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Interactions between black-tailed prairie dogs (*Cynomys ludovicianus*) and vegetation in habitat fragmented by urbanization

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Abstract

Although prairie dogs may function as keystone species in natural systems, little is known about their impacts in urban settings. We measured vegetative cover, vegetative height and density, and slope on isolated black-tailed prairie dog (*Cynomys ludovicianus*) colonies in semi-arid habitat along a gradient of urbanization in Denver, CO. We compared these measurements with data taken within the same colonized fragments but in areas unused by prairie dogs, and with data taken on habitat fragments entirely unoccupied by prairie dogs. As predicted, prairie dog colonies had reduced grass and litter layers, but increased forb and bare soil coverage. Plants were shorter and less dense on colonies, and slope was gentler. Grass cover was higher on uncolonized portions of fragments occupied by prairie dogs than on sites unoccupied by prairie dogs, suggesting that prairie dogs were more likely to be present on sites with high grass cover. In general, prairie dog–vegetation interactions we recorded were similar in urban fragmented landscapes to those observed in natural landscapes, providing evidence that some aspects of their ecological role are retained in urban systems.

Keywords: Habitat fragmentation; Herbivory; Plants; Urban development; Urban wildlife

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1. Introduction

Prairie dogs (*Cynomys* spp.) create important interactions in arid and semi-arid prairie and steppe ecosystems that may enhance total diversity (Bangert and Slobodchikoff, 2000; Detling, 1998; Miller et al., 1994, 2000) and are often designated as keystone species, highly interactive species, or ecosystem engineers (Bangert and Slobodchikoff, 2000; Kotliar, 2000; Kotliar et al., 1999; Miller et al., 1994, 2000; Soulé et al., 2003, 2005). For example, prairie dogs have been found to influence diversity of birds (Agnew et al., 1986; Manzano, 1996), small mammals (Ceballos et al., 1999; Hansen and Gold, 1977), herpetiles (Shipley and

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Reading, 2006), predators (Clark et al., 1982), and arthropods (Bangert and Slobodchikoff, 2006; Davidson and Lightfoot, in press; Russell and Detling, 2003).

Ecosystem-level impacts of prairie dogs also include effects on the vegetative community (Detling, 1998). Early studies focused on the degree to which prairie dogs might reduce forage for cattle (Hansen and Gold, 1977; Merriam, 1902; O'Meilia et al., 1982), but prairie dog colonies also have been shown to increase regional plant diversity (Bonham and Lerwick, 1976; Coppock et al., 1983). Prairie dogs decrease vegetative biomass both through consumption and clipping to facilitate predator detection (Hoogland, 1995). Prairie dogs can reduce grass cover and increase forb cover on colonies (Archer et al., 1987), increase amount of bare soil, and decrease standing litter (Coppock et al., 1983). In addition, prairie dog grazing has been found to significantly increase plant leaf nitrogen content (Coppock et al., 1983; Detling, 1998; Holland and Detling, 1990) and alter seed bank composition (Fahnestock et al., 2003).

The range of the prairie dog has been severely restricted by development, disease, and eradication by humans (Miller et al., 1990, 1994), and many of the remaining colonies are strongly affected by habitat fragmentation and urbanization (Johnson and Collinge, 2004; Lomolino and Smith, 2001). Although prairie dogs are considered ecosystem engineers in natural systems, it has been suggested that they may not perform keystone roles in highly fragmented habitat (Lomolino and Smith, 2003). Despite numerous studies documenting their impacts on plant communities, prairie dog–vegetation interactions have not been investigated in urban areas. Given the highly interactive nature of prairie dogs (Miller et al., 1994; Soulé et al., 2005) and the ongoing efforts to translocate them from and among urban patches (Farrar et al., 1998; Robinette et al., 1995), knowledge of how prairie dogs may impact vegetation or persist on patches with different habitat characteristics will help define target areas for priority removal, introduction, or management. In addition, wildlife/vegetation interactions in urban habitat patches may alter the important roles of these patches, which can include housing rare or endangered species (Crooks et al., 2001), facilitating bird migrations by providing stop-over sites (Fischer and Lindenmayer, 2002), providing wildlife corridors or stepping stones between undeveloped areas (Crooks and Sanjayan, 2006; Soulé, 1991), enhancing property values (Bolitzer and Netusil, 2000; Correll et al., 1978), and producing aesthetically pleasing landscapes (Garrod and Willis, 1995; Smith, 1993).

