance of many grassland species. Small mammal communities on black-tailed prairie dog colonies may aid in the spread of sylvatic plague (*Yersinia pestis*) by serving as a reservoir for infected fleas. I trapped rodents on and off black-tailed prairie dog colonies in Boulder County, Colorado to determine the effect of prairie dogs on small mammal communities. I captured, marked, and released small mammals on six grassland sites with prairie dog colonies and on six adjacent grassland sites without prairie dogs using large Sherman live-traps. Sites with and without prairie dogs had similar small mammal densities; however, sites with prairie dog colonies were dominated by deer mice (*Peromyscus maniculatus*) and had lower small mammal species diversity and richness. Western harvest mice (*Reithrodontomys megalotis*) were only found on grasslands without prairie dogs. Black-tailed prairie dogs significantly affected small mammal community composition in the mixed-grass prairies of Boulder County. Because deer mice were only trapped in grasslands with prairie dogs, deer mice may serve as a reservoir for sylvatic plague on prairie dog colonies.

Introduction

The black-tailed prairie dog (*Cynomys ludovicianus*) historically inhabited approximately 3 million hectares in Colorado (Gillette 1919, as cited in Colorado

Department of Natural Resources 2000) and now only occupies approximately 120,000 hectares (Colorado Department of Natural Resources 2000). Range-wide, disease, poisoning by cattle ranchers, agriculture, and most recently urban and suburban development have reduced prairie dogs to less than 2% of their original abundance (Miller et al. 1990, 1994; American Society of Mammalogists 1998), and prairie dogs now occupy less than 1% of the area in their estimated historic geographic range (Gober 2000). Poisoning and shooting of prairie dogs by ranchers has caused the majority of the prairie dog's decline (Miller et al. 1990, 1994). However, the recently introduced sylvatic plague (*Yersinia pestis*) kills up to 99% of prairie dogs in infected colonies (Cully et al. 1997; Cully & Williams 2001; Biggins & Kosoy 2001). The above factors, in combination with habitat loss from urbanization, were cited as sufficient reason to classify the prairie dog as "warranted, but precluded" on the United States Fish and Wildlife Service's threatened species list (Gober 2000).

Prairie dogs are considered a keystone species (sensu Paine 1969) and ecosystem engineer (sensu Jones et al. 1994; Ceballos et al. 1999) of short- and mixed-grass ecosystems (Miller et al. 1994; Kotliar et al. 1999). Keystone species are defined as those that have a disproportionate effect on the distribution and abundance of other species relative to their own abundance, and that perform a role unlike any other species or process in the same ecosystem (Power et al. 1996; Kotliar et al. 2000). When prairie dogs colonize a new area, they create a significant disturbance by reducing both dead and live vegetation cover and changing plant species composition (Agnew et al. 1986; Coppock et al. 1983a; Whicker & Detling 1988).

Differences in faunal species composition and abundance have been observed on prairie dog colonies when compared to grasslands without prairie dogs. Reduced vegetation height creates suitable habitat for species that prefer relatively open habitats, and unoccupied burrows create shelter for other semifossorial and opportunistic animals (Kotliar et al. 1999). For example, the endangered black-footed ferret's (*Mustela nigripes*) primary prey is the prairie dog and ferrets use prairie dog burrows for shelter; ferrets will not survive without large prairie dog colony complexes (Minta & Clark 1989; Miller et al. 1990, 1994; Kotliar et al. 1999). Burrowing owls (*Athene cunicularia*) and horned larks (*Eremophila alpestris*) have been observed at higher abundances on prairie dog colonies than on grasslands without prairie dogs; however, western meadowlarks (*Sturnella neglecta*) have been observed at higher abundances on undisturbed mixed-grass sites (Agnew et al 1986, Kotliar et al. 1999). Bison (*Bison bison*) and other large ungulates preferentially graze on prairie dog colonies probably due to the increased nitrogen content in the grasses (Coppock et al. 1983b).

Although the black-tailed prairie dog is considered to be a keystone species, in a recent literature review only nine out of a total of 208 species previously claimed to be dependent on prairie dogs were actually found to be strongly associated with grasslands with prairie dog colonies (Kotliar et al. 1999). In western Kansas there were no differences in amphibian and reptile species abundance between sites with and without black-tailed prairie dogs (Kretzer & Cully 2001). Furthermore, amphibian and reptile species diversity was higher on grasslands without prairie dogs, and species composition differed between sites (Kretzer & Cully 2001).

Nevertheless, prairie dogs have a proportionately larger effect on short- and mixed-grass prairie ecosystem structure than other grassland species, and they perform a role unlike any other grassland species, and may therefore be considered a keystone species (Kotliar et al. 1999, 2000).

The effect of prairie dogs on small mammal communities may have implications for disease transmission (i.e., sylvatic plague) in short- and mixed-grass prairie ecosystems (Wilson et al. 1994). Plague kills most black-tailed prairie dogs in affected colonies (Cully et al. 1997; Cully & Williams 2001). It is not known whether small mammal communities on prairie dog colonies serve as alternate host reservoirs for plague (Biggins & Kosoy 2001). Some small mammal species, such as deer mice (*Peromyscus maniculatus*), are more resistant to contracting plague from infected fleas than other small mammal species (Cully 1989; Biggins & Kosoy 2001). Resistant small mammal species may transmit fleas infected with plague to prairie dogs, whereas other small mammal species may die off before they have an opportunity to transmit plague. Therefore, it is important to determine what species are present on prairie dog colonies in order to make predictions about possible alternate hosts of plague and overall disease dynamics in this system.

The effect of prairie dog colonies on small mammal species richness and composition has been studied in Mexico, Oklahoma, and South Dakota, but the results are equivocal. Ceballos et al. (1999) reported that small mammal diversity was variable, but on average higher, on grasslands with black-tailed prairie dogs in northereastern Mexico. Density of small mammals was also significantly higher in grasslands with prairie dog colonies. However, the two sites with prairie dogs had variable species richness (four and ten species), whereas the site without prairie dogs had six species (Ceballos et al. 1999). A study on the Mexican prairie dog (*Cynomys mexicanus*) found higher small mammal species richness and abundance on inactive Mexican prairie dog colonies than on active colonies (Mellink and Madrigal 1993). In Oklahoma, O'Meila et al. (1982) found higher abundance but lower species richness of small mammals on black-tailed prairie dog colonies. Similarly, Agnew et al. (1986) found higher density of small mammals but lower species richness on prairie dog colonies in South Dakota.

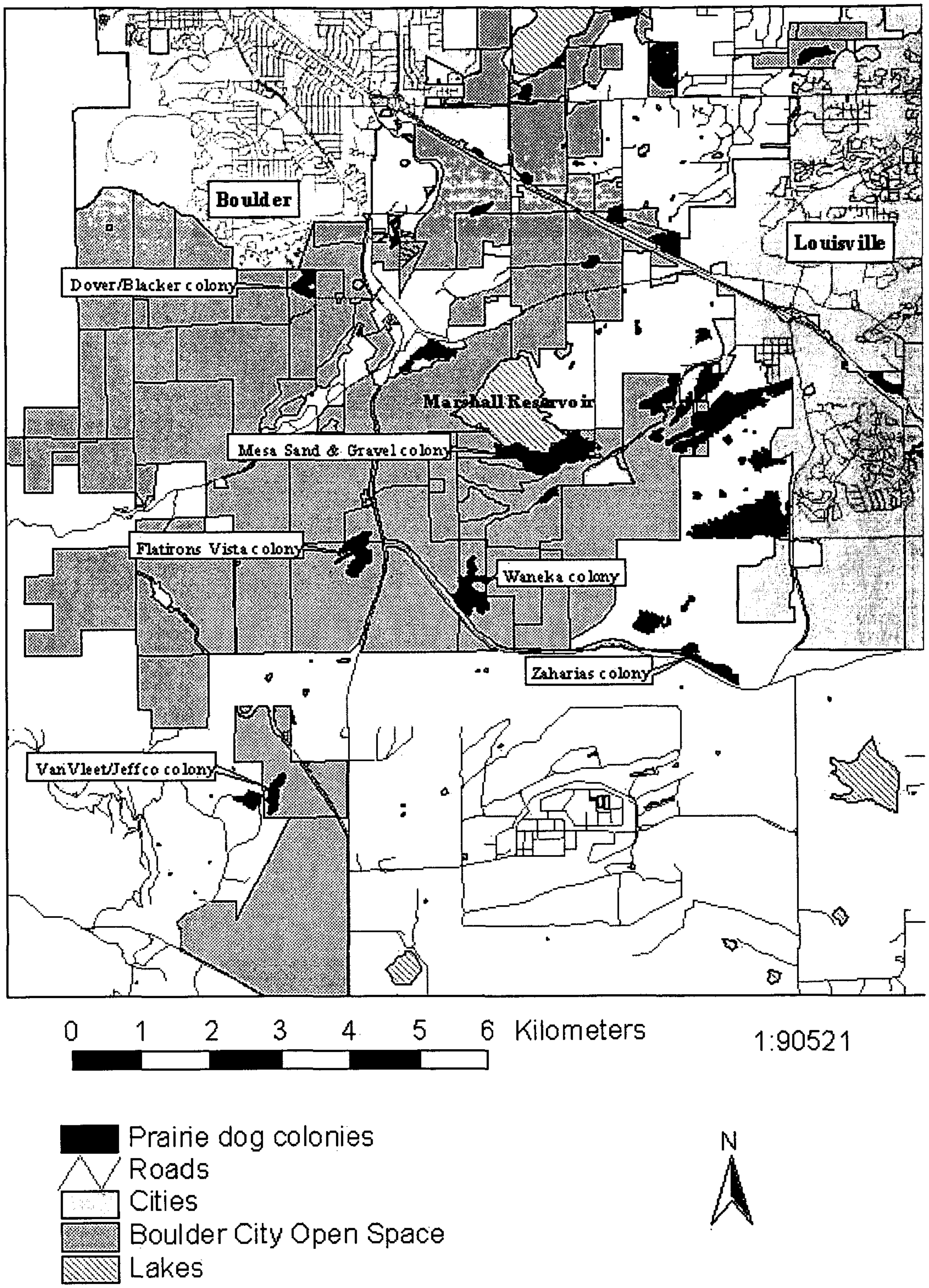
There have been no studies documenting small mammal species composition on and off black-tailed prairie dog colonies on the Colorado Piedmont. In the fall of 2001, I trapped small mammals on six sites with black-tailed prairie dogs and on six sites in similar habitat without black-tailed prairie dogs to test whether prairie dogs influence the distribution and abundance of other small mammals. Based on similar studies of small mammal communities on and off prairie dog colonies in other areas, I expected to find different densities and different species diversity of small mammals on sites with prairie dogs than on sites without prairie dogs.

Methods

I conducted my study in mixed-grass prairie of the Colorado Piedmont south of Boulder, Colorado, USA (all study sites were located between 39.88470° and 39.97151° N, and 105.16543° and 105.25980° W, and the average elevation of all sites was 1790m.). The Colorado Piedmont is the valley between the eastern border of the Rocky Mountains and the High Plains to the east. The City of Boulder has created a greenbelt of protected areas that surround the urban center. These areas, named "Open Space" properties, are protected from development and have various management protocols. For example, some properties are used only for grazing or agriculture, some properties have multi-use recreational trails, and other properties are habitat conservation areas with no public access. All of the Open Space properties that I used for my study allowed limited cattle grazing, but none of the prairie dog colonies have been subjects of control efforts. However, two of my six study sites were affected by plague within the last 10 years.

