DISSERTATION

THE PERSISTENCE OF PRAIRIE DOGS WITHIN URBAN HABITAT ISLANDS IN THE COLORADO FRONT RANGE

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY SETH MAGLE ENTITLED THE PERSISTENCE OF PRAIRIE DOGS WITHIN URBAN HABITAT ISLANDS IN THE COLORADO FRONT RANGE BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

THE PERSISTENCE OF PRAIRIE DOGS WITHIN URBAN HABITAT ISLANDS IN THE COLORADO FRONT RANGE

I investigated the ecology of black-tailed prairie dogs in fragmented urban habitat in the Denver, Colorado metropolitan area. My study area consisted of 387 habitat fragments, 54 of which were colonized by prairie dogs. These fragments were highly isolated and surrounded by roads and development, and my studies represent the first studies of prairie dogs in highly urban environments.

I evaluate the interactions between urban prairie dogs and vegetation and find that prairie dogs in urban areas tend to be present on sites with high grass coverage, though the grass layer is reduced in the immediate vicinity of the colonies. Prairie dogs interact with vegetation similarly in urban areas and natural habitat, providing evidence that the ecological role of prairie dogs as keystone species may be partly retained in human-dominated landscapes.

I provide the first study using mark-resight methodology to evaluate the local population density of prairie dogs, and find it more accurate than traditional methods of burrow counts or visual indices. I observed extremely high densities for prairie dogs in urban settings, probably because of a fence effect where animals are restricted to available habitat due to the difficulty of dispersal in an urban environment.

I compare connectivity metrics to determine which have the best predictive power for the occurrence of colonies in this area, and find that complex methods incorporating area of patches and cost-weighted distance surfaces perform best. In general, inclusion of biological information improves the ability of metrics to predict wildlife distribution. This study provides a rare opportunity to compare the performance of connectivity metrics using empirical data on wildlife distribution and will be of benefit to future spatial and landscape analyses.

Finally, I evaluate a series of landscape and local variables to determine which have the most importance to the distribution of prairie dogs across our study system. Fragment area and local variables such as litter coverage have the most explanatory power, but all tested metrics had importance to prairie dog occurrence. My results can be used to target potential habitat for prairie dog conservation and to inform future research on wildlife in urban areas.

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Seth B. Magle
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CHAPTER 1

INTERACTIONS BETWEEN BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*) AND VEGETATION IN HABITAT FRAGMENTED BY URBANIZATION

Abstract

Although prairie dogs may function as keystone species in natural systems, little is known about their impacts in urban settings. I measured vegetative cover, vegetative height and density, and slope on isolated black-tailed prairie dog (*Cynomys ludovicianus*) colonies along a gradient of urbanization in Denver, Colorado. I compared these measurements with data taken away from colonies, but within the colonized fragments, and with data taken on habitat fragments 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 may be more likely to be present on sites with high grass cover. In general, prairie dog-vegetation interactions I recorded are similar in fragmented landscapes to those observed in natural landscapes, providing evidence that some aspects of their keystone role are retained in urban systems.

Introduction

Prairie dogs (*Cynomys* spp.) create important interactions in prairie and steppe ecosystems that may enhance total diversity (Miller et al. 1994; 2000; Detling 1998; Bangert and Slobodchikoff 2000) and are often designated as keystone (Miller et al. 1994; 2000; Kotliar et al. 1999; Kotliar 2000) or highly interactive (Soulé et al. 2003; 2005) species, or ecosystem engineers (Bangert and Slobodchikoff 2000). For example, prairie dogs have been found to influence diversity of birds (Agnew et al. 1986; Manzano 1996), small mammals (Hansen and Gold 1977; Ceballos et al. 1999), reptiles and amphibians (Shipley and Reading 2006), predators (Clark et al. 1982), and arthropods (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 (Merriam 1902; Hansen and Gold 1977; O'Meilia et al. 1982), but prairie dog colonies also have been shown to increase total 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; Holland and Detling 1990; Detling 1998) 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 (Lomolino and Smith 2001; Johnson and Collinge 2004). 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 (Robinette et al. 1995; Farrar et al. 1998), 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.

To characterize vegetative structure in fragmented habitat, I measured vegetative cover, vegetative height and density, and slope on isolated black-tailed prairie dog (*Cynomys ludovicianus*) colonies along a gradient of urbanization in Denver, Colorado. I also measured these variables within colonized fragments but off the prairie dog colonies, and on uncolonized habitat fragments within the same landscape. I 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, I 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 keystone role are retained in fragmented habitat.

Methods

The study area (ca. 374 km^2) is bounded to the north by Interstate-70, near downtown Denver, Colorado, and extends south to the edge of development in Denver's southern suburbs. This area represents a gradient of increasing urbanization south to north. The study boundaries are described by a rectangle approximately 13 km wide by 29 km long (Figure 1). In the summer of 2002, I 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 hectare that was not regularly landscaped, and that was embedded in a dissimilar, less-hospitable, human-modified matrix. Highway embankments were omitted due to inaccessibility. Fragments were identified from aerial photographs for 2000 obtained from Landiscor, Inc. (Denver, Colorado) that had 0.7 m pixel resolution and were verified via field reconnaissance; this constituted a complete census. Of the 389 fragments, 54 were colonized by prairie dogs.

Vegetative characteristics were compared among three fragment categories: 1) colonized – data from colonies within fragments occupied by prairie dogs, 2) uncolonized – data taken away from colonies, but in fragments colonized by prairie dogs, and 3) unoccupied – data from 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. I 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, I repeated all analyses including only 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 I present the full analyses including all surveyed fragments to maximize the proportion of the study area represented in the data set.

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 meters apart. Transects were either 100 m or the length of the colony/fragment, whichever was shorter. At 10 m intervals along each transect, I measured slope, vegetative cover, and vegetative height and density as described below. 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 by 50 cm 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, I did record any dominant species on a fragment, which was operationally defined as a plant species covering ≥ 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 6 categories: slope of 0-2% (1), 3-4% (2), 5-8% (3), 9-15% (4), 16-25% (5), and > 25% (6), following Proctor (1998).

Overall, the mean number of habitat variable measurements on colonized and uncolonized portions of occupied fragments was 26.4 (range = 2-30, s.d. = 6.34) and 28.4

(range = 7-30, s.d. = 4.53), respectively. On each of the 54 uncolonized fragments, I recorded an average of 28.6 measurements (range = 17-30, s.d. = 3.10).

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. 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 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, Figure 2).

Discussion

As predicted, prairie dogs in my 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; Whicker and Detling 1988; Day and Detling 1994; Hoogland 1995; Detling 1998; Fahnestock and Detling 2002; Fahnestock et al. 2003). However, uncolonized portions of colonized fragments had substantially more graminoid cover than fragments not occupied by prairie dogs (Figure 2). This suggests that prairie dogs are more likely to be present on sites with greater graminoid cover, even though the prairie dogs reduce graminoids in their colonies. This may have important implications for conservation or translocation of prairie dogs in urban settings (Robinette et al. 1995; Farrar et al. 1998), perhaps focusing efforts on patches with high grass content.

Additionally, graminoid cover in patches occupied by prairie dogs was negatively related to time since isolation of the fragment as determined by county assessor building records ($R^2 = 0.173$, regression coefficient = -0.1895, $p = 0.009$; Magle unpublished data), a relationship not evident in unoccupied fragments ($R^2 = 0.021$; regression coefficient = -0.027; $p = 0.292$). This 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 review) compared to typical densities of 10-35 prairie dogs/ha in rural areas (Koford 1958, Reading et al. 1989, Powell et al. 1994).

The gentler slope on prairie dog colonies in comparison with unoccupied fragments (Figure 2) is consistent with previous findings that prairie dogs prefer flat areas (Reading 1993; Reading and Matchett 1997; Proctor 1998). Notably, such flat areas are often the quickest to convert to urban development (Moser 1991; Whitley et al. 1993; Landis 1994; Kaplan et al. 2003). Indeed, prairie dogs in urban Denver appear to exist in grassland remnants susceptible to development and difficult to conserve. Between 2002 and 2006, 9 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 (Lomolino and Smith 2001; Johnson and Collinge 2004), urban refugia may become increasingly important for prairie dog conservation.

Isolated urban habitat fragments are often susceptible to invasion by non-native species (Soulé et al. 1992; Alberts et al. 1993; Hunter 2002). The most common dominant species in my urban fragments was field bindweed (*Convulvulus 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. Prairie dogs are known to consume field bindweed (Lehmer et al. 2006). Given that prairie dogs often provide a competitive advantage to forb species (Coppock et al. 1983; Day and Detling 1994; Detling 1998), it is conceivable that prairie dogs in this study system are influencing the spread of this invasive exotic species, though further studies are needed to confirm this relationship. 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 (Uresk 1984; Clippinger 1989), 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. In contrast, a normal shortgrass prairie ecosystem typically is dominated by native plants such as blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*) and prickly pear cactus (*Opuntius* spp.) (Sims et al. 1978; Singh et al. 1983; Brown 1989).

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), I am 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 (Uresk 1985; Cid et al. 1991; Davidson et al. 1999). 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 ecosystem engineers (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 my urban habitat fragments, however, were similar to those described in natural systems, suggesting that prairie dogs may retain some of their keystone role in urban areas, at least in terms of their impacts on local habitat. Their keystone effects, however, could be limited if animals and plants typically facilitated by prairie dog colonies in rural areas can not 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.