To characterize vegetative structure in urban fragmented habitat, we measured vegetative cover, vegetative height and density, and slope on isolated black-tailed prairie dog (*Cynomys ludovicianus*) colonies in semi-arid habitat remnants within urban Denver, CO. We also measured these variables within the same colonized fragments but in areas not colonized or used by prairie dogs, and on uncolonized habitat fragments within the same landscape. We evaluated differences in vegetative characteristics among these three fragment classes based on expectations derived from prior work on prairie dog–vegetation interactions in non-urban systems. Specifically, we tested the hypotheses that, as in natural systems, prairie dog colonies in urban fragments would be associated with elevated forb and bare ground layers, decreases in grass and litter layers, a decline in vegetative height and density, and flatter slopes. If prairie dogs influence vegetation similarly in urbanized and natural systems, it may provide evidence that some aspects of their ecological role are retained in grassland systems within urbanizing landscapes.

2. Material and methods

The study area (ca. 374 km^2) is bounded to the north by Interstate-70, near downtown Denver, CO, and extends south to the edge of development in Denver's southern suburbs. The study boundaries are described by a rectangle approximately 12 km wide by 31.2 km long (Fig. 1). In the summer of 2002, we identified every habitat fragment (387) within this area. A fragment was defined as any plot of undeveloped land, regardless of shape, with an area of at least 0.25 ha that was not regularly landscaped, and that was embedded in a dissimilar, less-hospitable, human-modified matrix. Fragments were identified from aerial photographs for 2000 obtained from Landiscor, Inc. (Denver, CO) that had 0.7 m pixel resolution and were verified via field reconnaissance; this constituted a complete census. Of the 387 fragments, 54 were colonized by prairie dogs.

Vegetative characteristics were compared among three fragment categories: (1) colonized—data from prairie dog colonies, (2) uncolonized—data collected within the same habitat fragments colonized by prairie dogs, but in areas the prairie dogs did not occupy or utilize for grazing, and (3) unoccupied—data from