I trapped small mammals at six paired sites in grasslands with and without prairie dogs during the months of October and November 2001 (Fig. 1). At the six sites with prairie dogs, prairie dog densities ranged from 32 to 63 individuals/ha, and active burrow entrance density ranged from 142 to 216 active burrows entrances/ha. I used a square, 7x7-trap grid (n = 49) of large non-folding Sherman live-traps spaced 5-meters apart within the boundaries of the colony ("colony" grid) and another 7x7-trap grid at a distance of 500-m to 2-km from the edge of the colony in similar habitat ("control" grid). I positioned the colony grid close to the center of the colony to minimize any edge effects (i.e., capturing animals that lived beyond the edge of the colony). I baited traps with molasses covered oats and added cotton bedding. I set traps at 1700 hours and checked traps at 0600 hours. I trapped for four nights, or 196 trap-nights, at each colony and control site for a total of 1176 trap-nights for each treatment. I individually marked each captured animal by positional hair-clipping (Johnson 2001) to determine the density of rodents on each study site, and if there individuals were moving between study colonies and treatments (colony and control

Fig. 1. Small mammal trapping sites. Study sites are labeled by property names.



sites). I identified each animal to species, recorded its sex, approximate age, and reproductive condition.

I calculated the density of animals trapped at each pair of sites by dividing the number of animals captured by the area of the trapping grid (1225-m^2). I also calculated Shannon-Weiner species diversity (H') and evenness (J') indices (Zar 1999) at each pair of sites and compared diversity and evenness between colony and control sites using a nonparametric Kruskal-Wallis test (Zar 1999). I compared species richness and abundance at the colony and control sites using a Chi-squared test (Zar 1999). All statistical analyses were performed with SAS (Statistical Analysis Software v.8.2, Cary, NC, USA) or JMP Statistical Software (Cary, NC, USA).

Results

I trapped a total of 26 animals at the colony sites and 25 animals at the control sites (Table 1). I observed more deer mice (*Peromyscus maniculatus*) and fewer hispid pocket mice (*Chaetodipus hispidus*) at the six colony sites than at the control sites. Western harvest mice (*Reithrodonomys megalotis*) were present at the control sites but not at the colony sites (Table 1). Density of small mammals did not differ between prairie dog colonies and adjacent grasslands (Table 2; $P < 0.10$); however, species diversity and evenness were significantly higher on grasslands without prairie dogs than on grasslands with prairie dogs (Table 2, $P < 0.05$).

Species composition of small mammal communities differed significantly on

Table 1. Small mammal species captured in black-tailed prairie dog colonies and adjacent grasslands near Boulder, CO.

	Colony			Control		
SITE	PEMA	CHHI	REME	PEMA	CHHI	REME
Dover/Blacker	2	0	0	1	0	0
Flatirons Vista	1	1	0	1	2	2
Mesa Sand & Gravel	5	0	0	1	1	3
VanVleet/Jeffco	5	0	0	0	0	0
Waneka/Kelsall	11	0	0	4	1	1
Zaharias	1	0	0	5	1	2
TOTAL	25	1	0	12	5	8

Species: deer mice (PEMA), hispid pocket mice (CHHI), and western harvest mice (REME)

Table. 2. Mean density, diversity, and evenness values of small mammal communities captured in black-tailed prairie dog colonies (Colony) and adjacent grasslands (Control) (Kruskal-Wallis test).

	Colony	Control	df	Chi-sq	P <
Density (mice/m^2)	0.0035	0.0034	1	0.0067	0.10
Diversity (H')	0.0510	0.2816	1	3.86	0.05
Evenness (J')	0.0457	0.2486	1	3.86	0.05

and off of black-tailed prairie dog colonies. Species richness and the abundance of the three species varied significantly on sites with prairie dogs and grasslands without prairie dogs ($X^2 = 9.01$; df = 2; $P < 0.05$). I found no significant difference in the number of deer mice between sites on and off prairie dog colonies, but there were significantly more hispid pocket mice and harvest mice on grasslands without prairie dogs (Figure 2, $P < 0.05$).

Discussion

Small mammal communities were less diverse on prairie dog colonies compared to adjacent grasslands. Species richness was lower on grasslands with prairie dogs. Small mammal densities, however, were similar in prairie dog colonies and adjacent grasslands. Prairie dog colonies were dominated by deer mice, and I observed more deer mice on prairie dog colonies than on grasslands without prairie dogs; however, the difference was not significant (Fig. 2).

Small mammal density did not differ between colony and control sites because of the high variance in captures from one site to the next. Similarly, there was no significant difference in the abundance of deer mice between grasslands with prairie dogs and without prairie dogs due to the high variance in deer mouse captures on prairie dog colonies. I trapped at more sites than previous studies, but my overall sample size was still small. Perhaps with a higher number of study sites my results would show higher density of small mammals and abundance of deer mice on prairie dog colonies.

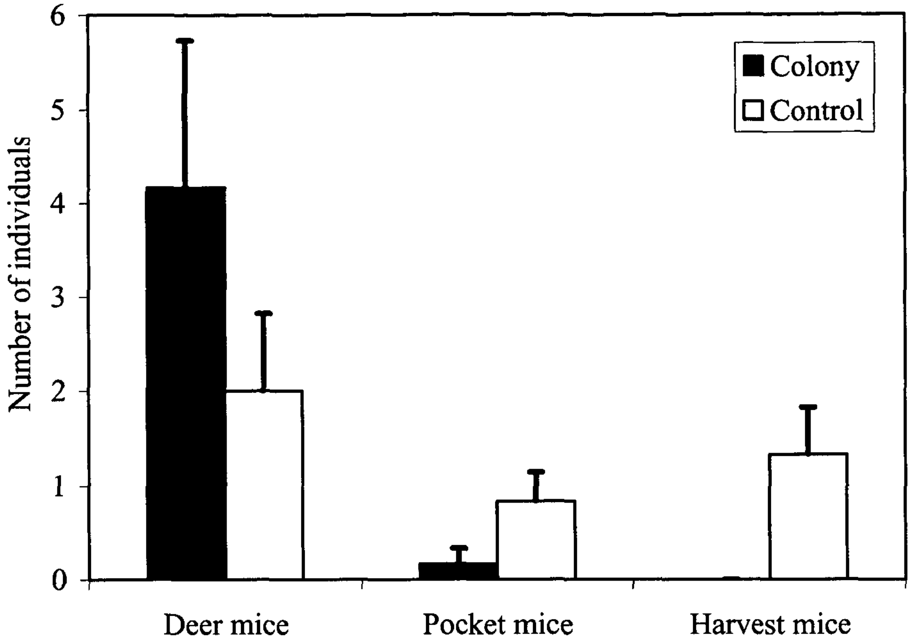


Fig. 2. The mean number and S.E. of individuals of each species at the colony and control sites.

Species richness in my study area was slightly lower than in previous studies. For example, I captured only three species of small mammals whereas Agnew et al. (1986) captured four species in South Dakota, and O'Meila et al. (1983) captured five species in Oklahoma. One potential reason for this difference may be due to timing. I trapped in the fall, while other investigators trapped in summer. Thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) are commonly observed on prairie dog colonies but are not found in high abundance in Boulder County (Bock et al. in press). Furthermore, thirteen-lined ground squirrels are diurnal, and I closed traps from 0700 hours to 1700 hours. Deer mice, hispid pocket mice, and western harvest mice are the most abundant species in Boulder Valley mixed-grass grasslands (Bock et al. in press). I did not expect to capture the northern grasshopper mouse (*Onychomys leucogaster*), another species associated with prairie dog colonies, because they are seemingly rare in Boulder County (D. M. Armstrong, personal communication).

Landscape context may also affect small mammal species composition in Boulder County grasslands. The Boulder Valley is becoming increasingly urbanized, and prairie dog colonies in the Boulder grasslands have higher prairie dog densities than found in non-urbanized landscapes (see Chapter II, this study). Even at large spatial scales (1256 ha), prairie dog colonies appear to be affected by urbanization and the density of roads in the surrounding landscape. Small mammal species richness at my study sites may be negatively affected by high prairie dog density and the resultant increased competition for resources. Perhaps only the most common species, the deer mouse, can persist when prairie dog density reaches a certain level.

The degree of urbanization in the landscape may also affect small mammal species abundance in more subtle ways. For example, Bock et al. (in press) found an abrupt decrease in the abundance of deer mice, hispid pocket mice, western harvest mice, and prairie voles (*Microtus ochrogaster*) at sites where only 5-10% of the surrounding landscape was urbanized. Perhaps even such a low degree of urbanization has locally extirpated the more sensitive species of small mammals from this landscape.

Sylvatic plague may explain why, in general, in previous studies deer mice and northern grasshopper mice were more abundant on prairie dog colonies than at sites without prairie dogs (O'Meila et al. 1983; Agnew et al. 1986). Although none of the colonies I studied was currently experiencing a plague epizootic, two of my six study sites have been affected by plague in the last 10 years. Deer mice and northern grasshopper mice are particularly resistant to plague whereas harvest mice are not (Cully 1989; Biggins & Kosoy 2001). This may explain why deer mice and northern grasshopper mice have proportionately higher abundances on prairie dog colonies than other species, and why I found only deer mice on prairie dog colonies. Moreover, deer mice are found in almost every habitat in higher abundances than any other species within their geographic range (Brown 1967). Deer mice have been observed in grazed and open areas more often than in areas with high grass cover, whereas western harvest mice avoided open areas and preferred sites with dense vegetation cover (Koford 1958; Davis et al. 2000; Matlack et al. 2001). Furthermore, western harvest mice and hispid pocket mice are predominately granivorous (Fitzgerald et al. 1994). Habitat generally denuded of vegetation, or kept at a low growth stage year round, as on prairie dog colonies, may not be preferable habitat for these species. Deer mice also may competitively exclude harvest mice in the short-grass steppe of Colorado (Stapp 1997).

The effect of prairie dogs on small mammal communities may vary between study areas within their geographic range. Agnew et al. (1986) found higher density but lower species diversity of small mammals on prairie dog colonies in the mixed-grass prairies of South Dakota. The same study found significantly more deer mice and northern grasshopper mice (*Onychomys leucogaster*) on prairie dog colonies, but found more hispid pocket mice, western harvest mice, prairie voles (*Microtus ochrogaster*), and thirteen-lined ground squirrels (*Spermophilus treidecemlineatus*) on sites without prairie dogs. Similarly, in the mixed-grass prairie of northwest Oklahoma, O'Meila et al. (1982) found higher abundance of small mammals but lower species diversity on prairie dog colonies. The increased abundance on prairie dog colonies was also primarily due to higher abundance of deer mice and northern grasshopper mice. As in my study, O'Meila et al. (1982) found no harvest mice and fewer hispid pocket mice on grasslands with prairie dogs. Interestingly, abundance of grasshoppers (Orthoptera) was significantly higher on grasslands without prairie dogs, which the authors attributed to the fact that prairie dog colonies had higher abundances of insectivorous species than grasslands without prairie dogs, such as the thirteen-lined ground squirrel, northern grasshopper mouse, and burrowing owl (O'Meila et al. 1982). A study on Mexican prairie dogs (*Cynomys mexicanus*), a very close relative to the black-tailed prairie dog (McCullough & Chesser 1987), reported different results than the above studies in Oklahoma and South Dakota. Mellink and

Madrigal (1993) found higher abundance and species richness of small mammals on an abandoned Mexican prairie dog colony than on an active prairie dog colony.

Although my study is a narrow slice in time and space of the small mammal communities observed on prairie dog colonies, combining the conclusions of the above studies gives insight into what may be a spatio-temporal response of small mammals to the presence of prairie dogs in the landscape. In the mixed-grass prairies of Colorado, South Dakota, and Oklahoma, black-tailed prairie dog colonies supported fewer small mammal species than surrounding grasslands (O'Meila et al. 1982; Agnew et al. 1986). Perhaps when prairie dogs first colonize an area species diversity decreases, and when prairie dogs abandon a colony species diversity increases. In this scenario older colonies would have lower species diversity than younger colonies, and abandoned prairie dog colonies would have species diversity values similar to grasslands never occupied by prairie dogs. Over time, this could maintain species diversity in the landscape by producing a shifting mosaic of habitat patches each with a unique small mammal community. This is consistent with the historical view of the relationship between bison (*Bison bison*) and prairie dogs. Bison and prairie dogs are believed to have had a relationship where both species would alter grassland structure in ways that were mutually beneficial (Koford 1958). Bison have been observed to preferentially graze in young prairie dog colonies, and secondarily at the edges of colonies (Coppock et al. 1983b). This was thought to facilitate the expansion and movement of prairie dog colonies across the landscape, while simultaneously providing a greater area of preferable habitat for bison and prairie dogs (Koford 1958; Coppock et al. 1983b). If prairie dogs did in fact move across the landscape with bison over time, then the accompanying small mammal assemblages would also change in response to changing habitat conditions.