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

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

Figure 1. Map of the study area, and associated habitat fragments along a gradient of urbanization.

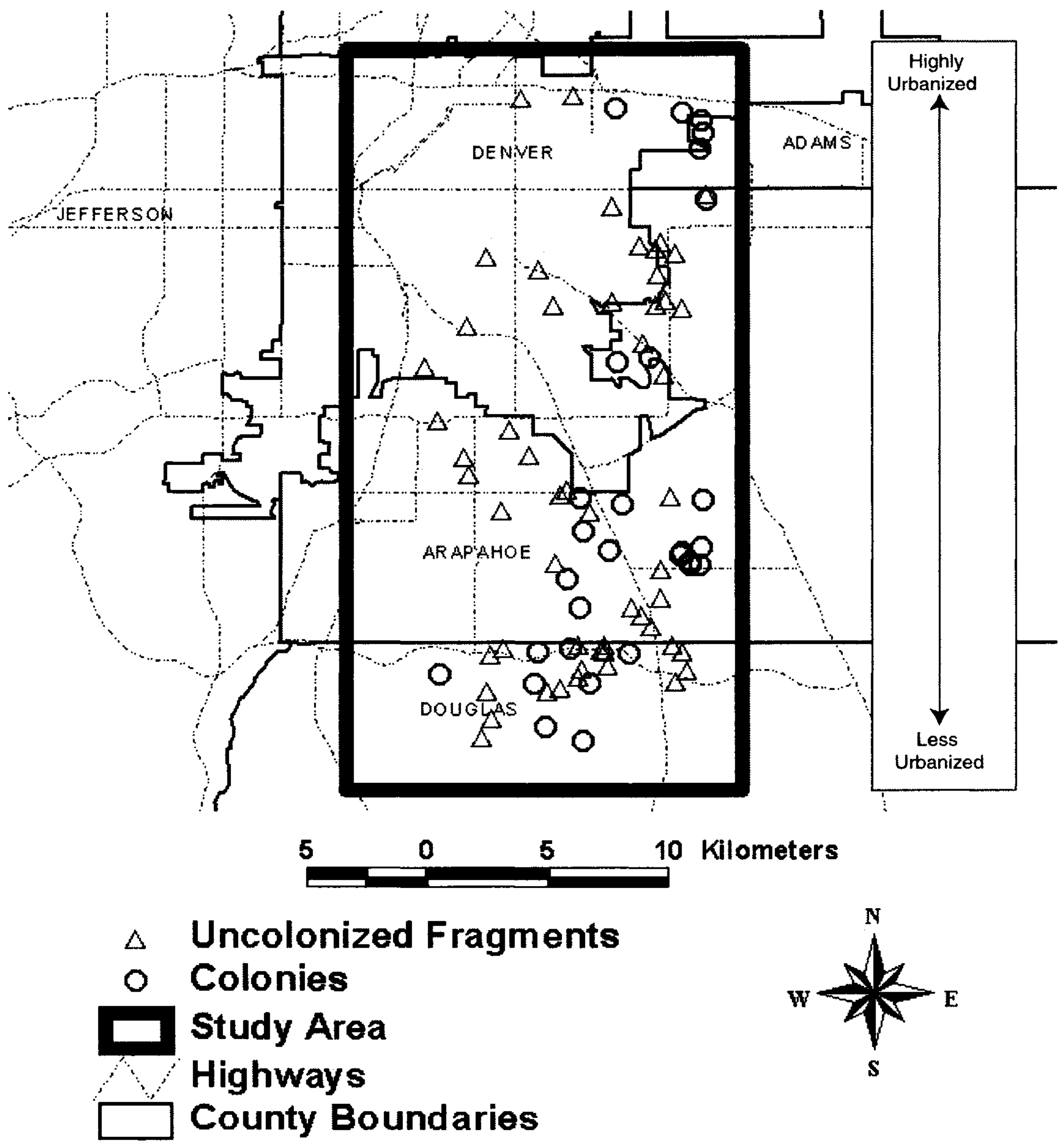


Figure 2. Comparisons of average value of (a) grass cover, (b) bare cover, (c) forb cover, (d) litter cover, (e) vegetation height and density, and (f) slope on prairie dog colonies, uncolonized portions of colonized fragments, and fragments unoccupied by prairie dogs. Errors bars represent standard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

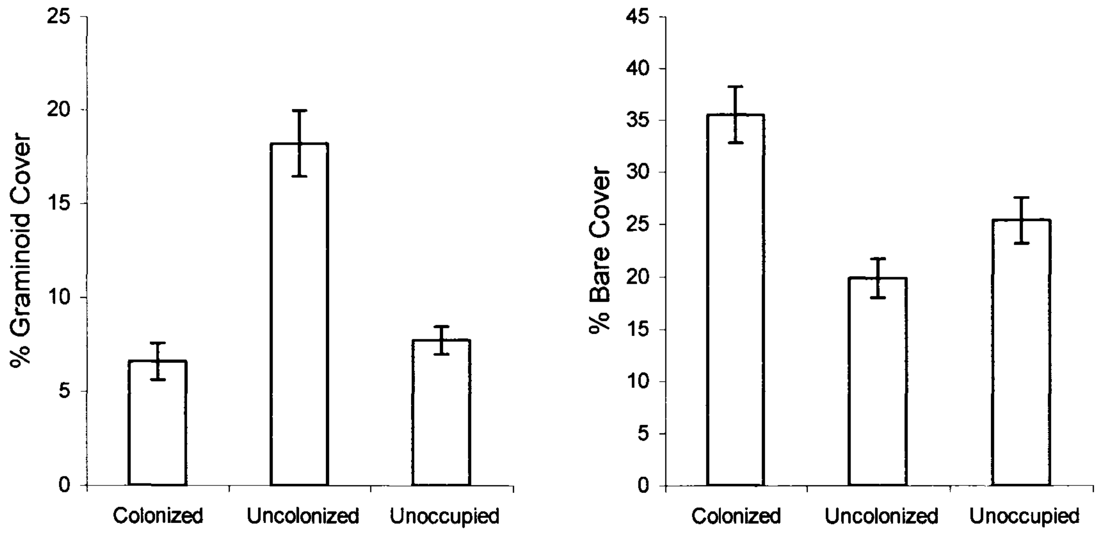


Figure 2a

Figure 2b

Figure 2 cont. 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.

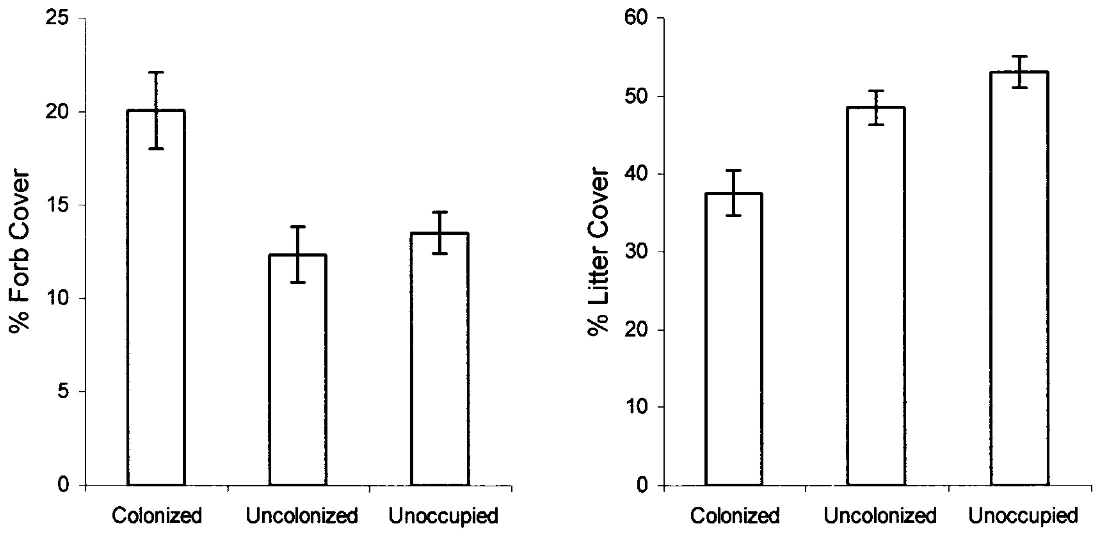
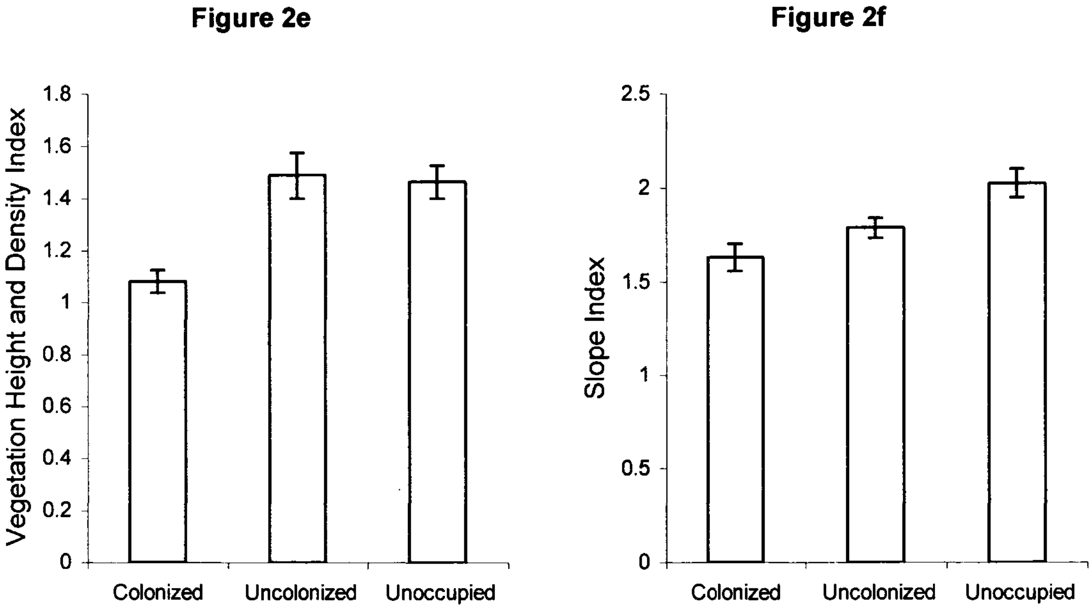


Figure 2c

Figure 2d

Figure 2 cont. 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.