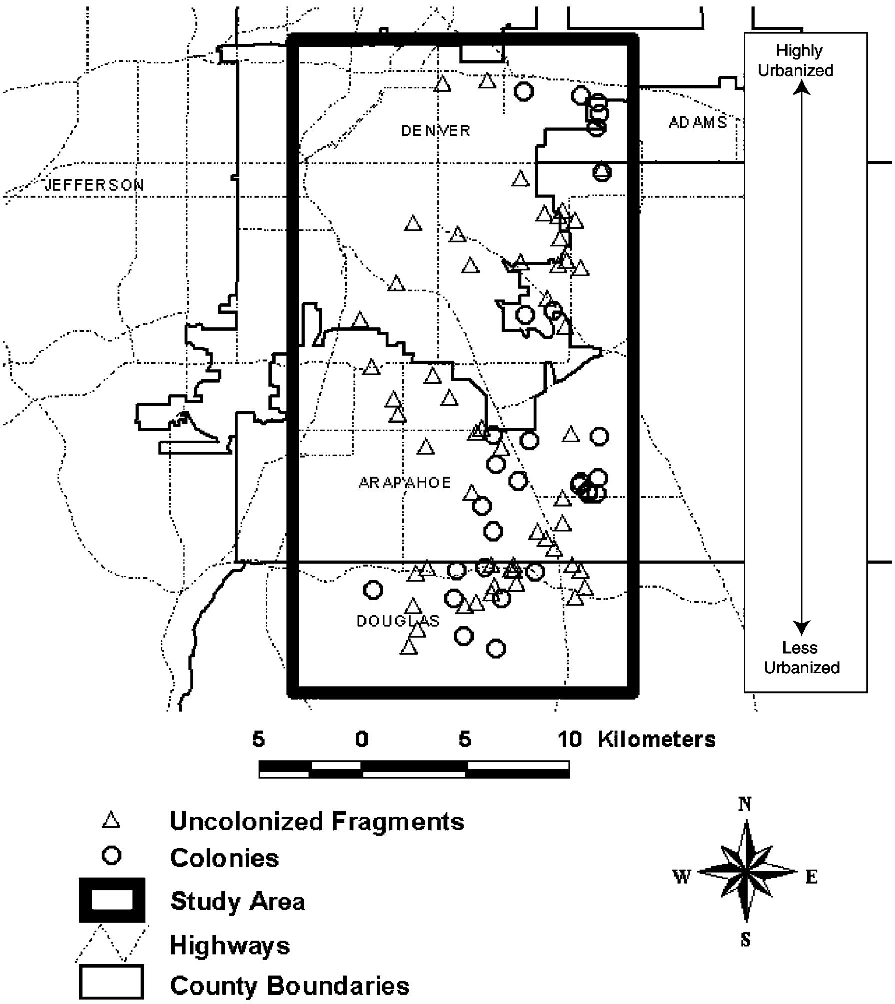

Fig. 1. Map of the study area.

fragments where no prairie dogs were present. Paired t-tests were used to compare variables on colonized and uncolonized portions of fragments containing prairie dogs. We used non-paired t-tests to compare variables between prairie dog colonies and unoccupied fragments, and to compare uncolonized portions of colonized fragments to fragments unoccupied by prairie dogs.

Habitat variables were measured between 1 July and 22 August 2002 on all fragments colonized by prairie dogs where permission to sample was granted, and which also had a significant uncolonized portion (29); sizes of colonized fragments that were surveyed (mean = 26.4 ha, SD = 34.9, $n = 29$) did not differ ($t = 0.97$; $p = 0.34$) from sizes of occupied fragments where habitat surveys could not be conducted (mean = 17.4 ha, SD = 30.6, $n = 25$) indicating no site selection bias by fragment area. For comparison, habitat surveys also were conducted on 54 fragments not occupied by prairie dogs. Unoccupied fragments were sampled when accessible, and where possible were selected based on having comparable areas and proximity to colonized fragments. However, for the largest colonized fragments, unoccupied fragments of comparable size were not available on the study area, and consequently, sizes of surveyed colonized fragments (mean = 26.4 ha, SD = 34.9) on average were larger ($t = 2.47$, $p = 0.019$) than surveyed unoccupied fragments (mean = 9.0 ha, SD = 15.6). To explore the possible effect of this size difference, we repeated all analyses only including unoccupied and colonized fragments of similar sizes (<33% difference), and conducted paired t-tests on the resulting 26 pairs. Statistical significance of all comparisons and resulting conclusions remained unchanged, so throughout we present the full analyses including all surveyed fragments in order to maximize the proportion of the study area represented in the dataset.

On each sampled site, three random transects were chosen, each parallel to the long axis of the colony or fragment and a minimum of 10 m apart. Transects were either 100 m or the length of the colony/fragment, whichever was shorter. At 10 m intervals along each transect, we measured slope, vegetative cover, and vegetative height and density as described here. All colonized fragments used in this study also contained a considerable uncolonized portion, so three transects were placed on both the colonized and uncolonized portions, for a total of six transects on those fragments.