In conclusion, small mammal communities on prairie dog colonies were significantly less diverse than grasslands without prairie dogs in Boulder County and had similar densities of small mammals. I only caught deer mice on sites with prairie dogs; therefore, deer mice may serve as a host reservoir for sylvatic plague in mixed-grass prairie ecosystems. The relationship between deer mice and the spread of plague in prairie dog-dominated ecosystems needs to be studied at greater depth. Additionally, because I did not find a positive effect of prairie dogs on grassland rodent communities, my results give insight into the definition of a keystone species. Power et al. (1996) stated that a keystone species has a disproportionately large effect on community structure and function when compared to its abundance, and Kotliar et al. (2000) added that a keystone species should "perform roles not performed by other species or processes" in the same ecosystem. Therefore, in the context of my study, the black-tailed prairie dog is still considered a keystone species because it had a disproportionately large effect on the distribution and abundance of other grassland small mammal species relative to the abundance of prairie dogs in the landscape, and prairie dogs fulfill a role unlike any other grassland species (Kolitar et al. 2000). To conserve native biodiversity in mixed-grass prairie ecosystems, managers must balance the preservation needs of prairie dog colonies and their associated small mammal communities with the preservation needs of species not found on prairie dog colonies. Allowing prairie dogs to abandon old colonies and colonize new areas contributes to landscape heterogeneity and may create patches of high and low small mammal species diversity at the landscape scale.

Literature Cited

Agnew, W., D. W. Uresk, and R. M. Hansen. 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.

Armstrong, D. M. 2002. Personal communication.

Biggins, D. E., and M. Y. Kosoy. 2001. Influences of introduced plague on North American mammals: implications from ecology of plague in Asia. Journal of Mammalogy 82:906-916.

Bock, C. E., K. T. Vierling, S. L. Haire, J. D. Boone, and W. W. Merkle. Patterns of rodent abundance on open-space grasslands in relation to suburban edges. Conservation Biology, *in press*.

Brown, L. N. 1967. Ecological distribution of mice in the Medicine Bow mountains of Wyoming. Ecology 48:677-680.

Ceballos, G., J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. Journal of Arid Environments 41:161-172.

Colorado Department of Natural Resources. 2000. Black-tailed prairie dog study of eastern Colorado. Prepared by EDAW, Inc. Fort Collins, CO. 49 pp.

Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983a. Plant-herbivore interactions 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., J. E. Ellis, J. K. Detling, and M. I. Dyer. 1983b. Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modifications of vegetation by prairie dogs. Oecologia 56:1-9

Cully, J.F. Jr., 1989. Plague in prairie dog ecosystems: mportance for black-footed ferret management. Pp 47-55 In: The prairie dog ecosystem: managing for biological diversity. eds. T.W. Clark, D. Hinkley, T. Rich. Montana BLM Wildlife Technical Bulletin No.2.

Cully, J.F., Jr., A.M. Barnes, T.J. Quan and G. Maupin. 1997. Dynamics of plague in a Gunnison's prairie dog colony complex from New Mexico. Journal of Wildlife Diseases 33:706-719.

Cully, J. F. Jr., and E. S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy 82:894-905.

Davis, S. S., R. B. Mitchell, and S. Demarais. 2000. Trap-revealed microhabitat use by small mammals in monoculture grasslands. Texas Journal of Science 52:195-200.

Fitzgerald, J. P., C. A. Meaney, and D. M. Armstrong. 1994. Mammals of Colorado. Denver Museum of Natural History and University Press of Colorado. 467pp.

Gober, P. 2000. 12-month administrative finding, black-tailed prairie dog. Federal Register 65:5476-5488.

Johnson, W. C. 2000. A new individual marking technique: Positional Hair Clipping. The Southwestern Naturalist 46: 126-129.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373-386.

Koford, C. B. 1958. Prarie dogs, whitefaces, and blue grama. Wildlife Monographs 3:1-78.

Kotliar, N. B., B. W. Baker, A. D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24:177-192.

Kotliar, N. B. 2000. Application of the new keystone species concept to prairie dogs: how well does it work? Conservation Biology 14:1715-1721.

Kretzer, J. E., and J. F. Cully Jr. 2001. Effects of black-tailed prairie dogs on reptiles and amphibians in Kansas shortgrass prairie. The Southwestern Naturalist 46:171-177.

Matlack, R. S., D. W. Kaufman, and G. A. Kaufman. Influence of grazing by bison and cattle on deer mice in burned tallgrass prairie. American Midland Naturalist 146:361-368.

McCullough, D. A., and R. K. Chesser. 1987. Genetic variation among populations of the Mexican prairie dog. Journal of Mammalogy 68:555-560.

Mellink, E, and H. Madrigal. 1993. Ecology of Mexican prairie dog, *Cynomys mexicanus*, in El Manantial, Northeastern Mexico. Journal of Mammalogy 74:631-635.

Miller, B., C. Wemmer, D. Biggins, and R. Reading. 1990. A proposal to conserve black-footed ferrets and the prairie dog ecosystem. Environmental Management 14:763-769.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology 8:667-681.

Minta. S. C. & T. W. Clark. 1989. Habitat suitability analysis of potential translocation sites for black-footed ferrets in northcentral Montana. Pp. 29-46 in The Prairie dog ecosystem: managing for biological diversity: Eds. T. W. Clark, D. Hinkley, and T. Rich. Montana BLM Wildlife Technical Bulletin No. 2.

O'Meila, M. E., F. L. Knopf, and J. C. Lewis. 1982. Some consequences of competition between prairie dogs and beef cattle. Journal of Range Management 35:580-585.

Paine, R.T. 1969. A note on trophic complexity and community stability. American Naturalist 103:91-93.

Powers, M. E, D. Tilman, J. A Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. BioScience 46:609-620.

Stapp, P. 1997. Community structure of shortgrass-prairie rodents: competition or risk of intraguild predation? Ecology 78:1519-1530.

Whicker, A. D., and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances: prairie dogs alter grassland patch structure, nutrient cycling, and feeding-site selection by other herbivores. BioScience 38:778-785.

Wilson, M.E., R. Levins and A. Speilman (eds.). 1994. Disease in evolution: global changes and emergence of infectious diseases. New York Academy of Sciences. Pg. 273

Zar, J. H. 1999. Biostatistical analysis. 4th ed. Prentice-Hall, Inc. New Jersey. 663pp.

Chapter II: Effects of landscape context on density of black-tailed prairie dogs

Abstract: Black-tailed prairie dogs (*Cynomys ludovicianus*) are increasingly coming into competition for available habitat with human development in the Colorado Front Range. Because the effects of increased urbanization on prairie dog colonies are unknown, I studied the how landscape context affects prairie dog density in Boulder County, Colorado. I used burrow density as a proxy for prairie dog density because these variables were highly correlated at my study sites ($r = 0.60$). Using remotely-sensed data and a GIS, I quantified percent urbanization, road density, and the percentage of other prairie dog colonies in the surrounding landscape at 200-, 1000-, and 2000-meters from the perimeter of 22 prairie dog colonies, and compared burrow density with each landscape variable at each scale. I also calculated Akaike's information criterion (AIC) to determine the most parsimonious models predicting burrow density. Burrow density was significantly higher in colonies surrounded by greater amounts of urbanization and roads. The degree that prairie dog colonies were immediately surrounded by unsuitable habitat, i.e., the "boundedness" of the colony, was negatively correlated with colony area and positively correlated with burrow density. Furthermore, a model based on boundedness, the density of roads at the 2000-m scale, and the amount of prairie dog colonies at the 200-m scale explained 73% of the variance in prairie dog burrow density. Increased prairie dog density may be related to decreased predator abundance in urbanized landscapes (i.e. Refuge Effect). If higher prairie dog density increases competition for available resources,

habitat quality may decline leading to population decline in highly urbanized landscapes. Furthermore, if dispersal is reduced in urbanized landscapes, then these colonies may not be recolonized after decline from plague epizootics.

Introduction

Prairie dogs (*Cynomys* spp.) are considered keystone species (sensu Paine 1969) and ecosystem engineers (sensu Jones et al. 1994; Ceballos et al. 1999) of short- and mixed-grass prairie ecosystems because of their disproportionately large effect on grassland ecosystem structure and function (Kotliar et al. 1999, 2000). Many different species, including badgers (*Taxidea taxus*), coyotes (*Canis latrans*), swift foxes (*Vulpes velox*), prairie rattlesnakes (*Crotalus viridis*), ferruginous hawks (*Buteo regalis*), golden eagles (*Aquila chrysaetos*), and black-footed ferrets (*Mustela nigripes*) all prey upon prairie dogs, and prairie dog burrows provide shelter for many invertebrates, reptiles, amphibians, burrowing owls (*Athene cunicularia*), and small mammals (Koford 1958; Agnew et al. 1986; Desmond & Savidge 1996; Goodrich & Buskirk 1998; Kotliar et al. 1999; Kretzer & Cully 2001).

Black-tailed prairie dogs (*Cynomys ludovicianus*) historically inhabited approximately 3 million hectares in Colorado (Gillette 1919, as cited in Colorado Department of Natural Resources 2000) and now only occupy approximately 120,000 hectares (Colorado Department of Natural Resources 2000). Range-wide, disease, competition with cattle ranching operations, agriculture, and most recently urban and suburban development have reduced prairie dogs to less than 2% of their original abundance (Miller et al. 1990, 1994; American Society of Mammalogists 1998), and prairie dogs now occupy less than 1% of the area in their estimated historical geographic range (Gober 2000). Poisoning and shooting of prairie dogs by ranchers and agricultural conversion of habitat are responsible for the majority of the prairie dog's decline (Miller et al. 1990, 1994). Furthermore, the recently introduced sylvatic plague (*Yersinia pestis*) kills up to 99% of prairie dogs in infected colonies (Cully et al. 1997; Cully & Williams 2001; Biggins & Kosoy 2001). The above factors, in combination with habitat loss from urbanization, helped the prairie dog reach "warranted, but precluded" status on the United States Fish and Wildlife Service's threatened species list (Gober 2000).

The historical range of the black-tailed prairie dog in Colorado included the entire eastern portion of the state west to the foothills of the Colorado Front Range (Fiztgerald et al. 1994). Although black-tailed prairie dog abundance and total habitat area have been reduced, the extent of their geographic range remains relatively unchanged. Prairie dog colonies historically were larger in size and less isolated from each other than they are today (Hoogland 1995; Lomolino & Smith 2001; Sidle et al. 2001), but it is unclear if prairie dog habitat has been fragmented enough to create non-interacting subpopulations of prairie dogs at large spatial scales.

Prairie dog colonies in Boulder County are located on the Colorado Piedmont. The Colorado Piedmont is located between the Great Plains and the Colorado Front Range. Urbanization and agriculture on the Colorado Piedmont have created areas dominated by human activity within once continuous grassland, thereby "perforating" the landscape (Forman 1995; Collinge & Forman 1998). The City of Boulder Open Space and Mountain Parks Department (OSMP) has created a "greenbelt" of preserved grassland properties around the city of Boulder to preserve native biodiversity along with traditional land uses such as cattle ranching and agriculture. However, these properties already exist within a highly perforated prairie ecosystem (Berry et al. 1998; Collinge & Forman 1998; Bock et al. in press). Urban and industrial development have replaced once continuous grassland, creating less habitat for prairie dog colony expansion. As a result, the majority of prairie dog colonies in Boulder County are on city- and county-owned land. Many of the remaining prairie dog colonies in Boulder have been displaced from their previous habitat and are now located on roadsides and on leftover portions of new urban developments. These "urban" prairie dog colonies are uncharacteristic of prairie dog colonies found in continuous grassland, yet they seem able to persist. However, it is unknown whether these urban prairie dog colonies can survive over the long term. I indirectly measured the effects of landscape perforation on prairie dog colonies, by studying prairie dog density in the perforated mixed-grass prairie ecosystem of Boulder County, Colorado.