CHAPTER 2

MARK-RESIGHT METHODOLOGY FOR ESTIMATING POPULATION DENSITIES FOR PRAIRIE DOGS

Abstract

Accurate assessments of local population size of the black-tailed prairie dog (*Cynomys ludovicianus*) are essential because of their overall decline and importance to prairie ecosystems. I describe the use of mark-resight methodology to estimate black-tailed prairie dog population size and density. Study colonies include isolated urban habitat fragments in Denver, Colorado, and unfragmented control colonies in the Pawnee National Grassland. I compare results from various mark-resight estimators to those derived from linear transformations of visual counts of active prairie dogs. My results suggest that mark-resight methods are feasible in both urban and rural systems, and reveal extremely high densities for isolated prairie dogs in urban sites. My methodology can be used to obtain reliable, unbiased estimates of local population size and density.

Introduction

Within the shortgrass prairie and steppe ecosystems, the black-tailed prairie dog (*Cynomys ludovicianus*) is an ecologically pivotal, and politically controversial, animal. Over the last century, government extermination programs, agricultural expansion, sylvatic plague, and commercial and residential development have emerged as threats to prairie dog populations (Miller et al. 1994, Antolin et al. 2002). Prairie dogs may be an essential part of a healthy prairie ecosystem (e.g. Miller et al. 2000, Forrest 2005) and are known to influence soil mixing and primary production of plants and increase plant and animal diversity and landscape heterogeneity (Holland and Detling 1990, Ceballos et al. 1999, Bangert and Slobodchikoff 2000). These interactions have led some researchers to characterize prairie dogs as keystone species (Miller et al. 1994, 2000, Forrest 2005, but see Stapp 1998, Vermeire et al. 2004).

The density of prairie dog colonies will likely affect at least some of these processes. Indeed, defining whether a species fulfills a keystone role involves estimates of whether its impacts are disproportionate to its abundance (Power et al. 1996). Traditional methods for estimating prairie dog densities have relied on burrow counts (Biggins et al. 1993, Johnson and Collinge 2004), which have been criticized as providing inaccurate or biased estimates (Powell et al. 1994, Biggins et al. 2006). Alternatively, researchers have suggested using visual counts of active prairie dogs, modified by a linear model relating prairie dogs visually counted to actual prairie dogs present (Powell et al. 1994, Severson and Plumb 1998). Both counts of burrows and visual counts of active prairie dogs, however, constitute indices of abundance, which are frequently unreliable for population estimation because of assumptions of constant probability of detection across space and time (Anderson 2003).

Debate is ongoing about the present and historical range of the prairie dog, and the current level of risk to the species (e.g. Vermeire et al. 2004, Forrest 2005, White et al. 2005). Given the potentially pivotal role of prairie dogs in ecological communities, and the ongoing disagreement about the magnitude of their decline, methods to accurately assess local populations are critically needed. My goal was to develop mark-resight methodology to obtain robust density estimates of prairie dog populations in urban, fragmented systems in the Denver, Colorado metropolitan area and in colonies in unfragmented habitat in the Pawnee National Grassland (PNG) in northeast Colorado. To my knowledge my study is the first to apply mark-resight methodology to prairie dog populations.

Study Area

Previous research (Magle 2003) identified a series of isolated habitat fragments bounded by human development and distributed along a gradient of urbanization in Denver, Colorado and its south suburbs. In 2002, this study area consisted of 387 habitat fragments, 54 of which contained prairie dog colonies. I selected 7 representative colonized fragments along this gradient where permission to trap prairie dogs could be obtained and that encompassed a range of fragment area (range 0.25–15.02 ha), age (time since isolation of a habitat fragment by development; range 24–44 yr), and isolation (edge-to edge distance to the nearest neighboring prairie dog colony; range 38–1203 m). I also selected 2 colonies on the PNG, approximately 40 km from the nearest urban area

(Greeley, Colorado) in the northeastern plains of Colorado to determine the feasibility of mark-resight methodology in large colonies in natural systems. These colonies were chosen based on accessibility, and differed in size (Colony 76: 28.54 ha, Colony 83: 94.71 ha).

Methods

Within urban colonies, I set traps in a grid pattern around the colony from May to October of 2004 and 2005, following methods outlined in Severson and Plumb (1998). On unfragmented colonies on the PNG, I set traps between July and September 2005 located near the closest burrows at 100 randomly selected points. I set traps from 0600 to 0700, left open throughout the day, and monitored continuously by on-site research assistants in urban areas, and in the early afternoon in unfragmented colonies. I individually marked all trapped animals with Nyanzol-D fur dye on their sides (Hoogland 1995:52-54), and released upon recovery from anesthesia. I marked animals with unique combinations of alpha-numeric characters, taking care to avoid symbols that could easily be mistaken for similar characters (Weiss et al. 1991). I marked adults as well as juveniles. I released all prairie dogs at the site of capture.

Before trapping began, I conducted visual counts of unmarked animals (minimum 3 counts per colony) and calculated naïve estimates of prairie dog populations using the linear regression model between visual counts and estimated population size described in Severson and Plumb (1998):

$$X = (Y - 3.04)/0.40 \qquad (1),$$

where *Y* is the maximum count of active prairie dogs from repeated sighting events (minimum 3) and *X* represents the population estimate. Based on simulations in Program NOREMARK (White 1996), I predicted that with 25 resightings per colony I needed to mark approximately 20% of the estimated population to maintain a total confidence interval length $\leq$10% of the population size. Thus, trapping ceased once approximately 20% of the estimated population had been marked. I recommend this procedure for sample size determination and power analysis prior to marking and resighting animals. Animal welfare protocols were approved by Colorado State University's Animal Care and Use Committee (04-085A-01).

In general, resighting methods followed recommendations of Severson and Plumb (1998). For small colonies ($\leq$10 ha), I conducted resightings adjacent to the colony from outside the responsive range of prairie dogs, which varied among colonies but could be determined in advance by approaching the colony and noting the response distance (Magle et al. 2005). For urban colony J15-10 and both PNG colonies (>10 ha), I placed some sampling locations inside the boundaries of the colony to ensure that I counted animals near the center. In these situations, observers remained motionless for at least 20 min upon arriving at each sampling location, after which animal behavior had resumed normal patterns. In instances where I could not sight an entire colony from one location, I conducted resightings from several different stations (maximum 3 on an urban colony [J15-10], and maximum 7 on an unfragmented colony [83]), with landmarks and radios used to guard against double counting. I eliminated double counting in the smaller colonies using one observer to perform the count and monitor all animals. I used binoculars to make counts, and counted only on days with no strong winds. In cases where I needed elevated stations to sight the entire colony, observers sat on vehicles (urban sites) or hilltops (unfragmented sites). I only counted prairie dogs within the colony area. I determined the number of observers and degree of elevation required by preliminary observation to assess difficulty of sighting animals throughout the colony.

I spaced resighting at least 30 min apart and I performed resightings within 3 weeks of marking to ensure dye mark visibility. During each resighting occasion, I noted any sighting of an individually marked animal and recorded the total number of unmarked individuals sighted. I recorded animals observed to be marked, but whose individual marking could not be identified. To improve precision, I conducted as many resighting events per colony as was logistically feasible. I resighted each urban colony at least 20 times, and I resighted unfragmented colonies 76 and 83, 11 and 10 times respectively. Resighting events occurred from late June – September and lasted at each colony on average 8.2 days, ranging from 2 days (Colony M15-14 in 2005) to 17 days (Colony L15-25 in 2004). In 2004, I marked and resighted animals on 4 urban colonies (L15-25, K15-36, M15-14 and M15-25). In 2005, I revisited 3 urban colonies sampled in 2004 (K15-36, M15-14 and M15-25) to perform new mark-resight surveys, and also marked and sighted animals on the 3 remaining urban colonies (J15-10, L15-4, L15-9) as well as the 2 colonies on the PNG (76 and 83). In total, I collected 12 sets of mark-resight data from 9 colonies (Table 1). Note that temporal variation between occasions does not bias estimators (White and Shenk 2001).