At each sampling point, the proportion of vegetative cover within $20 \times 50\,\mathrm{cm}^2$ quadrats was visually estimated to the nearest 1% using methods modified from Daubenmire (1959). Categories used for the modified Daubenmire analysis included graminoid (grasses, sedges, and rushes), forb, litter, and bare ground. Although individual species were not always noted, we did record any dominant species on a fragment, which was operationally defined as a plant species covering $\geqslant 50\%$ of a fragment.

Height and density of vegetation were measured using the Robel method (Robel et al., 1970). A Robel pole 150 cm long was painted black and white at alternating 1 dm intervals. At each sampling point, the Robel pole was placed vertically 10 cm to one side of the transect. The pole was then observed from the opposite side of the transect at a height of 1 m and at a distance of 4 m. The lowest decimeter mark visible on the pole was recorded; this value integrates height and density of the vegetation (Robel et al., 1970). Slope was estimated with an inclinometer at each sampling point. Slope measurements were placed into one of six categories: slope of 0–2% (1), 3–4% (2), 5–8% (3), 9–15% (4), 16–25% (5), and $>25\%$ (6) (Proctor, 1998).

Overall, the mean number of habitat variable measurements on colonized and uncolonized portions of occupied fragments was 26.4 (range = 2–30, SD = 6.34) and 28.4 (range = 7–30, SD = 4.53), respectively. On each of the 54 uncolonized fragments, we recorded an average of 28.6 measurements (range = 17–30, SD = 3.10).

3. Results

Colonized components of fragments had less graminoid and litter cover and more forb cover and bare ground than uncolonized portions of the same fragments (Table 1, Fig. 2). Vegetation was shorter and/or less dense in the colonized areas, and colonies tended to have flatter slopes than uncolonized portions of their fragments.

The comparisons of colonies to unoccupied fragments revealed higher bare ground and forb coverage on colonies. Litter layer was reduced on colonies, which also had shorter and sparser vegetation and gentler slopes compared to fragments unoccupied by prairie dogs. Graminoid coverage did not significantly differ between colonies and fragments without prairie dogs.

When evaluating differences between uncolonized portions of colonized fragments and fragments unoccupied by prairie dogs, there was significantly more grass on uncolonized portions. Uncolonized areas

Table 1
Results of statistical analyses of habitat variables on urban fragments in Denver, CO

Treatment comparison	N	Graminoid cover	Forb cover	Litter cover	Bare ground	Robel measure	Slope
Colonized vs. uncolonized	29	$T=-6.49$, $p<0.001$	$T=3.95$, $p<0.001$	$T=-3.99$, $p<0.001$	$T=5.40$, $p<0.001$	$T=-4.52$, $p<0.001$	$T=-1.82$, $p=0.080$
Colonized vs. unoccupied	29, 54	$T=-0.93$, $p=0.360$	$T=2.80$, $p=0.005$	$T=-4.41$, $p<0.001$	$T=2.92$, $p=0.005$	$T=-4.95$, $p<0.001$	$T=-3.79$, $p<0.001$
Uncolonized vs. unoccupied	29, 54	$T=5.51$, $p<0.001$	$T=-0.630$, $p>0.5$	$T=-1.55$, $p=0.130$	$T=-1.94$, $p=0.056$	$T=0.23$, $p>0.5$	$T=-2.64$, $p=0.010$

Paired t-tests were used for comparisons of colonized areas with uncolonized areas, unpaired t-tests were used for comparing colonized areas to unoccupied areas and uncolonized areas to unoccupied areas.