In this study, I report on characteristics of black-tailed prairie dog colonies in the mixed-grass prairie of Boulder County in the urbanized Colorado Piedmont. My research goal was to uncover relationships between two dependent variables: the density of active burrow entrances (burrow density) and prairie dog density, and multiple independent variables: the area of the colony, and the amount of urbanization, roads, and other prairie dog colonies in the surrounding landscape at three spatial scales. I also determined the best, most parsimonious models to predict burrow density using the above independent variables. I predicted that the amount of urbanization, roads, and prairie dog colonies in the surrounding landscape would not affect prairie dog density.

Methods

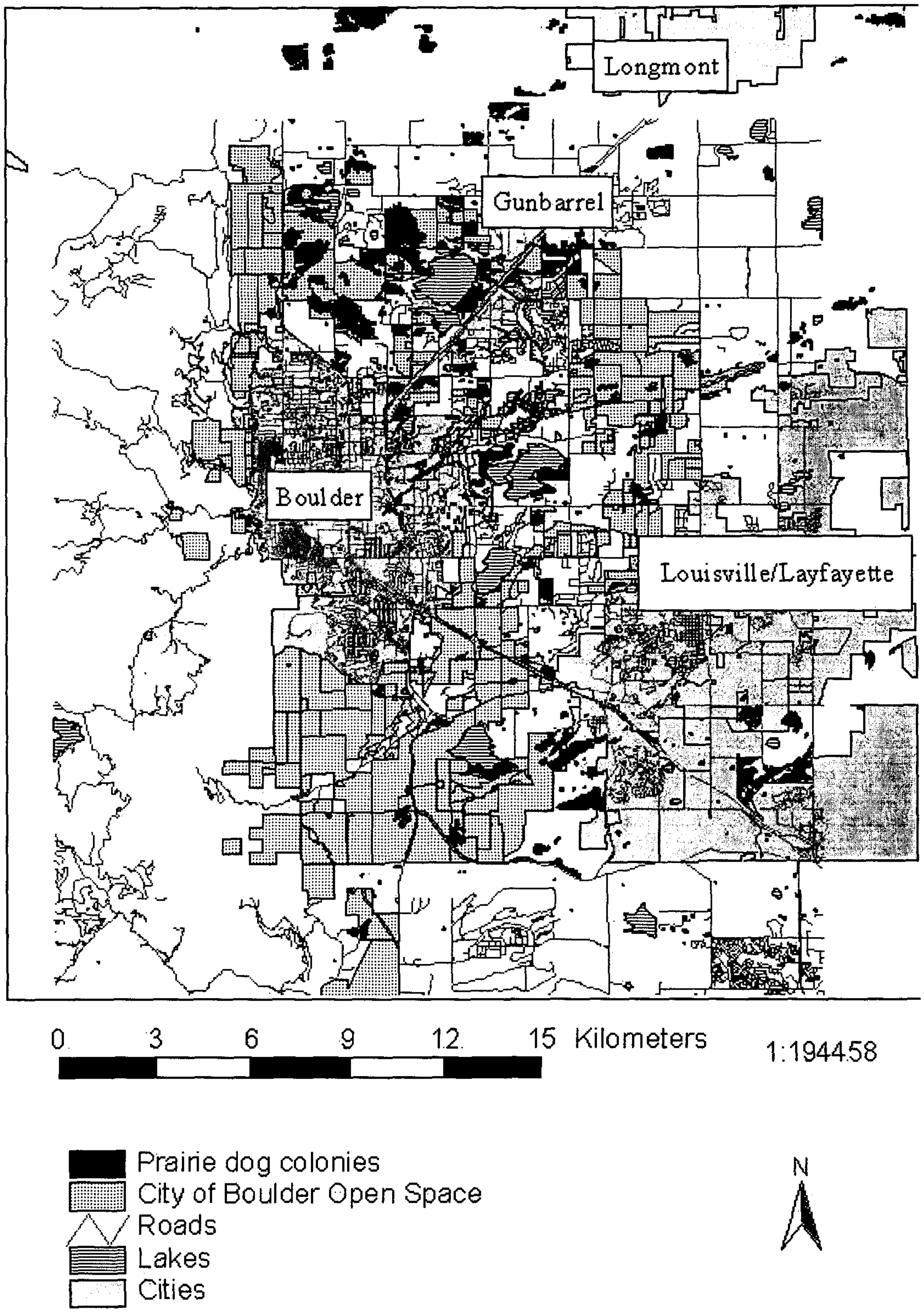
Study area

I conducted my study on the mixed-grass prairie ecosysem of the Colorado Piedmont in Boulder County, Colorado. Within the city of Boulder there are 440 preserved "Open Space" properties making up a total of approximately 12,000-ha of land. There are approximately 1,200 ha of active prairie dog colonies that lie within these preserved properties (Fig. 1). Colony size ranges from 0.5- to 100-ha with an average colony size of only 8-ha (Johnson, W. C., unpublished data).

Prairie dog density and burrow density

I estimated the density of prairie dogs using two methods: the belt-transect method to calculate the density of active burrow entrances (hereafter "burrow density") (Biggins et al. 1993; Powell et al. 1994; VanDruff et al. 1996), and the visual count method to calculate prairie dog density (Fagerstone & Biggins 1986; Menkens et al. 1990; Menkens & Anderson 1993; Powell et al. 1994). I strategically chose a sample of prairie dog colonies that spanned the full range of landscape contexts. I sampled burrow density in the months of June-August 2000, and September 2001-January 2002 using 3x50-m belt transects (Biggins et al. 1993; Powell et al. 1994; VanDruff et al. 1996). I randomly placed the belt transects within each colony rather than using regular spacing intervals because I did not want to under-sample small colonies. I included all three burrow opening types as classified by Hoogland (1995) in my estimate of burrow density: burrow entrances with no mound, dome craters, and rim craters. Active burrow entrances are characterized as

Fig. 1. Prairie dog colonies in a perforated landscape



having new scat (Biggins et al. 1993; Hoogland 1995). I calculated burrow density, area, and "boundedness" (see definition below) for 36 colonies in 2000, and 40 colonies in 2001 (Table 1). In 2000, I randomly placed 2, 3x50-m belt-transects within 36 colonies and counted the number of active burrow entrances that fell within each transect's footprint. In 2001, I randomly placed 10, 3x50-m belt-transects within 40 colonies and recorded all active burrow entrances. I used the number of active burrow entrances per hectare to estimate burrow density in these colonies. I analyzed the 2000 and 2001 datasets separately because boundedness, burrow density, and area all change year to year (Hoogland 1995).

In 2001, I quantified the density of prairie dogs in 15 colonies using the timed visual count method (Fagerstone & Biggins 1986; Menkens et al. 1990; Powell et al. 1994) during the months of September 2001-January 2002. I strategically selected 15 out of the 40 colonies in order to get a range of boundedness values. My purpose was to determine if there was a significant linear correlation between prairie dog density and burrow density (Biggins et al. 1993; Powell et al. 1994; Reading & Matchett 1997). I counted prairie dogs using 10x24mm binoculars at a distance of 100-m from the colony perimeter. Depending on access to each colony, I remained in a vehicle or on a camping chair for the duration of the count. Because I was unable to count every prairie dog in each colony, I staked out between one and eight 50x50-m grids within each of 15 colonies prior to surveying. I used wooden survey sticks with red flagging to mark the four corners of each grid and wooden survey stakes with no flagging to mark the middle of each side of the grids. I used one grid for very small colonies and up to eight for the largest colonies. I counted the number of

Table 1. Number of sites sampled (N) for each variable for each year.

Year	*2000*	*2001*
Boundedness	36	40
Burrow density	36	40
Prairie dog density	0	15
% Urbanization	0	22
% Road density	0	22
% Other prairie dog colonies	0	22

prairie dogs in each grid, three times an hour, two hours a day, for three days in a row. Counts at each colony were performed between 0900 and 1200 hours on days with no precipitation and temperatures above 10 C. I arrived at least 15 minutes before 0900 to allow the prairie dogs to acclimate to my presence. I used the average of the maximum count of each grid to estimate prairie dog density of each colony. Maximum average is the average of the highest number of prairie dogs counted in each grid over the three-day sampling period, and is the best predictor of actual prairie dog density (Severson & Plumb 1998).

Landscape Context

In 2000 and 2001 I determined the boundedness of 36 and 40 colonies, respectively, on a scale of zero to five depending on the colony's surroundings. I strategically chose each of the prairie dog colonies to represent the entire range of boundedness values in Boulder County. Boundedness represents the amount of unsuitable habitat immediately surrounding a colony, and may be considered an estimate of the relative permeability of the colony to emigration and immigration. In effect, this is an estimation of the amount of urban and industrial development and roads directly adjacent to each prairie dog colony. For example, if the colony was bounded on all sides by short- or mixed-grass grassland, then the boundedness value would be zero (Fig. 2). Conversely, if the colony was bounded on all sides by high density urban development, then the boundedness value would be five. I classified a colony as a one if there was unsuitable habitat on one side of the colony. If the colony was bounded on two sides with unsuitable habitat, then the boundedness value

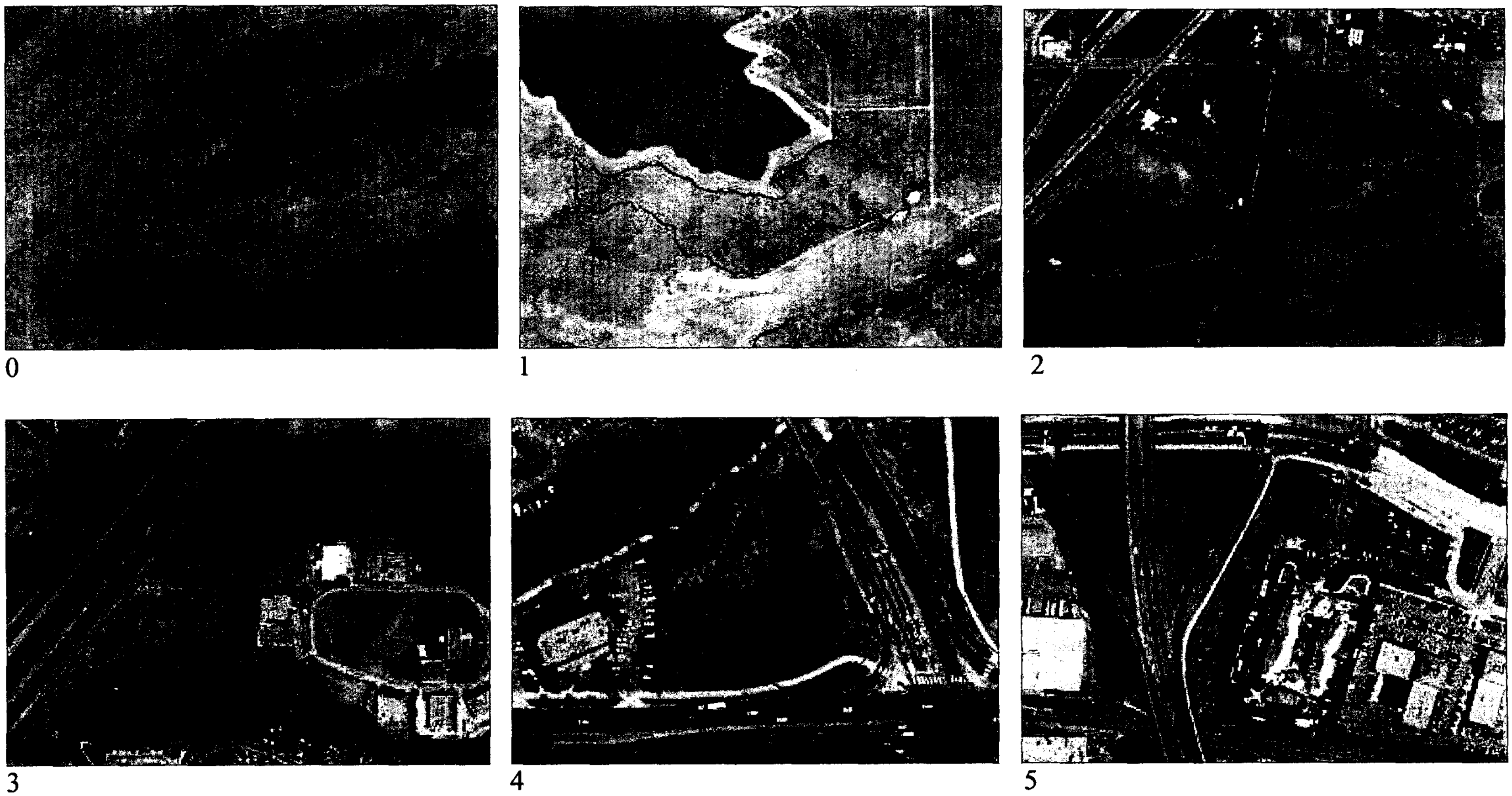


Figure 2. Examples of boundedness values (0-5) for six colonies. See text for explanation of boundedness. Colonies are circumscribed by the thin black lines in each figure. Aerial photos taken in 1999.

was two. This continued until the colony was bounded on all four sides by unsuitable habitat (North, East, South, and West). I reserved a boundedness value of five for colonies that were completely surrounded by a high density of buildings and roads on all sides. Unsuitable habitat includes most non-grassland habitats: the foothills of the Front Range, lakes and reservoirs, dirt and paved roads, freeways, and urban and industrial developments.