I used data from each resighting occasion to estimate total prairie dog population sizes (e.g. all sex-age classes) on each colony with the Beta-binomial mark-resight abundance estimator (BBE). The BBE (details in McClintock et al. 2006) is based in likelihood theory and tolerates both individual heterogeneity and temporal variation in sighting probabilities including observer heterogeneity. The model provides maximum likelihood estimates of abundance (N), mean sighting probability (μ) and individual heterogeneity (σ). BBE parameterizations allow μ and σ to remain constant (.) or vary (t) between primary sampling occasions. With 2 primary sampling occasions (groups), the 4 possible parameterizations are models $\{\mu(.)\ \sigma(.)\ N(t)\}$, $\{\mu(t)\ \sigma(.)\ N(t)\}$, $\{\mu(.)\ \sigma(t)\ N(t)\}$, and $\{\mu(t)\ \sigma(t)\ N(t)\}$. I used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to assign Akaike weights to the 4 models and computed model-averaged parameter and unconditional variance estimates (Burnham and Anderson 2002:448). All reported densities and population estimates from the BBE are model-averaged from all 4 models. Grouping for parameterization for the BBE took place as follows: I grouped colonies 76 and 83 because both were colonies located in the PNG. I grouped urban colonies L15-4 and L15-9 because of geographic proximity (distance apart 1.2 km) and comparable areas (0.65 ha and 0.92 ha, respectively; 34% difference). For colonies K15-36, M15-14, and M15-25, 2004 and 2005 I grouped data within each colony. Grouping is intended only to more efficiently estimate resighting probability parameters, and varied grouping criteria for these nuisance parameters do not bias inferences on population size. I did not group urban colony J15-10 (15.02 ha) because comparably sized colonies were not present in the data set (Table 1). I did not estimate colony L15-25 with the BBE because individual marks were not utilized on this colony due to poor legibility of dye-marks. Because I did not pool these data with other colonies, this does not impact other estimates.

The assumptions of the model are: 1) demographic and geographic closure; 2) no loss of marks; 3) no error in identifying marked and unmarked animals; 4) independently and identically distributed resighting probabilities for marked and unmarked animals; and 5) sampling without replacement within sampling occasions. The model requires marked animals to be individually identifiable. A common problem in mark-resight studies occurs when a marked individual is detected but its individual identity is unknown. If ignored, this violation can cause substantial overestimation of N due to the underestimation of sighting probabilities. I proposed and employed an extension of BBE where μ is inflated to accommodate any unidentified marks (Appendix A).

I transformed abundance estimates provided from the BBE $(\hat{N})$ to densities $(\hat{D} = \hat{N} / A)$. I constructed confidence intervals as logarithm transformed 95% normal with the lower bound constrained to be greater than the known number of marked individuals. I computed colony area by GPS mapping to the extent of the prairie dog clipped vegetation (Plumb et al. 2001), or to the extent of bare ground surrounding burrows when clipped vegetation boundaries were not apparent, or to the edge of human development when burrows were adjacent to roads or structures. For comparison, I also conducted population estimation analysis using data from each resighting occasion with Program NOREMARK (White 1996), using two commonly used mark-resight estimators: Bowden's estimator (Bowden and Kufeld 1995) and the joint hypergeometric maximum likelihood estimator (JHE) (Bartmann et al. 1987). I chose Bowden's estimator because it allows modeling of individual heterogeneity in sighting probabilities of prairie dogs, and preliminary analysis indicated substantial heterogeneity. Bowden's estimator has similar assumptions as the BBE, although Bowden's estimator does not allow pooling of data across time or groups for efficient parameter estimation. Further, although Bowden's estimator is unbiased, it is not a maximum likelihood estimator as is BBE. I also included the JHE because it allows for estimation without individually identified marks, such as for colony L15-25. JHE also is a maximum likelihood estimator, although it makes the assumption of no individual heterogeneity in sighting probabilities and this assumption should be tested. I also compared results from all estimators to naïve population estimates derived by transforming the maximum visual count of prairie dogs on each colony by equation 1 (Severson and Plumb 1998) (Table 2). I converted these naïve population estimates to naïve density estimates by dividing the result by colony area.

Results

Densities measured on urban colonies ranged from approximately 65–194 prairie dogs/ha across all estimators (Table 2). Density estimates for urban prairie dogs were similar across estimators; mean urban prairie dog density was 114.2 (SE = 14.2), 113.3 (SE = 14.2), and 116.8 (s.e. = 13.2) prairie dogs/ha based on the BBE, Bowden's estimator, and the JHE, respectively. Density estimates of prairie dogs on the 2 unfragmented colonies ranged from approximately 22.5 – 26.5 prairie dogs/ha. I estimated mean density on the 2 unfragmented colonies as 26.0 and 23.5 (BBE), 26.4 and 22.6 (Bowden's) and 26.5 and 22.9 (JHE) for Colonies 76 and 83, respectively.

Average % confidence interval length relative to density was 32.4% (SE = 2.45) for the BBE and 36.7% (SE = 2.66) for Bowden's estimator. These values provide an indication of the relative precision of each method for prairie dog population estimation.

The JHE yielded an average confidence interval length of only 18.9% (SE = 1.39) relative to density, but these estimates do not take into account individual heterogeneity in sighting probabilities for prairie dogs. Point estimates for the σ term, which represents individual heterogeneity, ranged from 0.09 – 0.18 on colonies, with a mean value of 0.13, which represents a moderate to high level of heterogeneity (McClintock et al. 2006)

Naïve density estimates, derived by transforming maximum visual counts of prairie dogs using Equation 1 (Severson and Plumb 1998), were within the confidence intervals provided by my robust estimators only for 4 of 11 colonies (36%) when using both the BBE and Bowden's estimator; 3 of these 4 colonies (L15-9; M15-25 in 2004; 83) were the same between BBE and Bowden's estimator (Table 2). This indicates fairly low concurrence between traditional methods and mark-resight methodology. Compared to the BBE, the naive estimator underestimated density for 3 colonies by an average difference of 31% (range 18-49%; s.e. = 9%) and overestimated density for 4 colonies by an average difference of 35% (range 32-42%; s.e. = 2%), with 4 colonies estimated within the confidence intervals provided by the mark-resight estimator (average difference 12%, range -17% – +20%, s.e. = 3%). Compared to Bowden's estimator, the naïve estimates were low for 2 colonies (average difference 38%; range 26-50%, s.e. = 12%) and high for 5 colonies (average difference 48%; range 22-77%; s.e. = 9%), with 4 colonies within the provided intervals (average difference 10%, range -3% – -18%, s.e. = 4%). Only 2 of 12 colonies (16.7%) had naïve density estimates within the confidence intervals provided by the JHE (4% and 6% underestimates), with equal numbers of colonies (5 and 5) demonstrating low (average difference 30%; range 17-51%, s.e. = 6%) and high (average difference 45%; range 20-72%, s.e. = 9%) estimates; however, these confidence intervals are inappropriately narrow due to the assumption of no individual heterogeneity.

In 2004, the proportion of sighted marked animals that could be identified to individual was only 65% on the first colony sampled, but improved to approximately 90% on colonies sampled later in the summer due to research personnel gaining experience in creating legible marks. Average proportion of marked animals identified to individual was 76% (range 65–90%) and 91% (range 75–99%) in 2004 and 2005, respectively. This change in identification rates does not bias my estimates for the BBE or Bowden's estimators because they do not assume detection probability to be constant. Incorporating unidentified individual marks into my BBE estimates decreased my population estimates by an average of 12% (s.e. = 2.5%).

Discussion

I present a mark-resight technique for prairie dogs that avoids the uncertainties associated with indices such as simple burrow or prairie dog counts (e.g. Severson and Plumb 1998, Johnson and Collinge 2004), but that is less labor-intensive than a full mark-recapture study. My method was successful and generated robust local density estimates and respective confidence intervals. When comparing the results derived from my estimators to those obtained through simple transformations of visual counts of prairie dogs (Severson and Plumb 1998), the naïve estimates fell outside the confidence intervals of my robust estimates in a majority of instances, and were both over and underestimates in various cases, suggesting that robust methods (e.g. mark-resight or mark-recapture) may be necessary for reliable prairie dog population estimation. It is likely that the burrowing habit of prairie dogs, where animals spend much time underground and out of sight, led to the moderate to high level of heterogeneity I observed in sighting probabilities, which in turn, might create misleading estimates from estimators based on counts of animals or burrows that do not incorporate this heterogeneity. It should be noted, however, that Severson and Plumb (1998) indicate that their model, calibrated to one specific study colony, may perform poorly when applied to dissimilar areas, which my study may represent.

The 3 mark-resight estimators I used in this study – the BBE, Bowden's estimator, and the JHE – each harbor a suite of assumptions that are important to consider and discuss (White and Shenk 2001, McClintock et al. 2006). My study design was determined *a priori* to attempt to minimize any violations of model assumptions. Common assumptions of mark-resight models include:

1) *Demographic and geographic closure*—Resighting events in this study began in late June in an attempt to avoid juvenile emergence and dispersal events (Hoogland 1995:249), and occurred over relatively brief time periods (2-17 d). Violation of the closure assumption, if present, is not as serious for the BBE or Bowden's estimators because they allow animals off the study area to have a sighting probability of 0 for a given occasion.