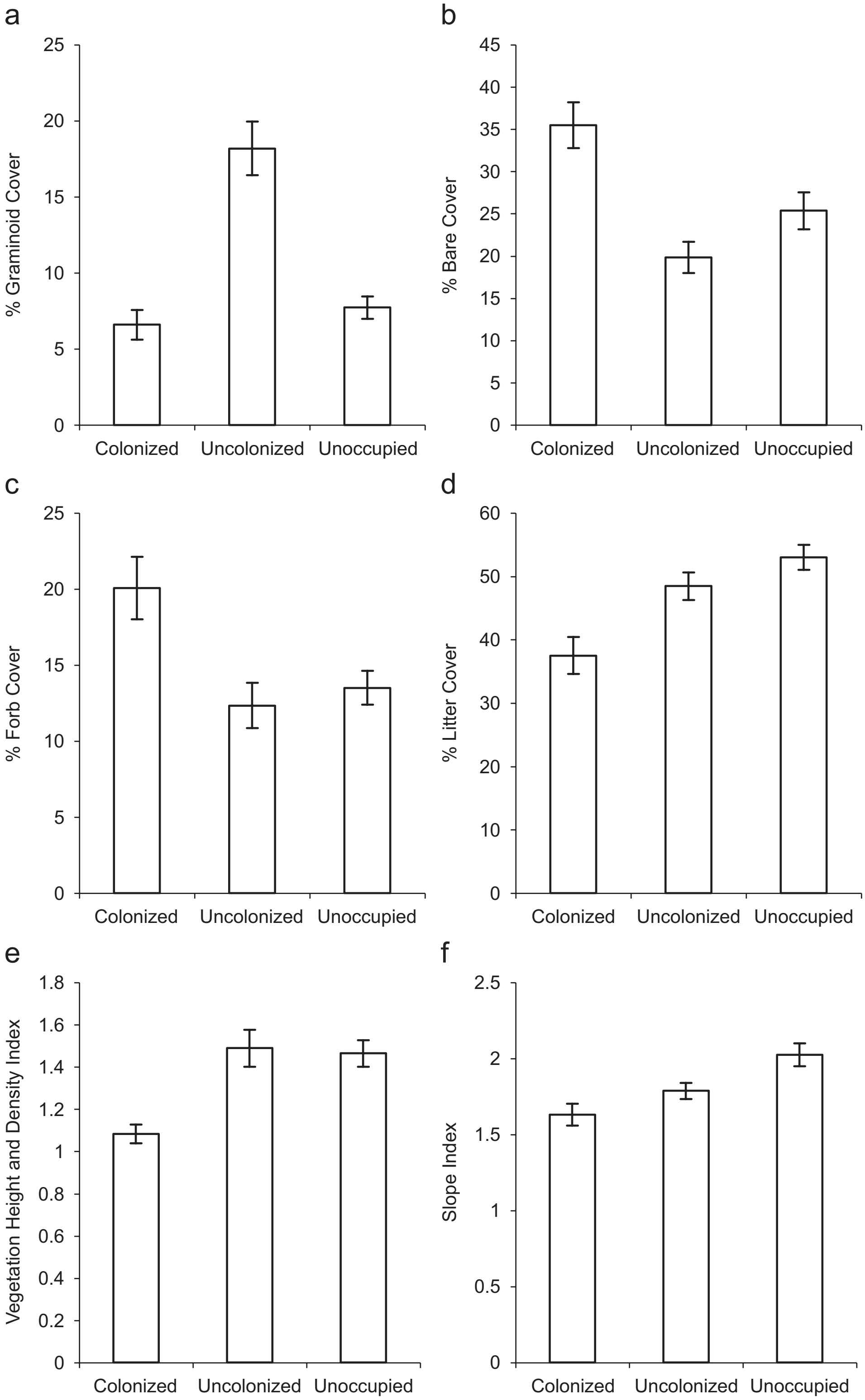

Fig. 2. Comparisons of average value of: (a) grass cover, (b) bare cover, (c) forb cover, (d) litter cover, (e) vegetation height and density, and (f) slope on prairie dog colonies, uncolonized portions of colonized fragments, and fragments unoccupied by prairie dogs. Errors bars represent standard errors.

also had gentler slopes and a trend for less bare ground than fragments that were unoccupied. There were no significant differences in forb coverage, litter coverage or vegetative height and density between uncolonized portions of colonized fragments and unoccupied fragments (Table 1, Fig. 2).