I further determined landscape context for 22 prairie dog colonies using remotely-sensed data and GIS analyses (Table 1). In November 2000 and 2001, I received a GIS layer (ArcView Shapefile) for all colonies found on Boulder City and County Open Space properties. I used Global Positioning Systems (GPS, Trimble GeoExplorer II) to map the perimeter of prairie dog colonies that were not found on City or County of Boulder Open Space properties. I merged the above data into one complete GIS layer incorporating all prairie dog colonies found in Boulder County over both the 2000 and 2001 seasons. In 2001, there were approximately 260 active colonies, and these colonies were further separated by streams, topography, or unpaved roads into approximately 480 wards (W C Johnson, unpublished data). Most colonies have subcolonies, or wards, that are separated by a stream or other minor topographic feature such as a hill (Hoogland 1995).

I quantified three landscape features in relation to prairie dog colonies at three spatial scales: urbanization, road density, and the amount of other prairie dog colonies at 200-, 1000-, and 2000-m from the perimeter of each colony. First, I digitized urban-, suburban-, and industrial-development (hereafter, urbanization) in Boulder County using 62 digital orthoquad images (DOQs) with 1-meter resolution. I defined urbanization as any anthropogenic landscape feature. This included residential and industrial buildings, parking lots, urban vegetation, and roads encompassed by the previous features. Second, I calculated road density using a GIS layer for all roads that occurred within Boulder County. Third, I calculated the area of other prairie dog colonies using the above-mentioned prairie dog GIS layer. I considered the area of other prairie dog colonies within the surrounding landscape as an indication of colony isolation.

I strategically chose 22 colonies out of the 40 colonies on which to perform landscape context analyses. Each of the 22 colonies was surrounded by varying amounts of urbanization, roads, and other prairie dog colonies. I did not randomly select colonies because highly urbanized colonies are fewer in number than other colonies. Using ArcView GIS (ArcView v.3.2, ESRI Inc., Redlands, CA), I created a buffer around each colony at three spatial scales (200-, 1000-, and 2000-meters). This created three zones (polygons) extending outwards 200-, 1000-, and 2000-meters from the perimeter of each of 22 prairie dog colonies. The largest spatial scale of 2-km was chosen because intercolony prairie dog dispersal rarely exceeds 2-3 km (Garrett & Franklin 1988; Hoogland 1995). I then used the "Clip" function in the GeoProcessing Wizard extension (ArcView v.3.2, ESRI Inc., Redlands, CA) to select all urbanization, roads, and other prairie dog colonies that fell within the boundary of each buffer zone. The Clip function acts like a cookie cutter for each buffer zone. For example, any urbanized feature that falls within the buffer zone boundary is clipped to the portion that falls within the buffer zone. I then created a new theme of the clipped features and their new associated lengths or areas. I then calculated percent urbanization, road density, and percentage of other prairie dog colonies within each buffer by dividing the area (urbanization and prairie dog colonies) or length (roads) of the clipped theme by the area of the buffer theme and multiplying by 100. In this way, I could determine at which of the three spatial scales each of these three independent variables affected the dependent variables: prairie dog density and burrow density.

Data analysis

For the 2000 field season, I compared boundedness to burrow density using Spearman rank correlation (N = 36). For the 2001 field season, I first compared boundedness and prairie dog colony area to prairie dog density (N = 15 colonies) and burrow density (N = 40 colonies) using Spearman rank correlation (Table 1). Secondly, I compared all three scales of each landscape context variable to burrow density (N = 22 colonies) using Spearman rank correlation. Thirdly, I used Akaike's Information Criterion (AIC) to determine the most parsimonious models predicting burrow density (Burnham & Anderson 1998; Roach et al. 2001). I combined 11 independent variables to create a number of possible linear regression models. The predictor variables I used in the AIC analysis were: (1) area of colony, (2) 200-m % urbanization, (3) 1000-m % urbanization, (4) 2000-m % urbanization, (5) 200-m % road density, (6) 1000-m % road density, (7) 2000-m % road density, (8) 200-m % prairie dog colonies, (9) 1000-m % prairie dog colonies, (10) 2000-m % prairie dog colonies, and (11) boundedness. I did not use all combinations of all 11 independent variables. I excluded models that used more than one scale of urbanization, roads, or prairie dog colonies together because each landscape variable is not independent of one another (i.e., the three scales of urbanization, road density, and the percentage of other prairie dog colonies are nested). For example, I did not use models that combined variable (2) and (3), (2) and (4), or (3) and (4). Using SAS (Statistical Analysis Software v.8.2, Cary, NC, USA), I calculated the standard error of the regression for each possible regression and used this standard error to calculate AIC for each regression (see Burnham & Anderson 1998 for equation). Each regression has its own AIC value and the lowest AIC value is the model that best, and most parsimoniously, explains the variance in the data (Burnham & Anderson 1998). Because of low sample size (N = 22), I calculated the corrected AIC (AIC_c) for all models (Burnham & Anderson 1998). To compare models, I computed ÄAIC_i, the difference in AIC values between model *i* and the best model. The best model has the lowest AIC_c value and therefore a ÄAIC value of zero. Models with ÄAIC less than four should be considered useful candidates for explaining variance in the dependent variable (Burnham & Anderson 1998). Models with a ÄAIC of less than or equal to two should be considered the best, most parsimonious models. Lastly, I ranked each model based on its calculated "Akaike Weight" value, a measure of relative likelihood (Burnham & Anderson 1998).

I used ArcView v.3.2 for all spatial analyses (ESRI, Redlands, CA, USA), and all statistical analyses were performed on SAS (Statistical Analysis Software v.8.2, Cary, NC, USA).

Results

Burrow density for the 22 colonies ranged from 100 to 674 burrows/ha, and prairie dog density ranged from 32 to 120 prairie dogs/ha (Table 2). Burrow density and prairie dog density were positively correlated (Fig. 3; $N = 15$; Spearman correlation, $r = 0.60$, $P < 0.05$; Kendall's Tau, $r = 0.41$, $P < 0.05$). In 2000, burrow density was positively correlated with boundedness ($N = 36$; Pearson correlation, $r = 0.34$, $P < 0.05$). In 2001, burrow density and prairie dog density were both positively correlated with boundedness (Fig. 4a & b, Spearman correlation, N = 40 & 15, r = 0.66 & 0.81, respectively, $P < 0.001$). Colony area was negatively correlated with boundedness (Fig. 5; Spearman correlation, $N = 40$; $r = -0.37$; $P < 0.05$), but was not correlated with burrow density ($P > 0.10$).

In the landscape analyses, burrow density was positively correlated with urbanization at the 200-, 1000-, and 2000-meter spatial scales (Fig. 6a; Table 3; N = 22, r = 0.63, 0.67, 0.65 & P < 0.005, 0.001, 0.001, respectively). Similarly, burrow density was positively correlated with road density at all three spatial scales (Fig. 6b, Table 3; N = 22, r = 0.43, 0.63, 0.67, & P < 0.05, 0.005, 0.001, respectively). However, the percentage of the landscape covered by prairie dog colonies was not correlated with burrow density at any scale (Fig. 6c, Table 2; r = 0.14, 0.07, 0.003, respectively; $P > 0.5$). In the AIC analysis, the most parsimonious model was based on boundedness, the density of roads at the 2000-m scale, and the percentage of the landscape covered by prairie dog colonies at the 200-m scale (Fig. 7a, $N = 22$). This model explained 73% of the variance in burrow density (Table 4). The second best model included boundedness and road density at the 2000-m scale, and explained

Table 2. Active burrow entrance density and prairie dog density for 22 black-tailed prairie dog colonies in Boulder County.

Dependent variable	Mean (#/ha)	SE	Range (#/ha)
Active burrow entrance density	255	21.15	100-674
Prairie dog density	68	7.26	32-120

Table 3. Landscape context variables and partial correlation coefficients with active burrow entrance density (* = P < 0.05, ** = P < 0.01, *** = P < 0.001).

Independent variable	N	r
Prairie dog density (prairie dogs/ha)	15	0.60*
Area of colony (ha)	40	-0.37*
Boundedness	40	0.81***
% Urbanization (200-m scale)	22	0.63**
% Urbanization (1000-m scale)	22	0.67***
% Urbanization (2000-m scale)	22	0.65***
Road density (200-m scale)	22	0.43*
Road density (1000-m scale)	22	0.63**
Road density (2000-m scale)	22	0.67***
Prairie dog colonies (200-m scale)	22	0.14
Prairie dog colonies (1000-m scale)	22	0.07
Prairie dog colonies (2000-m scale)	22	0.003

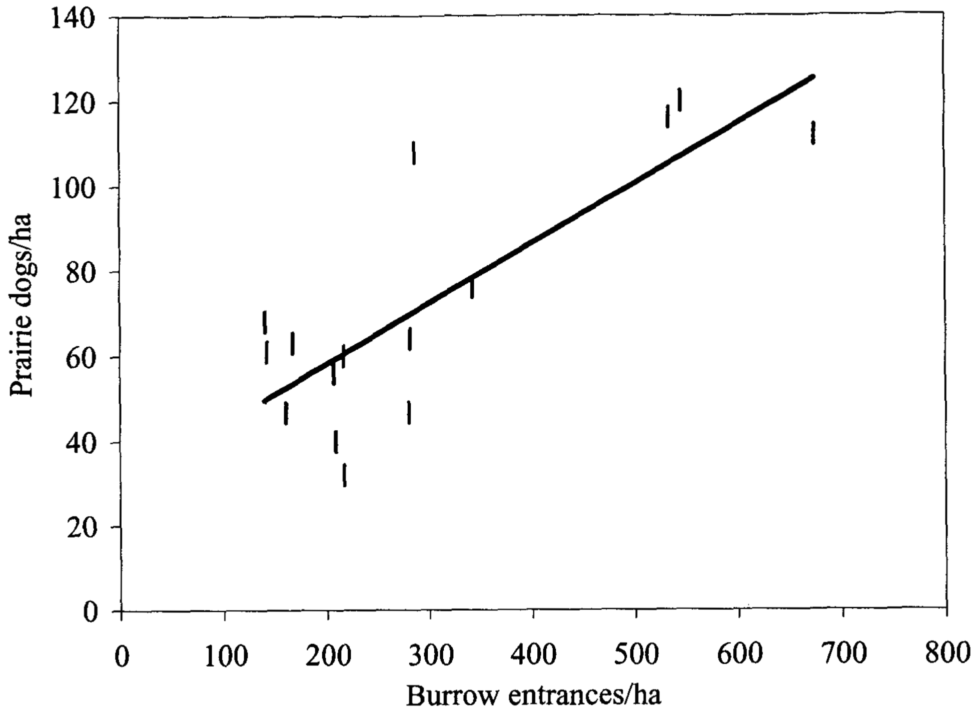


Fig. 3. Prairie dog density is significantly positively correlated with active burrow entrance density (r = 0.60, P < 0.05).