2) *No loss of marks.* The dye I used (Nyanzol-D) is permanent and is lost only when animals molt (spring and fall) (Hoogland 1995:56). Prairie dogs began to molt in mid-August, but I completed most observations by that time.

3) *Independently and identically distributed resighting probabilities for marked and unmarked animals.* Above-ground prairie dogs were highly visible and the

black fur dye did not render marked animals especially visible compared to unmarked animals.

4) *Sampling without replacement within sampling occasions.* I used landmarks and radios to avoid double-counting unmarked and marked but unidentified individuals.

5) *No errors in identifying marked and unmarked animals.* Technicians generally had little difficulty distinguishing marked and unmarked animals.

6) *Individual marks are unidentified randomly.* When I could not identify marks, it was typically because marked animals retreated into a burrow, which I believe is a primarily random process.

The 3 mark-resight estimators produced similar point estimates of population size, most likely indicating that none of the estimators had large bias, consistent with previous findings (McClintock et al. 2006). Despite similar density estimates, I endorse use of the BBE because it has the advantages that mark-resight data can be pooled across time or groups for more efficient parameter estimation, and model estimation and parameterization can be performed and compared in an information-theoretic framework (Burnham and Anderson 2002:60-64; McClintock et al. 2006). The BBE also provides a maximum likelihood estimate for individual heterogeneity, which the other models cannot. Since the code is readily available, the BBE model is not appreciably harder to use and interpret than the Bowden's, and both have the same data collection requirements (individually identifiable marks). The Bowden's estimator is also a good choice and is widely available through Program NOREMARK. While the JHE has the narrowest confidence intervals in this study, and has the additional advantage of not requiring individual marks on animals, the individual heterogeneity present in the data represents a serious failure to meet the assumptions of the JHE model. Though no consistent rules exist regarding an unacceptable level of heterogeneity, I recommend a conservative approach and feel a moderate level is a cause for concern. We, therefore, do not recommend use of the JHE for prairie dog population estimation unless researchers can demonstrate that specific colonies have negligible individual heterogeneity.

Although the confidence intervals achieved in this study were wider than the initial goal of 10% of the mean due to lower mean sighting probabilities and higher heterogeneity than expected, I feel the estimates are precise enough to be of value to managers and conservationists who need to estimate prairie dog populations. Indeed, many prior studies estimating animal densities report no confidence intervals at all. The larger colonies were more difficult to resight because with limited field personnel it was at times challenging to sight animals in the center of the colony without alarming peripheral animals. Overall, mark-resight methodology may be more efficient with smaller prairie dog colonies, particularly if personnel are limited, though these methods are still substantially less time-consuming than mark-recapture techniques. Studies intended to estimate population size for very large prairie dog colonies should anticipate using numerous field technicians at numerous counting stations, with field landmarks (e.g. painted wooden stakes) used to avoid double-counting of prairie dogs. Of course, in situations where estimates of distribution and population size are necessary across extremely large spatial scales (e.g. regionally or the range of a species), mark-resight methodology likely will be infeasible or cost-prohibitive, and I will need to rely on other techniques such as aerial surveys of prairie dog colonies or burrows (White et al. 2005).

Estimates of prairie dog density for urban colonies in this study area ranged from ~65–187 (Mean 114.2) prairie dogs/ha based on the BBE. These densities are dramatically higher than the usual estimates for prairie dog density in natural systems (10–35 prairie dogs/ha: Reading et al. 1989, Powell et al. 1994, Derner et al. 2006), and also higher than density estimates derived for sites in urban Boulder, Colorado (32–120 prairie dogs/ha: Johnson and Collinge 2004). In contrast, prairie dog densities in my two unfragmented colonies were estimated at 23.5–26.0 prairie dogs/ha, which is within the range of typical estimates. Increased density in urban areas, if present, is probably not related to higher quality habitat, but may result from either a refuge effect, because predation may be reduced in urban settings, or a fence effect (Krebs et al. 1969), because the prairie dogs were restricted into available habitat by urban development (Johnson and Collinge 2004).

Management Inplications

My comparisons of local density estimates derived from simple visual counts of prairie dogs to robust estimates based on mark-resight methodology indicate that results can be quite disparate. Although previous research (Severson and Plumb 1998, Menkens et al. 1990) demonstrated a positive correlation between mark-recapture methodology and visual sighting of prairie dogs, robust methods such as mark-recapture yield more precise and unbiased data (Biggins et al. 2006). I demonstrate the use of mark-resight methodology as a reliable means of prairie dog population estimation at a local scale, which can help guide prairie dog conservation and management efforts that rely on rigorous measurements of population and density.

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Table 1. Prairie dog colonies in the Colorado Front Range where mark-resight methodology was conducted May 2004-Oct 2005. .

Colony[a]	Year	Colony area (ha)	n[b]	t[c]
J15-10	2005	15.02	117	47
K15-36	2004	0.25	13	34
K15-36	2005	0.25	9	46
L15-4	2005	0.65	28	48
L15-9	2005	0.92	28	52
L15-25	2004	1.86	45	20
M15-14	2004	1.16	21	49
M15-14	2005	1.16	19	25
M15-25	2004	0.59	22	64
M15-25	2005	0.59	15	46
76 (PNG)	2005	28.54	80	11
83 (PNG)	2005	94.71	45	10

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[a] PNG = Pawnee National Grassland control colony.
[b] Number of animals marked on each colony.
[c] Number of resighting events conducted.

Table 2. Prairie dog population density estimation (# prairie dogs/ha) for colonies in the Colorado Front Range based on the Beta Binomial Estimator (BBE), Bowden's Estimator, and the Joint Hypergeometric Estimator (JHE).

Colony[a]	Year	Naïve density[b]	BBE density[c]	BBE CI[c,d]	BBE % CI length[c,e]	Bowden's density	Bowden's CI[d]	Bowden's % CI length[e]	JHE density	JHE CI[d]	JHE % CI length[e]
J15-10	2005	33.3	67.8	57.8-79.7	32.4	66.5	57.2-77.6	30.8	67.4	63.3-71.8	12.7
K15-36	2004	199.6	135.3	122.9-149.7	19.8	135.2	120.9-152.5	23.4	140.9	131.1-152.0	14.9
K15-36	2005	169.6	112.8	98.5-130.4	28.2	111.4	94.1-133.8	35.6	111.4	101.1-123.3	20.0
L15-4	2005	111.4	136.1	112.8-167.1	39.9	131.5	*104.2-170.9	50.8	134.7	124.2-146.5	16.6
L15-9	2005	154.8	187.3	*152.4-232.3	42.7	188.6	*148.2-242.8	50.2	194.3	176.9-213.8	19.0
L15-25	2004	84.6	N/A	N/A	N/A	N/A	N/A	N/A	128.0	114.2-145.7	24.6
M15-14	2004	112.0	65.5	58.3-73.9	23.8	63.3	55.6-72.5	26.9	64.9	61.7-68.4	10.4
M15-14	2005	99.1	67.5	58.5-78.4	29.5	70.6	60.8-82.6	30.9	71.4	64.8-78.9	19.8
M15-25	2004	143.9	152.6	*128.5-183.0	35.7	151.5	*125.8-184.9	39.0	152.5	*139.9-166.8	17.6
M15-25	2005	122.7	102.7	*85.2-125.5	39.2	100.9	84.8-121.5	36.4	102.4	92.3-114.1	21.2
76 (PNG)	2005	19.5	26.0	21.8-31.1	36.0	26.4	22.1-31.5	35.7	26.5	23.7-29.7	22.4
83 (PNG)	2005	22.0	23.5	*18.7-29.5	46.3	22.6	*18.2-28.1	43.9	22.9	*20.0-26.2	27.2

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[a] PNG indicates a Pawnee National Grassland control colony.

[b] Derived from maximum counts of unmarked prairie dogs, modified by the equation of Severson and Plumb (1998). Asterisks indicate that the naïve estimate was within the confidence interval provided by the mark-resight estimator.

[c] Density estimates and CI values from BBE are model averaged based on AIC weights of available models.

[d] CI refers to a 95% confidence interval.

[e] The percentage of the mean density value represented by the confidence interval.

Appendix A.