The most common dominant species in our urban fragments was field bindweed (*Convolvulus arvensis*), an introduced forb that was dominant in over 70% of prairie dog colonies, over 30% of uncolonized portions, and over 50% of unoccupied fragments. The most common grass recorded on urban fragments was also an introduced species, smooth brome (*Bromus inermis*), which was dominant in over 10% of prairie dog colonies, over 60% of uncolonized portions, and over 30% of unoccupied fragments. Although non-native vegetation was common, scarlet globemallow (*Sphaeralcea coccinea*), a native forb known to be a preferred forage item for prairie dogs (Clippinger, 1989; Uresk, 1984), was dominant on over 40% of prairie dog colonies but on less than 5% of uncolonized portions or unoccupied fragments. Overall, approximately 50% of dominant species recorded on both prairie dog colonies and uncolonized portions of their fragments were non-native, compared to approximately 60% for unoccupied fragments.

Additionally, after review of initial results indicating complex dynamics for graminoid species we used simple linear regression to relate colony graminoid cover to fragment age, defined as time since isolation of the fragment (which we determined by review of county assessor building records), and revealed a significant negative relationship ($R^2 = 0.173$, regression coefficient $= -0.1895$, $p = 0.009$), which is not evident in unoccupied fragments ($R^2 = 0.021$; regression coefficient $= -0.027$; $p = 0.292$).

4. Discussion and conclusions

As predicted, prairie dogs in our isolated urban habitat fragments were associated with a decline in graminoid and litter layers and an increase in forb and bare ground coverage, as well as shorter, less dense vegetation and flatter slopes. Such patterns are consistent with interactions recorded in natural systems, and are attributed to prairie dogs clipping vegetation and preferentially consuming grass, providing forb species a competitive advantage (Coppock et al., 1983; Day and Detling, 1994; Detling, 1998; Fahnestock and Detling, 2002; Fahnestock et al., 2003; Hoogland, 1995; Whicker and Detling, 1988). However, uncolonized portions of colonized fragments had substantially more graminoid cover than fragments not occupied by prairie dogs, which was not expected. This suggests that prairie dogs are more likely to be present on sites with greater graminoid cover, even though the prairie dogs locally reduce graminoids in their colonies. This finding could be a product of colonizing prairie dogs initially selecting fragments with more grass, higher persistence of colonies on sites with greater graminoid cover, and/or more complex ecological interactions, for example presence of prairie dogs excluding species such as 13-lined ground squirrels (*Spermophilus tridecemlineatus*) that preferentially forage on graminoid seeds (as in Stapp, 2007). Whatever the cause, this relationship has important implications for conservation or translocation of prairie dogs in urban settings, and suggests that efforts should perhaps focus on habitat patches with high grass content.

The finding that graminoid cover is negatively related to time since isolation of fragments suggests that prairie dogs may hasten reduction in graminoid cover as urban habitat fragments age. Indeed, reduction of vegetative cover by prairie dogs in urban fragments may be especially pronounced because urban prairie dogs often have elevated densities, exceeding 100 animals/ha (Johnson and Collinge, 2004; Magle et al., in press) compared to typical densities of 10–35 prairie dogs/ha in rural areas (Koford, 1958; Powell et al., 1994; Reading et al., 1989).