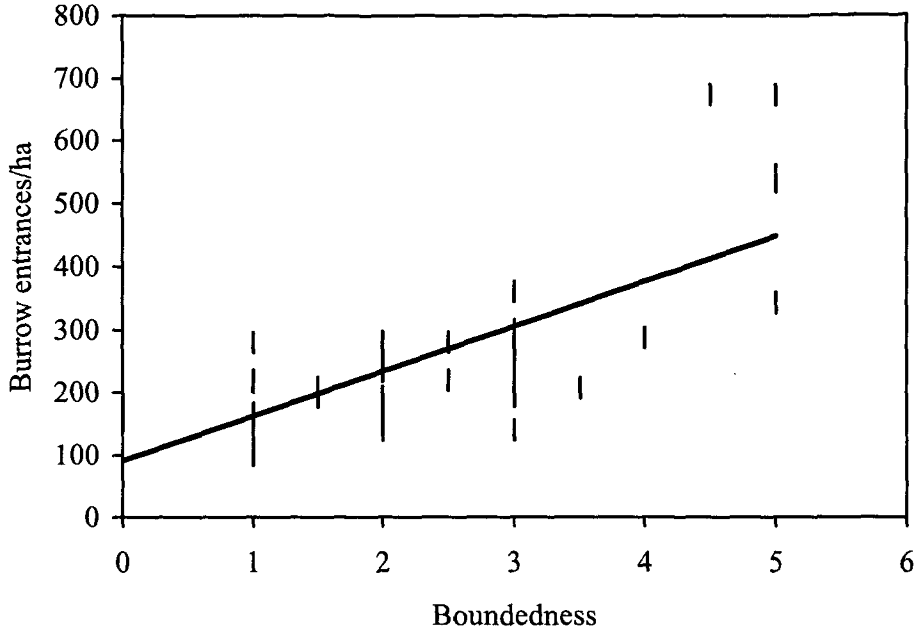


Figure 4a. Burrow density increases (burrows/ha) as boundedness increases (r = 0.66).

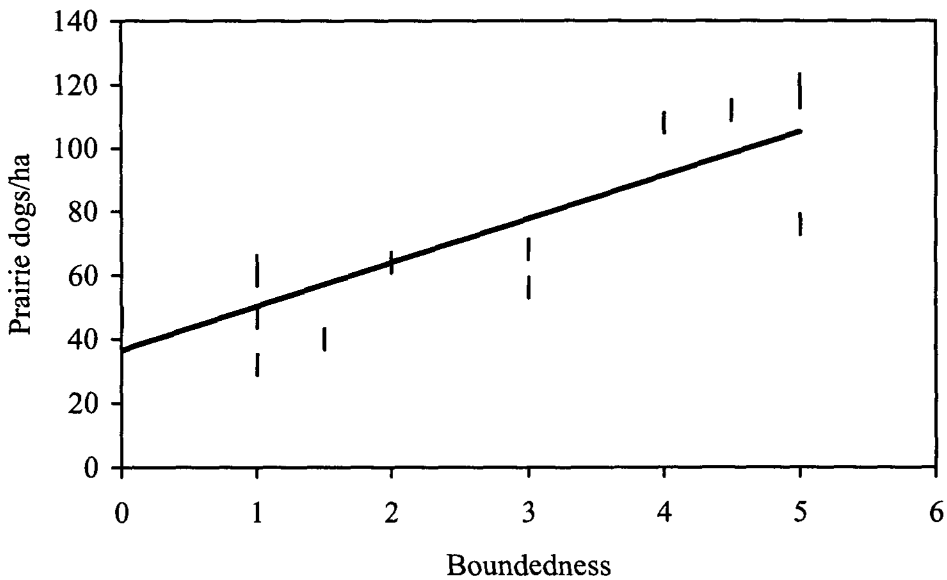


Fig. 4b. Prairie dog density (prairie dogs/ha) increases as boundedness increases (r = 0.81).

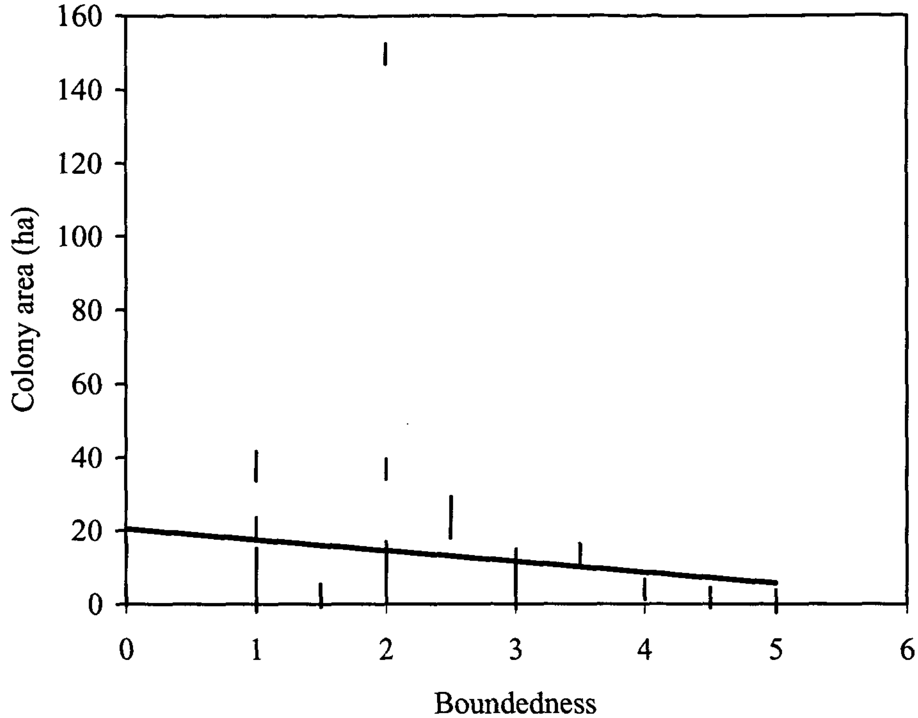
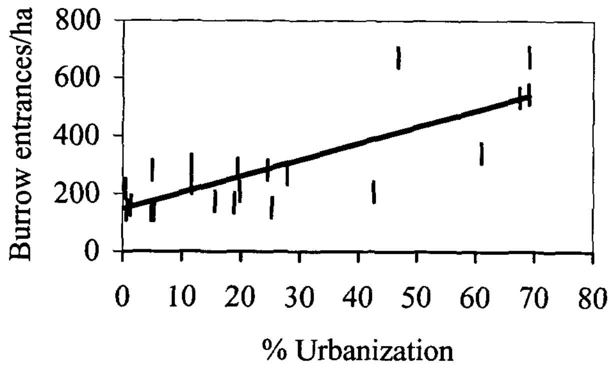


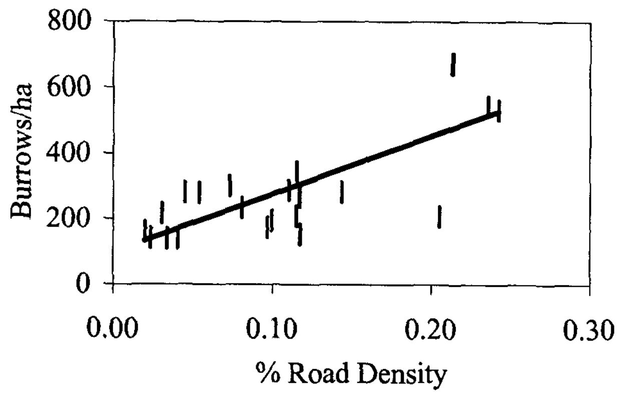
Figure 5. Colony area decreases as boundedness increases (r = -0.37, P < 0.05).

Figure 6. Spearman correlations of the landscape context of prairie dog colonies at the 2000-m scale. Burrow density increased with (a) percent urbanization, (b) percent road density, and was not correlated with (c) percent of the landscape covered in other prairie dog colonies.

a)



b)



c)

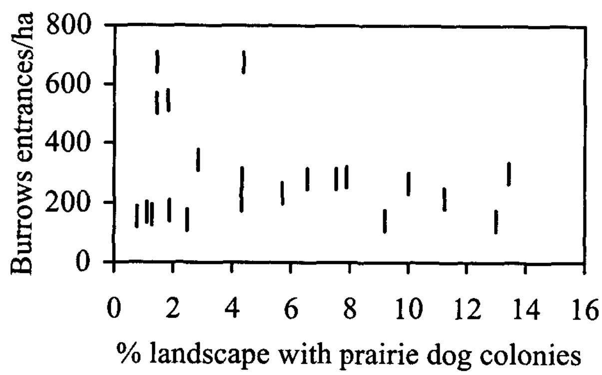
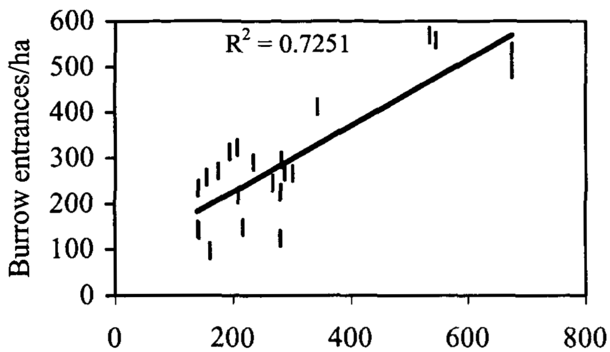
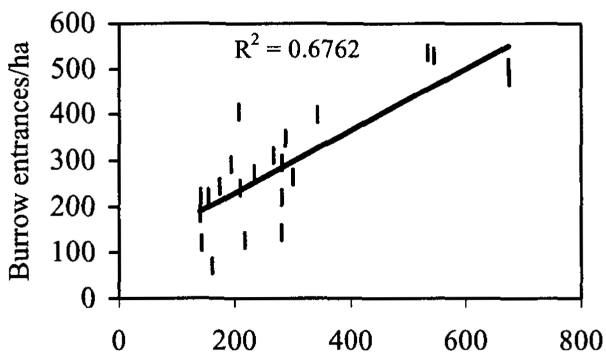


Fig. 7. The three best models determined by AIC_c: (a) Boundedness, road density at the 2000-m scale, and the percentage of other prairie dog colonies in the landscape at the 200-m scale, (b) Boundedness, and road density at the 2000-m scale, and (c) road density at the 2000-m scale and the percentage of other prairie dog colonies in the landscape at the 200-m scale.

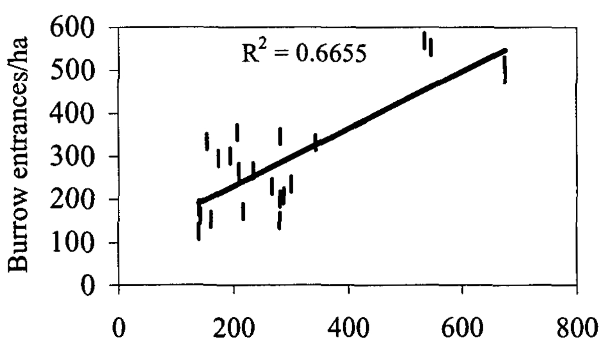
a)



b)



c)



68% of the variance in burrow density (Fig. 7b; Table 4). The third best model was based on road density at the 2000-m scale and the percentage of the landscape covered by prairie dog colonies at the 200-m scale, and explained 67% of the variance in burrow density (Fig. 7c; Table 4).