I propose an extension of the beta-binomial estimator (BBE) to incorporate unidentified marks, where μ is inflated to accommodate any unidentified marks. This inflated mean sighting probability is:

$$\mu' = \left(\frac{\alpha}{\alpha+\beta}\right) + \frac{\varepsilon}{kn},$$

where α and β are the beta distribution parameters, and ε = the total number of unidentified marks across the k distinct resighting occasions. The beta distribution parameters are adjusted accordingly, such that

$$\alpha' = \frac{(\mu')^2(1-\mu')}{\sigma^2} - \mu',$$

and

$$\beta' = \frac{\sigma^2(\mu'-1) + \mu'(\mu'-1)^2}{\sigma^2}.$$

The adjusted parameters are then substituted into the BBE likelihood as follows:

$$L(N,\alpha,\beta \mid T_u,k,x_i,n) = \prod_{i=1}^{n} \binom{k}{x_i} \frac{\mathrm{B}(\alpha+x_i,\beta+k-x_i)}{\mathrm{B}(\alpha,\beta)}$$

$$\times \frac{1}{\sqrt{2\pi\cdot\mathrm{Var}(T_u)}} \exp\left(\frac{-(T_u-\mathrm{E}(T_u))^2}{2\mathrm{Var}(T_u)}\right),$$

where

$$\mathrm{E}(T_u) = (N-n)\,k\frac{\alpha'}{\alpha'+\beta'},$$

and

$$\mathrm{Var}(T_u) = (N-n)\,k\frac{\alpha'}{\alpha'+\beta'}\left(1-\frac{\alpha'}{\alpha'+\beta'}\right)\left(\frac{k+\alpha'+\beta'}{1+\alpha'+\beta'}\right).$$

The critical assumption of this extension is that individual marks are unidentified according to some random process. In other words, the probability of a mark not being individually identifiable must be the same for all marked individuals. In limited simulations with lower levels of individual heterogeneity ($\sigma < 0.15$), the modified estimator remained unbiased with nominal 95% confidence interval coverage of N as long as 75% of marked individuals were identified. Although the model remained unbiased with 75% identified marks with high individual heterogeneity ($\sigma = 0.25$), confidence interval coverage in these simulations fell as low as 88%. On average, in order to achieve nominal coverage with high levels of heterogeneity, at least 90% of marks need to be identified. The extension is easily incorporated into the robust sampling design model of McClintock et al. (2006) for t primary sampling occasions by substituting the adjusted beta distribution parameter vectors $\alpha' = \{\alpha'_1, \alpha'_2, \ldots, \alpha'_t\}$ and $\beta' = \{\beta'_1, \beta'_2, \ldots, \beta'_t\}$ into the likelihood.

CHAPTER 3

COMPARING ISOLATION METRICS PREDICTING THE DISTRIBUTION OF A HIGHLY INTERACTIVE SPECIES ALONG AN URBAN GRADIENT

Abstract

Many wildlife species persist in fragmented habitat where movement between patches is essential for long term demographic and genetic stability. In the absence of direct observation of movement, isolation metrics are a useful method of characterizing potential patch-level connectivity. However, multiple metrics exist and no general consensus has been reached about what level of metric complexity is desirable. I compare 12 isolation metrics of varying degrees of complexity to determine which best predict the distribution of prairie dog colonies for my study system of 384 isolated habitat patches in Denver, Colorado. I found that a nearest neighbor metric including area-weighting of patches and a cost parameterized surface had the best predictive power, where I assumed roads were fairly impermeable to movement, and low-lying drainages provide dispersal corridors. Thus, both patch area and the composition of the surrounding matrix effected the presence of prairie dog colonies. My results provide

guidance for wildlife distribution modeling in fragmented landscapes and can help identify target habitat for conservation and management of prairie dogs in urban habitat.

Introduction

Habitat fragmentation is a worldwide phenomenon that threatens many species (Wilcox and Murphy 1985, Wilcove et al. 1998). When habitat becomes discontinuous, movement of organisms among resource patches is essential to maintain demographic and genetic stability of populations (Hanski 1994, 1998, Hanski and Gaggiotti 2004), and the degree to which a patch is isolated is frequently a key determinant of species abundance and distribution (Soulé et al. 1988, Bolger et al. 1991, Taylor et al. 1993, Crooks 2002, Crooks et al. 2004, Crooks and Sanjayan 2006). Numerous metrics exist to quantify patch isolation or its inverse, connectivity, ranging from simple (e.g., distance to the nearest neighbor) to complex (e.g., multivariate models involving cost surfaces and/or graph theory) (Moilanen and Nieminen 2002, Calabrese and Fagan 2004). These metrics can measure "structural" connectivity—the simple physical configuration of habitat patches; "potential" connectivity, by incorporating basic or indirect information about animal movement; or "functional" connectivity, actual movement of organisms among patches (Calabrese and Fagan 2004, Crooks and Sanjayan 2006, Fagan and Calabrese 2006). Isolation metrics can stand as a proxy for biological events that are difficult to measure, such as dispersal and extinction, and can also be used in multivariate models to control for spatial correlation in data (M. Antolin, unpublished data). Ongoing debate centers on which isolation metrics are preferred, with no single metric having gained widespread acceptance (Tischendorf and Fahrig 2000, 2001, Moilanen and Hanski 2001, Murphy and Lovett-Doust 2004), but when used properly isolation metrics have been shown to correlate with actual biological events such as immigration (Tischendorf et al. 2003). Ultimately, connectivity depends on the structure of the individual landscape and the movement behavior of the study organism(s) (Tischendorf and Fahrig 2000). Because no single measure applies to all situations, testing multiple metrics is recommended (Goodwin 2003).

Biologists frequently use straightforward metrics to predict abundance of species, including distance to nearest neighbor (e.g. Crooks et al. 2001, Lomolino and Smith 2001, Crooks 2002, Lomolino et al. 2003, Collinge et al. 2005) and amount or proportion of the landscape within various buffer distances consisting of other wildlife habitat (Lomolino and Smith 2001, 2003, Lomolino et al. 2003, Johnson and Collinge 2004). However, some researchers criticize these simple metrics for being poor representations of connectivity compared to more complex metrics that include factors such as average distance to all adjacent neighbors, area of habitat patches, and cost pathways that model the effects of different landscape components on animal movement (Moilanen and Nieminen 2002, Calabrese and Fagan 2004). Very few studies have used empirical data on wildlife distribution to compare the performance of connectivity metrics (Tischendorf and Fahrig 2000, but see Moilanen and Nieminen 2002).

Grassland ecosystems are experiencing high levels of fragmentation and urbanization (Samson and Knopf 1994, 1996, Bock et al. 1999, Johnson and Collinge 2004), and an understanding of connectivity and dispersal patterns for species in these system is essential. In the Colorado Front Range, the black-tailed prairie dog (*Cynomys ludovicianus*) is an ecologically pivotal and politically controversial animal that may function as a keystone (Miller et al. 1994, 2000, Kotliar et al. 1999, Kotliar 2000, Forrest 2005, but see Stapp 1998, Vermeire et al. 2004) or a highly interactive (Soulé et al. 2003, 2005) species, with many other organisms associated with their colonies. Over the last century, government extermination programs, sylvatic plague, agricultural expansion, and commercial and residential development have reduced prairie dog populations drastically, to less than 5% of their historic range (Miller et al. 1990, 1994, Kotliar et al. 1999). Many remaining black-tailed prairie dog colonies exist within small isolated patches in urban and suburban areas (Lomolino and Smith 2001, 2003, Lomolino et al. 2003, Magle 2003, Johnson and Collinge 2004). Increasing our understanding of wildlife ecology in urban areas is critical because urban habitat patches often perform important roles (Kellert 1980), such as maintaining rare and endangered species (Bolger et al. 1997, Crooks et al. 2001, 2004, Crooks 2002), providing stepping stones for dispersal (Soulé 1991, Estrada 1993, Stouffer and Bierregaard 1995, Turner and Corlett 1996, Fischer and Lindenmayer 2002), opportunities for education (Savard et al. 2000, DeStefano and DeGraff 2003), and enhancing property values and aesthetics (Correll et al. 1978, Smith 1993, Garrod and Willis 1995, Bolitzer and Netusil 2000). Ecological relationships observed in natural areas do not always apply in urban ecosystems (Miller and Hobbs 2002, Garden et al. 2006), so research in these areas is essential.

In this study, I compare several patch-based, structural and potential isolation metrics used to predict the distribution of prairie dogs in isolated habitat patches in the Denver, Colorado metropolitan area. At present, rates of prairie dog dispersal and factors that influence their distribution in highly fragmented urban habitat are poorly understood (Magle 2003, Johnson and Collinge 2004, Magle and Crooks in submission). Complexes of prairie dog colonies can function as metapopulations (Roach et al. 2001) and their patch-level isolation may influence their long-term persistence. Identifying the best performing isolation metrics for this system is important to future spatial analysis for this species; can provide insight into which urban landscape elements influence wildlife persistence and dispersal; and will assist efforts to conserve these populations and associated biotic communities.

Methods

Identifying fragments

In the summer of 2002 I used aerial photography maps to identify a section of the Denver Metropolitan Area (13 x 29 km, ~374 km^2) spanning from downtown Denver south through Highlands Ranch (a southern suburb of Denver), isolating a gradient of decreasing urbanization north to south (Figure 1). At the time of surveying, the southern boundary represented the outer edge of urban development. I performed a census that identified 387 habitat fragments within this study area, 54 of which were colonized by prairie dogs. A habitat fragment was defined as any plot of undeveloped land with an area of at least 0.25 ha that was not regularly landscaped or manicured by humans, and that was embedded in a dissimilar, less-hospitable, human-modified matrix. Highway embankments were omitted due to inaccessibility. Average fragment area was 7.86 ha (range: 0.25-139.1 ha, SE = 0.87). When spatial extent of an ecological study is defined by arbitrary human boundaries, patch-based metrics can be influenced by boundary choice, particularly if patches are bisected by the boundaries (Turner et al. 1989, O'Neill et al. 1996). I defined all four study area boundaries by highways or roads with heavy traffic density such that no habitat patch spanned a study boundary. I expect dispersal of prairie dogs across these boundaries to be difficult, and thus the boundaries have biological relevance. Given also the high number of fragments and the relatively large study area, I believe boundary definitions did not cause unusual behavior in my metrics.