The gentler slope on prairie dog colonies compared with unoccupied fragments (Fig. 2) is consistent with previous findings that prairie dogs prefer flat areas (Proctor, 1998; Reading, 1993; Reading and Matchett, 1997). Notably, such flat areas are often the quickest to convert to urban development (Kaplan et al., 2003; Landis, 1994; Moser, 1991; Whitley et al., 1993). Indeed, prairie dogs within urban Denver appear to exist in grassland remnants susceptible to development and difficult to conserve. Between 2002 and 2006, nine of the 54 prairie colonies (16.7%) in this study area were eliminated by humans and their habitat fragment was developed (Magle, unpublished data). Unoccupied patches were also susceptible to development: 105 out of 333 (31.5%) of the habitat fragments without prairie dogs were also developed during this time frame. Thus, not only is existing prairie dog habitat vanishing within this study system, but sites that provide potential for colonization are being developed as well. Since destruction of natural habitat for prairie dogs is ongoing

(Miller et al., 1994, 2000), and because urban colonies may be isolated from plague (Johnson and Collinge, 2004; Lomolino and Smith, 2001), urban refugia may become increasingly important for prairie dog conservation, particularly if urban colonies are genetically and demographically stable and retain ecological functionality.

Isolated urban habitat fragments are often susceptible to invasion by non-native species (Alberts et al., 1993; Hunter, 2002; Soulé et al., 1992), and field bindweed, an invasive forb, was most commonly found on prairie dog colonies in this study. While it is known that prairie dogs often provide a competitive advantage to forb species (Coppock et al., 1983; Day and Detling, 1994; Detling, 1998), and it is thus conceivable that prairie dogs in this study system are enhancing the spread of this invasive exotic species, further studies are needed to confirm this relationship. In addition, prairie dogs are known to consume field bindweed (Lehmer et al., 2006), and thus may actually have potential to limit its spread.

Differences in vegetative characteristics on and off prairie dog colonies may be due to prairie dogs selecting or persisting on sites due to local vegetative factors, altering habitat through herbivory and ecosystem impacts, or a combination thereof. Although prior studies have experimentally examined the ecological impacts of prairie dogs via exclosures (Cid et al., 1991; Fahnestock and Detling, 2002; Fahnestock et al., 2003) or introductions (Davidson et al., 1999), we are not aware of similar manipulations in urbanizing systems. Experimental studies could take advantage of ongoing prairie dog control and translocation activities common in urban areas and would clarify the causality of the relationship between prairie dogs and vegetation in these systems. However, these studies may need to be monitored for many years since vegetative changes induced by herbivores often happen slowly (Cid et al., 1991; Davidson et al., 1999; Uresk, 1985). For example, some studies have found that 1 year after introduction (Davidson et al., 1999) and 4 years after exclusion (Uresk, 1985) of prairie dogs is not sufficient time to allow for significant vegetative changes, though others (Cid et al., 1991) reported responses in vegetation only 2 years after exclusion.

Finally, it has been suggested that, unlike prairie dogs in natural systems, prairie dogs in small habitat fragments may not function as keystone species (Lomolino and Smith, 2003). Specifically, Lomolino and Smith (2003), studying prairie dogs in fragmented agricultural landscapes in Oklahoma, found that the community-level effects of prairie dogs on non-volant terrestrial vertebrates varied greatly based on landscape context rather than colony size or isolation, and concluded that if prairie dogs persist only in isolated communities in anthropogenic habitats, their keystone role would cease. Interactions between prairie dogs and vegetation in our urban habitat fragments, however, were similar to those described in natural systems. Thus, our study suggests that prairie dogs may retain some aspects of their traditional ecological role in urban areas, at least in terms of their impacts on local habitat, although assessments of proportional abundance (Magle et al., in press) and ecological importance would be needed to confirm keystone status. Further, any keystone effects could be limited if animals and plants typically facilitated by prairie dog colonies in rural areas cannot persist within the urban matrix or within fragments heavily denuded by elevated population densities of urban prairie dogs. Additional research on the direct and indirect effects of prairie dogs on ecosystem processes and animal and plant community structure within urban fragments will be necessary to further evaluate to what degree black-tailed prairie dogs function as keystone species in urban systems. If findings indicate that a considerable portion of their ecological role is retained, conservation of prairie dogs in urban areas will be an important first step towards maintaining functional grassland systems in urban areas, representing an important step forward for the conservation of biodiversity in these human-dominated landscapes.

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