Discussion

Urbanization and roads in the immediate surroundings of prairie dog colonies (boundedness), and in the surroundings of prairie dog colonies at larger spatial scales, were positively correlated with, and best predicted, increased densities of black-tailed prairie dogs. Conversely, nearby prairie dog colonies appeared to slightly lower prairie dog density within colonies.

Burrow density and prairie dog density

Colonies with more active burrow entrances had more prairie dogs. The average burrow entrance density at my study sites was 255 active burrow entrances/ha, and the average number of prairie dogs was 68 prairie dogs/ha. The averages and ranges in my study area are higher than the ranges of 10-250 burrows/ha and 10-35 prairie dogs/ha that have been documented in other studies (Koford 1958; Reading et al. 1989; Powell et al. 1994). Previous studies may have used different protocols to sample active burrow entrance densities. Prairie dog burrows usually have more than one entrance and there is more than one type of burrow entrance (Hoogland 1995). Therefore, researcher bias may have contributed to the inconsistent relationship between active burrow density and prairie dog density (Reading et al.

Table 4. AIC analysis: the 8 regression models that best explain burrow density.

Model #	Variables	R^2	adj R^2	AICc	ΔAICc	Akaike Weight
1	Boundedness, road density at 2000m scale, prairie dog colonies at 200m scale	0.7251	0.6793	212.9	0*	0.1913
2	Boundedness, road density at 2000m scale	0.6762	0.6421	213.1	0.2086*	0.1724
3	Road density at 2000m scale, prairie dog colonies at 200m scale	0.6655	0.6303	213.8	0.9212*	0.1207
4	Boundedness	0.5753	0.554	216.1	3.159	0.0394
5	Area of colony, Boundedness, road density at 2000m scale, prairie dog colonies at 200m scale	0.7314	0.6682	216.2	3.343	0.0397
6	Area of colony, Boundedness, road density at 2000m scale	0.6766	0.6227	216.5	3.576	0.0320
7	Boundedness, road density at 2000m scale, prairie dog colonies at 2000m scale	0.6763	0.6224	216.5	3.596	0.0317
8	Area of colony, road density at 2000m scale, prairie dog colonies at 200m scale	0.6725	0.6179	216.8	3.857	0.0278

* = models with ΔAICc less than two were considered the best, most parsimonious models predicting prairie dog burrow density.

1989; VanHorne et al. 1997; Severson & Plumb 1998). I counted active burrow entrances using the same methodology as Powell et al. (1994), yet found over twice as many active burrow entrances/ha. Koford (1958) did not state how burrow density was calculated. Reading et al. (1989) counted all burrow entrances using the belt-transect method but they counted all burrows within an "arm's width" of the transect, instead of the 3-m used by Biggins et al. (1993) and Powell et al. (1994). Nevertheless, at least three studies have found a significant relationship between active burrow density and prairie dog density (Biggins et al. 1993; Powell et al. 1994; Reading & Matchett 1997). Because I also found a significant correlation between these variables, I conclude that the discrepancy found in this relationship among different studies may be due to different sampling techniques, observer bias as to what constitutes an active burrow entrance, or to differences in particular landscape contexts.

Landscape context of Boulder County

The effects of habitat loss and perforation on prairie dog colonies are not well known. In Boulder County, mixed-grass prairies, along with the prairie dog colonies within these grasslands, have been perforated by urbanization and agriculture forcing prairie dogs to survive wherever they can. There are numerous small, bounded colonies along roadsides and both large and small colonies in areas of continuous grassland. Historically, soil structure, topography, and vegetation structure restricted prairie dog colonies from expanding (Koford 1958; Reading & Matchett 1997). Currently, urbanization and other forms of human development restrict prairie dog colony size and spatial distribution more than any other factor, especially in Boulder County. There are prairie dog colonies on steep slopes, in small openings in woodlands, on roadsides and medians, and on top of isolated buttes (W. C. Johnson, personal observation).

In Boulder County, the effects of increased urbanization on other grassland species are variable. Increased urbanization was negatively correlated with the abundance of grassland nesting songbirds (Haire et al. 2000), small mammals (Bock et al. in press), and wintering raptors (Berry et al. 1998), but not correlated with the abundance of butterflies (Collinge et al. in press), and grasshoppers (Orthoptera) (Craig et al. 1999). In the same landscape I found that active burrow density (and prairie dog density) increased as colonies became more bounded, and as the percentage of urbanization and road density in the surrounding landscape increased. The percentage of the landscape covered with other prairie dog colonies, an index of isolation from other colonies, was not correlated with burrow density at any spatial scale, but at the 200-m scale was a variable in the most parsimonious model predicting burrow density (Table 4). Moreover, urbanization and the percentage of the landscape covered with other prairie dog colonies were not correlated at any scale indicating that urban and rural colonies were surrounded by similar amounts of prairie dog colonies. These data indicate that prairie dog colonies within 200-m of other colonies may play a part in mediating the effects of increased urbanization by decreasing the density of prairie dogs.

A recent study in Montana found that distance to roads did not affect prairie dog density or the area of colonies (Reading & Matchett 1997). In my study, road density strongly affected prairie dog density. Although our two studies found contrary results, our indicies of landscape context were calculated differently. Reading and Matchett (1997) used the distance of each colony to a road in estimating the effect of roads on prairie dog density. In comparison, I calculated the density of roads at three spatial scales surrounding each colony to estimate the effect of roads on prairie dog density. Furthermore, Reading and Matchett (1997) conducted their study in comparatively undisturbed grassland in Montana, whereas my study was conducted in landscape perforated by urbanization. It is possible that their range in distance-to-road values may have been too small to detect a significant effect on prairie dog density.

A study of the Mexican prairie dog (*Cynomys mexicanus*), found lower burrow density on small colonies that had been fragmented by agriculture (Trevino-Villarreal & Grant 1998). The authors speculated that habitat loss and fragmentation were responsible for the local extirpation of six out of 88 colonies because of decreased connectivity of the landscape. These results contrast with the higher densities of prairie dogs on smaller colonies in my study area. Nevertheless, if smaller, more fragmented colonies are in fact more vulnerable to extinction, then the smaller, higher-density, and more perforated colonies in my study may have a higher extinction risk than colonies in less perforated landscapes.

In Boulder County, landscape context has been observed to have threshold effects on the abundance of other rodent species. Deer mice, prairie voles, and hispid pocket mice were found to decrease abruptly in abundance at only 5-10% urbanization in the surrounding landscape (Bock et al. in press). Similar studies found that the abundances of four wintering raptors (Berry et al. 1998) and grassland nesting songbirds (Haire et al. 2000) also decreased significantly with as little as 5-7% urbanization in the surrounding landscape. The authors of these studies hypothesized that a critical landscape threshold (Andren 1994; With & Crist 1995) exists at 5-7% urbanization of the landscape where the abundance of these species sharply decreases. Interestingly, the opposite effect occurred in my study on prairie dogs, but without a noticeable threshold effect. Prairie dog burrow density increased linearly in areas surrounded by more urbanization, at all three spatial scales. The increase in prairie dog density that I observed may be due to a "Refuge Effect" in urbanized landscapes. For example, nest predation was significantly higher at greater distances from recreational trails in Boulder County riparian areas, presumably due to human presence on recreational trails (Miller & Hobbs 2000). Similarly, many potential prairie dog predators may decline in urbanized landscapes enabling prairie dog colonies to achieve higher densities.

Habitat quality and demography of prairie dogs

The increased density of prairie dogs in my study could result in multiple changes in their demography. Higher density of animals does not necessarily indicate higher habitat quality (VanHorne 1983), especially for prairie dogs in Boulder County. In a non-urbanized landscape, Gunnison's prairie dog (*Cynomys gunnisoni*) was observed to have similar densities at good and poor habitat quality sites, but prairie dogs at the poor habitat quality site had lower body mass, delayed sexual maturity, and delayed dispersal when compared to a site with higher habitat quality (Rayor 1985). Similarly, in the urbanized landscape of Boulder County, "urban" adult males, and adult and juvenile females had significantly lower body mass than the same age groups at a "rural" colony (Dawson 1991). Dawson's (1991) urban site was surrounded by buildings and the rural colony was located in relatively undisturbed grassland. Interestingly, Dawson (1991) found no difference in prairie dog densities between the urban and rural prairie dog colonies, contrary to what I found in my study. However, he had a sample size of only one urban and one rural colony. Even without higher densities, if urban prairie dogs have decreased body mass (Dawson 1991) and prairie dogs in poorer habitat quality sites have decreased body mass (Rayor 1985), then prairie dogs in urban colonies may have decreased body mass due to poor habitat quality. More research is necessary to determine if high-density prairie dog colonies in urbanized landscapes actually have lower food resources than colonies in non-urbanized landscapes--even though this relationship seems obvious.

In highly urbanized colonies, prairie dog density may also be related to decreased dispersal rates. In colonies not bounded by urbanization, dispersal rates increased as available food resources decreased (Garret & Franklin 1988). If the dispersal rate of prairie dogs is reduced in urban colonies because of barriers such as roads and buildings, and increased density of prairie dogs decreases food resources in urban colonies, then prairie dogs may have lower dispersal rates in areas of low food resources. Over the long term, high-density colonies may not be able to sustain high amounts of herbivory, and habitat quality may become degraded leading to population decline.

Another factor that could limit black-tailed prairie dog density is infanticide. Up to 39% of litters are affected by infanticide in black-tailed prairie dogs (Hoogland 1995). In non-urbanized landscapes, infanticide rate appears to be independent of prairie dog density (Hoogland 1995). However, the effects of increasing boundedness, urbanization, and road density on infanticide rate are unknown. Infanticide rate may increase at abnormally high prairie dog densities.

Plague and its possible implications for prairie dog demography

In addition to fragmentation and perforation effects on prairie dog colonies, the introduced sylvatic plague (*Yersinia pestis*) may now have created metapopulations of prairie dog populations (Roach et al. 2001). Prairie dog colonies are not thought to have experienced periodic extinctions before the introduction of plague. Colonies are now periodically extripated by plague and later recolonized by dispersers from nearby colonies (Hanski & Simberloff 1997; Cully & Williams 2001; Roach et al. 2001). Colonies with higher prairie dog density have higher plague transmittance rates than less-dense colonies (Cully & Williams 2001). Therefore, in my study area, the smaller urban colonies should be the first colonies to be extirpated by plague. However, during the 1994 plague outbreak in Boulder County, the relatively larger rural prairie dog colonies were the ones most severely affected by plague.

The size of a colony may also affect transmission rates of plague between colonies. Cully and Williams (2001) found that larger colonies greater than 3 km apart were more likely to experience plague during an outbreak. They suggested that smaller colonies that are farther apart tend to persist longer when plague is present in the landscape. In Boulder County, there are not many colonies that are disconnected by more than 3 km; colonies are dispersed throughout the landscape like stepping-stones. Therefore, the limiting factor affecting disease transmittance in Boulder County may not be whether the colonies are isolated by distance, but whether they are isolated by their surroundings (i.e., their landscape context).

In my study, high-density colonies were in highly developed areas, surrounded by habitat not conducive to high dispersal success. This observation suggests that dispersal mortality would be much higher at the urban prairie dog colonies than at the rural prairie dog colonies. This may be one reason why urban colonies have higher densities: in the short term, prairie dogs have adapted behaviorally to higher densities because dispersal is unsuccessful. Furthermore, because there may be decreased dispersal success, intraspecific plague transmission may also be decreased. Cully & Williams (2001) suggested that plague is carried to colonies interspecifically by animals such as coyotes, deer mice, and raptors. Interspecific disease transmission may also be decreased by urbanization; thus, transmitting plague to these urban prairie dog colonies could prove difficult (i.e. Refuge Effect). Studies are currently underway to determine the dynamics of plague transmission between and within prairie dog colonies and the effect of landscape context on plague transmission.