All fragments were verified via field reconnaissance, and characterized as colonized or not colonized by prairie dogs. Because prairie dogs are diurnal, colonies are conspicuous (Hoogland 1995), terrain was reasonably flat, and surveys were thorough, I am confident that I accurately assessed colonization status of all fragments. Colonized fragments in this area ($\bar{X} = 21.8$ ha, n = 54, SE = 4.5) were significantly larger (T = 3.55, $p < 0.001$) than uncolonized fragments ($\bar{X} = 5.6$ ha, n = 333, SE = 0.65). All fragments and prairie dog colonies were digitized using digital aerial photographs (Landiscor, Inc.) and ArcGIS software (ESRI, Inc.) at 2 m resolution. All data layers were analyzed in a projected coordinate system (UTM Zone 13 N, NAD 1927).

Spatial Distribution

To determine which connectivity metrics might be relevant for this system, I first evaluated whether the fragments and prairie dog colonies were clustered spatially, using the Average Nearest Neighbor tool in the spatial statistics toolbox in ArcGIS 9.1 (ESRI, Inc). This tool compares the distance (centroid-to-centroid) between nearest neighbors to the average distance between neighbors in a hypothetical random distribution to determine if features are located closer together than expected by chance. I found that the colonies were clustered in space ($Z = -3.81, p < 0.01$), as were both colonized and uncolonized habitat fragments ($Z = -6.1, p < 0.01$). Because my dependent variable was colonization status of fragments (1/0), I decided not to test connectivity metrics that described distance to other colonies (as opposed to other fragments). Because the colonies are clustered on the landscape, distance to nearest colony would be a statistically strong predictor of colonization status for a fragment, but this is simply a description of their spatial distribution rather than a landscape-level metric of connectivity that could be applied to other landscapes and organisms. I also rejected centroid-to-centroid distance connectivity metrics in favor of those based on edge-to-edge distances because I found that the larger fragments were more likely to contain prairie dogs ($T = -3.59, p < 0.001$), and large fragments had larger centroid-to-edge distances, inflating centroid-to-centroid distances for these fragments.

Connectivity Metrics

I employed several criteria in selecting my connectivity metrics. I chose measures that would span a range of complexity, with roughly equal representation of simple and complex metrics. I included commonly used metrics when possible to increase the comparability of my results to past and ongoing research. I also decided to test only a small number of models because I used model selection protocols to delineate the best performing models, and these methods function best when the number of models is small compared to the amount of data (Burnham and Anderson 2002).

Twelve connectivity metrics were calculated for each fragment (Table 1). The first was a nearest neighbor metric that calculated edge-to-edge Euclidean distance to the closest fragment (designated Euclidean Nearest Neighbor, or ENN). This is a purely structural connectivity metric (Fagan and Calabrese 2006). The next three metrics represented isolation of fragments by creating buffers around each fragment (0.2 km, 1 km and 2 km, designated Buffer or B0.2, B1.0, and B2.0, respectively), following distance categories from Johnson and Collinge (2004). The tested metric for each is the percentage of each buffer comprised of habitat fragments. Because these metrics are fractions of recorded prairie dog dispersal distances, they are potential connectivity metrics (Fagan and Calabrese 2006). These initial four metrics represent simple connectivity metrics that other researchers frequently use (e.g. Lomolino and Smith 2001, 2003, Johnson and Collinge 2004).

I then tested more complex connectivity metrics. I used an "Adjacent Neighbors Distance Statistics Tool" (D. Theobald) to calculate a structural metric consisting of the average Euclidean distance to all first order (adjacent) neighbors for each patch based on edge-to-edge distance (Euclidean Adjacent Neighbors, or EAN). This tool calculates omni-directional patch-to-patch distance using Voronoi polygons, which represent the distance from a target patch to its neighbors in all directions by making equidistant polygons between them (Krebs 1989, Bender et al. 2003). For this analysis I rasterized my vector-based features with 10 m resolution.

I also calculated isolation metrics that were weighted by the area of a patch, including the area-weighted minimum nearest neighbor distance (Area-Weighted Euclidean Nearest Neighbor, or AEN), and the area-weighted average adjacent neighbors distance, calculated using Voronoi polygons as above (Area-Weighted Adjacent Neighbors, or AAN). These area-weighted metrics used a modification of the proximity index (Gustafson and Parker 1992, Moilanen and Nieminen 2002, Bender et al. 2003) where I summed the area of each patch (in hectares) in a pair of neighbors and divided this sum by the edge-to-edge Euclidean distance between the patches. These are potential connectivity metrics (Calabrese and Fagan 2006) because they implicitly model the interaction of organisms and habitat. Based on findings that species frequently respond in a non-linear fashion to changes in habitat area or isolation (Kerkhoff et al. 2000, Brown et al. 2002), I raised the product of the area terms to the 0.7 power and raised the edge-to-edge distance between the patches to the 1.7 power before performing calculations (Theobald 2006), thus:

$$C = (A_i A_j)^{0.7} / d_{ij}^{1.7} \qquad (1.0)$$

This equation relates connectance (C) of two neighboring patches (*i* and *j*) to the area of each patch in a neighboring pair (*Aj* and *Ai*) and the Euclidean distance between them (d_{ij}). The values 0.7 and 1.7 were used based on their superior performance in simulated studies where they exhibited stable behavior over a wider range of areas and distance than traditionally used scaling metrics such as 0.5 and 1.5 (B. Milne, personal communication).

Euclidean distance may not be the ideal way to measure the isolation of fragments, due to its assumption that the matrix between patches is homogenous (Knaapen et al. 1992, Murphy and Lovett-Doust 2004). To differentiate the landscape elements that may impact movement of animals (e.g. Roach et al. 2001), I also created a cost surface raster for the study area, which was used to calculate 4 cost-weighted metrics. A cost surface is a raster layer where each cell is parameterized with a cost value representing how difficult it may be for an organism to move across. Thus, the "cost" for an organism to move from one patch to another is the least cost of possible pathways, represented as the sum of the costs of each cell that must be traversed. Cost surfaces are typically constructed based on known movement or habitat selection data (e.g., Petit and Burel 1998, Ferreras 2001, Adriaensen et al. 2003).

My cost surface raster was created beginning with land cover data from the Colorado Vegetation Model (CVM) dataset, which has 30 m resolution (Table 2, Theobald et al. 2004). I grouped values from this raster as follows: residential, commercial, industrial, and bare rock/sand/clay layers were grouped as "urban"; pasture/hay, row crops, small grains, fallow land, and urban/recreational grasses were combined as "agricultural"; and foothills, woodland, shrubs, and prairie were grouped as "habitat". This layer was resampled to 10 m resolution before analysis to match the resolution of the fragment layer. Then, I added the following features over the underlying land cover value: road and highway data from the Colorado Department of Transportation (1:100000 scale) starting with local roads, then medium volume roads (collectors and arterials), and ending with highways. Next, I overlaid hydrologic features (streams and water bodies) from the National Hydrography Dataset (1:24000 scale) obtained from the United States Geological Survey. I finished by buffering these hydrologic features by one cell (30 m) and designating this buffer "stream banks". This step differentiated land adjacent to water due to the finding of Roach et al. (2001) that prairie dogs frequently disperse along drainages. Most water features in this study area represented agricultural drainages that were dry most of the year, and were thus comparable to previous findings (Roach et al. 2001). Features added later overrode the previous value for a given cell.

Because information regarding the permeability of various terrain for prairie dogs and their habitat selection in urban environments was highly limited (but see Roach et al. 2001), I estimated cost values based on my knowledge of movement behavior. I assigned cost values for landscape features using Analytic Hierarchy Process (AHP: Saaty 1980, 1990, 1994). For this process, pairwise comparisons of each possible pair of habitat features were quantified using my expert opinion on a -9 to 9 scale based on their relative impermeability to prairie dog movement. For example, to represent that element A is maximally more impermeable than element B, a value of 9 would be assigned. Alternatively, if element A is slightly easier to traverse than element B, a value of -1 or -2 could be assigned. A 0 value indicates that both features are equally permeable. AHP provides a derived relative cost for each feature based on the provided relative values. My values were 91.5% internally consistent, above the 90% recommended level (Saaty 1980). After I obtained AHP values for each of these terrain features, I adjusted the "habitat" layer to a cost of 1 to represent a basic cost of movement, and adjusted other cost values proportionally (Table 2). The stream banks layer was the only layer assigned an adjusted movement cost less than 1. My cost layer was used to calculate potential connectivity metrics comprised of a minimum cost distance (edge-to-edge) to nearest neighbor (Cost-weighted Nearest Neighbor, or CNN) and average cost distance to adjacent neighbors calculated through Voronoi polygons (Cost-weighted Adjacent Neighbors, or CAN).

Based on preliminary analyses that revealed high explanatory power for cost and area-weighted metrics, I also combined the cost-weighting and area-weighting tools to create models that were weighted by both area of patches and differing permeabilities of matrix elements. For this, I substituted the derived cost value for movement between patches in the d_{ij} term in equation 1.0 above. I then calculated the area-weighted cost-distance to the nearest neighbor (ACN) and the average area-weighted cost-distance to all adjacent neighbors (ACA), derived using Voronoi polygons.