In conclusion, prairie dog colonies in urbanized areas of Boulder County have an abnormally high density of prairie dogs. The long-term implications for prairie dog demography are unknown although many predictions arise from my study. With no room for colony expansion, abnormally high prairie dog density could create increased competition for available food and space, lower dispersal rates, and higher infanticide rates. In the event of plague, high density colonies may experience increased plague transmission rates and decreased recolonization rates. However, the effects of urbanization on plague transmission will depend on what species are carrying plague between colonies, and how these species are affected by potential dispersal barriers, such as roads. Plague may effectively extirpate urban black-tailed prairie dog colonies from the landscape if prairie dogs cannot recolonize highly urban colonies.

Literature Cited

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.

Agnew, W., D. W. Uresk, and R. M. Hansen. 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.

American Society of Mammalogists. 1998. American Society of Mammalogists' resolution on the decline of prairie dogs and the grassland ecosystem in North America. Journal of Mammalogy 79:1447-1448.

Berry, M. E., C. E. Bock, and S. L. Haire. 1998. Abundance of diurnal raptors on open space grasslands in an urbanized landscape. The Condor 100:601-608.

Biggins, D., B. Miller, L. Hanebury, B. Oakleaf, A. Farmer, R. Crete, and A. Dood. 1993. A system for evaluating black-footed ferret habitat. Pages 73-92 in J. Oldemeyer, D. Biggins, B. Miller, and R. Crete, eds. Management of prairie dog complexes for black-footed ferret reintroduction. U. S. Fish and Wildlife Service Biological Report 13.

Biggins, D. E., and M. Y. Kosoy. 2001. Influences of introduced plague on North American mammals: implications from ecology of plague in Asia. Journal of Mammalogy 82:906-916.

Bock, C. E., K. T. Vierling, S. L. Haire, J. D. Boone, and W. W. Merkle. Patterns of rodent abundance on open-space grasslands in relation to suburban edges. Conservation Biology, in press.

Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference. A practical information-theoretic approach. Springer-Verlag New York Inc. New York, NY.

Collinge, S, K, and R. T. T. Forman. 1998. A conceptual model of land conversion processes: predictions and evidence from a microlandcape experiment with grassland insects. Oikos 82: 66-84.

Collinge, S. K., K. L. Prudic, and J. C. Oliver. Effects of local habitat characteristics and landscape context on grassland butterfly diversity. Conservation Biology, in press.

Colorado Department of Natural Resources. 2000. Black-tailed prairie dog study of eastern Colorado. Prepared by EDAW, Inc. Fort Collins, CO. 49 pp.

Craig, D. P., C. E. Bock, B. C. Bennett, and J. H. Bock. 1999. Habitat relationships among grasshoppers (Orthoptera:Acrididae) at the western limit of the Great Plains in Colorado. American Midland Naturalist 142:314-327.

Cully, J.F., Jr., A.M. Barnes, T.J. Quan and G. Maupin. 1997. Dynamics of plague in a Gunnison's prairie dog colony complex from New Mexico. Journal of Wildlife Diseases 33:706-719.

Cully, J. F. Jr., and E. S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy 82:894-905.

Dawson, R. E. 1991. Comparison of body mass and demography between urban and rural populations of black-tailed prairie dogs (*Cynomys ludovicianus*). Masters Thesis, University of Colorado at Boulder. 71pp.

Desmond, M. J., and J. A. Savidge. 1996. Factors influencing burrowing owl (Speotyto cunicularia) nest densities and numbers in western Nebraska. American Midland Naturalist 136:143-148.

Fagerstone, K.A., and D. E. Biggins. 1986. Comparison of capture-recapture and visual indices of prairie dog densities in black-footed ferret habitat. Great Basin Naturalist Memoirs 8:94-98.

Fitzgerald, J. P., C. A. Meaney, and D. M. Armstrong. 1994. Mammals of Colorado. Denver Museum of Natural History and University Press of Colorado. 467pp.

Forman, R. T. T. 1995. Land Mosaics: the ecology of landscapes and regions. Cambridge University Press, New York, NY.

Garrett, M. G., and W. L. Franklin. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. Journal of Mammalogy 69:236-250.

Gober, P. 2000. 12-month administrative finding, black-tailed prairie dog. Federal Register 65:5476-5488.

Goodrich, J. M., and S. W. Buskirk. 1998. Spacing and ecology of North American badgers (*Taxidea taxus*) in a prairie-dog *(Cynomys leucurus)* complex. Journal of Mammalogy 79:171-179.

Haire, S. L., C. E. Bock, B. S. Cade, and B. C. Bennett. 2000. The role of landscape and habitat characteristics in limiting abundance of grassland nesting songbirds in an urban open space. Landscape and Urban Planning 48:65-82.

Hanski, I., and D. Simberloff, 1997. The Metapopulation Approach, its history, conceptual domain, and application to conservation. Pp. 5-26, In:

Metapopulation Biology: Ecology, Genetics, and Evolution. Eds. I.A. Hanski, and M.E. Gilpin. Academic Press, San Diego, CA.

Hoogland, J.L. 1995. The Black-Tailed Prairie Dog, Social life of a Burrowing Mammal. The University of Chicago Press, Chicago, IL.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373-386.

Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildlife Monographs 3:1-78.

Kotliar, N. B., B. W. Baker, A. D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24:177-192.

Kotliar, N. B. 2000. Application of the new keystone species concept to prairie dogs: how well does it work? Conservation Biology 14:1715-1721.

Kretzer, J. E., and J. F. Cully Jr. 2001. Effects of black-tailed prairie dogs on reptiles and amphibians in Kansas shortgrass prairie. The Southwestern Naturalist 46:171-177.

Lomolino, M. V., and G. A. Smith. 2001. Dynamic biogeography of prairie dog (*Cynomys ludovicianus*) towns near the edge of their range. Journal of Mammalogy 82:937-945.

Menkens, G. E. Jr., and S. H. Anderson. 1993. Mark-recapture and visual counts for estimating population size of white-tailed prairie dogs. Pages 67-72 in J. Oldemeyer, D. Biggins, B. Miller, and R. Crete, eds. Management of prairie dog complexes for black-footed ferret reintroduction. U.S. Fish and Wildlife Service Biological Report.

Menkens, G. E. Jr., D. E. Biggins, and S. H. Anderson. 1990. Visual counts as an index of white-tailed prairie dog density. Wildlife Society Bulletin 18:290-296.

Miller, B., C. Wemmer, D. Biggins, and R. Reading. 1990. A proposal to conserve black-footed ferrets and the prairie dog ecosystem. Environmental Management 14:763-769.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology 8:667-681.

Miller, J. R., and N. T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. Landscape and Urban Planning 50:227-236.

Minta. S. C. & T. W. Clark. 1989. Habitat suitability analysis of potential translocation sites for black-footed ferrets in northcentral Montana. Pp. 29-46 in The Prairie dog ecosystem: managing for biological diversity: Eds. T. W. Clark, D. Hinkley, and T. Rich. Montana BLM Wildlife Technical Bulletin No. 2.

Paine, R.T. 1969. A note on trophic complexity and community stability. American Naturalist 103:91-93.

Powell, K.L., Robel, R.J, Kemp, K.E., M.D. Nellis. 1994. Aboveground Counts of Black-Tailed Prairie Dogs – Temporal Nature and Relationship to Burrow Entrance Density. J. Wildl. Manage. 58:351-355.

Rayor, L. S. 1985. Effects of habitat quality on growth, age of first reproduction, and dispersal in Gunnison's prairie dogs (*Cynomys gunnisoni*). Canadian Journal of Zoology 63:2835-2840.

Reading, R. P., S. R. Beissinger, J. J. Grensten, and T. W. Clark. 1989. Attributes of black-tailed prairie dog colonies in northcentral Montana, with management recommendations for the conservation of biodiversity. Pp. 13-28 in The Prairie dog ecosystem: managing for biological diversity: Eds. T. W. Clark, D. Hinkley, and T. Rich. Montana BLM Wildlife Technical Bulletin No. 2.

Reading R. P., and R. Matchett. 1997. Attributes of black-tailed prairie dog colonies in northcentral Montana. Journal of Wildlife Management 61:664-673.

Roach, J. L., P. Stapp, B. VanHorne, and M. F. Antolin. 2001. Genetic structure of a metapopulation of black-tailed prairie dogs. Journal of Mammalogy 82:946-959.

Severson, K. E., and G. E. Plumb. Comparison of methods to estimate population of black-tailed prairie dogs. Wildlife Society Bulletin 26:859-866.

Sidle, J. G., D. H. Johnson, and B. R. Euliss. 2001. Estimated areal extent of colonies of black-tailed prairie dogs in the northern great plains. Journal of Mammalogy 82:928-936.

Trevino-Villarreal, J., and W. E. Grant. 1998. Geographic range of the endangered Mexican prairie dog (*Cynomys mexicanus*). Journal of Mammalogy 79:1273-1287.

VanDruff, L. W., E. G. Bolen, and G. J. San Julian. 1996. Management of urban wildlife. Pages 507-530 in Research and management techniques for wildlife and habitats. ed. T. A. Bookhout. Fifth ed., rev. The Wildlife Society, Bethesda, Md.

VanHorne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Van Horne, B, Schooley, R.L., Knick, S.T., Olson, G.S., K.P. Burnham. 1997. Use of burrow entrances to indicate densities of Townsend's ground squirrels. Journal of Wildlife Management 61:92-101.

With, K. A., and T. O. Crist. 1995. Critical thresholds in species responses to landscape structure. Ecology 76:2446-2459.

Zar, J. H. 1999. Biostatistical analysis. 4th ed. Prentice-Hall, Inc. New Jersey.

Conclusion

In Chapter I, I found that black-tailed prairie dogs significantly affected small mammal species composition on the grasslands of Boulder County. There was no difference in small mammal density on and off prairie dog colonies; however, small mammal communities in grasslands with prairie dogs were significantly less diverse than in grasslands without prairie dogs. Although there were proportionately more deer mice on prairie dog colonies, the difference was not significant due to high variation in the number of deer mouse captures on prairie dog colonies. Western harvest mice were not found on grasslands with prairie dogs perhaps because harvest mice prefer sites with dense vegetation cover. Furthermore, deer mice may competitively exclude harvest mice from short- and mixed-grass prairies. Land managers need to preserve grasslands with and without prairie dog colonies in order to conserve the unique small mammal communities found on each. Furthermore, the presence of prairie dog colonies may increase landscape heterogeneity by creating a mosaic of habitat patches with high and low small mammal species diversity. In Boulder County, deer mice may serve as a reservoir for sylvatic plague, because they are the only species of small mammal species that I captured in abundance on prairie dog colonies.

In Chapter II, I observed a positive correlation between urbanization and prairie dog burrow density and road density and prairie dog burrow density. The percentage of other prairie dog colonies in the landscape, an index of isolation from other colonies, was not significantly correlated with prairie dog density. Prairie dog density and colony area were correlated with boundedness, an index of the amount of unsuitable habitat immediately adjacent to a colony. Prairie dogs appeared to be highly sensitive to the amount of urbanization in the landscape, at least up to 2-km from the perimeter of a colony. Interestingly, the scale at which I examined urbanization and road density did not matter. Increased urbanization appears to create smaller prairie dog colonies that have higher densities of prairie dogs. Finally, boundedness, road density at the 2000-m scale, and the percentage of the surrounding landscape covered in other prairie dog colonies at the 200-m scale best predicted burrow density ($R^2 = 0.73$). Anthropogenic landscape features immediately surrounding prairie dog colonies and up to 2-km away from a colony appear to increase prairie dog densities. Prairie dog colonies within 200-m of a colony may provide easy dispersal destinations, slightly lessening the increase in prairie dog density related to urbanization and road density. Over the long term, with no place for urban colonies to expand, increased competition for resources could cause population declines. Other density-dependent factors may also intensify under high prairie dog densities, such as increased infanticide and inbreeding. If plague extirpates an urban colony, recolonization may prove difficult in highly urbanized colonies because of dispersal barriers. More studies are needed to determine the long-term effects of landscape context on prairie dog demography and plague susceptibility.