I was also interested in fitting a modified version of the incidence function model (the T-statistic, designated TST) to these data to assess its ability to predict the presence of prairie dogs (Hanski et al 1996, Hanski 1998, Moilanen and Hanski 2006, Theobald 2006). The model I fit is defined by:

$$T_i = \sum_{k=1}^{n} w_{ik} A_k (A_i / \overline{A}) \qquad (2.0)$$

A_k is the area of the focal patch, $\overline{A}$ is the mean area of all patches, and w_{ik} is an interaction term that describes the interaction between patch i and all other patches n, using cost distances based on cost allocation paths to all other patches, as well as area of each patch (A_i). The tool finds the cost paths to each patch that fall in the lowest 10th percentile of all possible cost paths (Q_{10}, Theobald 2006), creating multiple pathways between patches. This may be a more realistic depiction because animals use multiple routes to travel between habitat. These cost distances are raised to the 1.7 power to represent a non-linear relationship between distance and colonization. This tool also differs from the area and cost weighted tool in that it incorporates the distance to all other patches in the study system rather than just the nearest or adjacent neighbors. I used the T-statistic rather than the classic form of the IFM ($S_i = \sum_{i=1}^{k} A_j \exp^{-\alpha d_{ij}}$, Hanski et al. 1996, Hanski 1998, Moilanen and Hanski 2006) in order to calculate multiple pathways between patches and because when distances between patches are large, the exponential term in the IFM model frequently generates metric values large enough to create numerical instability (Theobald 2006). These final three tools (CAN, ACA, TST) were tested after preliminary results were reviewed and thus should be interpreted cautiously (Burnham and Anderson 2002). Finally, I also fit a null model, which was a logistic regression containing only a constant intercept term without any dependent variables, to determine whether my 12 models had more explanatory power than a model with no relationship.

Statistical analysis

I analyzed data in a likelihood-based framework. Each connectivity metric was used as an independent variable to predict the presence of prairie dogs in habitat fragments (1/0 data) in simple logistic regressions. With the exception of the buffer-based metrics (B0.2, B1.0, B2.0), metrics were log-transformed before analysis was performed. Buffer metrics were percentages, and thus were arcsin square-root transformed.

I derived -2 log likelihood values from these logistic regressions. To determine the most efficient explanatory connectivity metric, I used AIC (Akaike's Information Criterion, Akaike 1973, Burnham and Anderson 2002), based on these derived likelihood values. AIC is not based on acceptance or rejection of null models or arbitrary significance levels (e.g. 0.05). Instead, it is used to determine the relative ability of tested models to predict observed patterns (Burnham and Anderson 2002). I used the version of AIC corrected for low sample size (AIC_c) (Burnham and Anderson 2002). The model with the lowest relative AIC_c value is the model that most parsimoniously explains the observed patterns. Models are compared using ΔAIC_c values, which are the difference in AIC_c values between a given model and the "best" (lowest AIC_c) model. Thus the top model has a ΔAIC_c value of 0. Models also were assigned Akaike weights (Burnham and Anderson 2002), which are measures of the relative likelihood of each model given the data. Akaike weights allow inference from more than one model based on the relative strength of each model rather than using only the top model, which may not be overwhelmingly superior to others.

Results

My best performing model was the area and cost-weighted distance to nearest neighbor (ACN, Table 3). This model, though superior based on AICc model selection, did not hold a majority of the model weight (48.9%), indicating some uncertainty regarding which connectivity metric most parsimoniously predicts prairie dog occurrence. The relationship between colony occurrence and connectivity in this model was in the direction expected; prairie dog colonies were more likely to be found in large fragments with low-cost distances to a large neighboring fragment. There was also considerable support for my area and cost-weighted distance to all adjacent neighbors metric (ACA, 44.6% of model weight). These two models cumulatively held 93.5% of the model weight, and all other tested metrics had a ΔAICc value > 4, indicating that they have moderate to low support from the data (Burnham and Anderson 2002). Logistic regression results for the top two models were as follows; ACN: area and cost-weighted distance to nearest neighbor ($\chi^2 = 20.07$, $\beta = 0.208$, -2 log likelihood = 288.17, $p < 0.001$) and ACA: area and cost-weighted distance to all adjacent neighbors ($\chi^2 = 19.88$, $\beta = 0.248$, -2 log likelihood = 288.36, $p < 0.001$).

Discussion

The relatively strong performance of an area-weighting term in my study (as in Moilanen and Nieminen 2002, Bender et al. 2003) indicates that patches of large area should be a conservation priority for both existing and potential future prairie dog habitat. Many studies found area of habitat to have an impact on wildlife communities (e.g. MacArthur and Wilson 1967, Bolger et al. 1997, 2000, Crooks et al. 2001, Crooks 2002). In addition, colonized fragments in this area were substantially larger than uncolonized fragments.

Because my top models also incorporated cost-based distance, there is evidence that in addition to simple distance to other fragments, the content of the intervening matrix is also important to the distribution of prairie dogs (Roach et al. 2001). Thus, the matrix matters (Ricketts 2001, Murphy and Lovett-Doust 2004). These results suggest that the parameterization of my cost surface is a reasonable one for prairie dogs. My AHP-based method assigned roads a high cost, with costs relative to the size of roads (local, arterial, highway), while buffers around drainages had a particularly low cost. My cost allocation was only one possible variable set and parameterization, to avoid data dredging and a biased model set, I chose to include only one set of a priori cost variables (Burnham and Anderson 2002). Clearly, researchers with more specific research questions could test more parameterizations of a cost surface, changes to an area-weighting equation, or additional metrics altogether, but such alterations were beyond the scope of this study.

My top performing isolation metrics were relatively complex. I added complexity to the models by increasing the degree to which the biology of the study organism was incorporated. Thus, I included buffers based on known prairie dog dispersal distances, weighted metrics by area because larger areas may be more detectable or suitable for wildlife, and used cost surfaces based on my presumption of varying landscape permeability. Past research finds that isolation models incorporating biological information preformed better (Calabrese and Fagan 2004, Fagan and Calabrese 2006). The few strictly structural metrics I tested (Euclidean Nearest and Euclidean Adjacent Neighbors, ENN and EAN) performed fairly poorly (Fagan and Calabrese 2006), in keeping with studies that discourage use of simple interpatch distance (Moilanen and Nieminen 2002, Bender et al. 2003). However, the T-statistic, a modified Incidence Function Model (Hanski 1994, Calabrese and Fagan 2004, Moilanen and Niemenen 2002), was arguably my most complex metric, but ultimately held almost none of the final model weight, suggesting that the relative impact of each patch on every other may be an unnecessary level of complexity for this study system and animal.

The next logical step towards including biological information in my isolation metrics might be to parameterize them based on the configuration of prairie dog colonies on the landscape, perhaps using distance to colonies rather than habitat. I did not test colony-distance based metrics because I wanted to compare a balanced set of metrics applicable to other organisms and study areas, but the finding that colonies are clustered on the landscape may suggest that urban colonies persist when located near other colonies, which could facilitate demographic and genetic flow and metapopulation dynamics (e.g. Roach et al. 2001). Indeed, in an analysis of the combined effect of local and landscape variables on prairie dog distribution, Magle (Chapter 4) finds simple distance-to-colony based metrics to have extremely high explanatory power for prairie dog distribution in this area.

It is important to note the limitations of my model set and the assumptions I made. I am assuming that my models represent a useful simplification of reality, such that patch area and isolation are factors that help describe the distribution of prairie dogs, as with other wildlife (e.g. Soulé et al. 1988, Bolger et al. 1991, Taylor et al. 1993, Crooks 2002, Crooks et al. 2004, Crooks and Sanjayan 2006). My null (intercept-only) model held virtually no weight among the top models, indicating that my tested isolation metrics do indeed provide explanatory power. I am assuming that the relationship between prairie dog presence and patch area or isolation is not defined by thresholds or discontinuous functions, which are not tested by my methodology. I also make the assumption that similar matrix elements (e.g. local roads, urban development) are homogenous. Interpretation of isolation metrics frequently can be challenging in ecology, and these metrics should be used with a full knowledge of their expected behaviors (Tischendorf et al. 2003). Despite my assumptions and simplifications, this study provides a wide range of isolation metrics fitted to wildlife distribution data, and is the first attempt to compare these metrics for urban habitat.

The pattern of prairie dog colonies currently present in an urban landscape is a function of both biological factors (e.g., local extinction and colonization) and historical human control (development and poisoning of colonies). As such, my metrics predict a distribution that results from complex interactions of social and ecological variables, with the relative effects of each unknown. Nonetheless, I found that a cost-surface and area-weighted nearest neighbor metric was the strongest predictor of prairie dog distribution in my study area in urban Denver. Comparisons of isolation metrics using empirical data on wildlife distribution are rarely preformed, and this study provides important information regarding their relative predictive power. In addition to providing guidance for landscape modeling, my results have implications for conserving and managing of urban prairie dog colonies. Features such as roads and land cover (parameterized via a cost surface) and the area of fragments were important determinants of the distribution of prairie dogs in urban areas. My findings suggest that large fragments and those near drainages should thus be targets for prairie dog conservation activity, while small patches strongly bordered by roads and other dispersal barriers warrant lower priority.

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Table 1. Summary of connectivity metrics tested to examine distribution of prairie dogs in urban habitat fragments in the Denver Metropolitan area. See methods section for specific details of how each metric was calculated. Distance to all adjacent neighbors was derived through Voronoi polygons. Connectivity types follow Fagan and Calabrese (2006).

Metric	**Description**	**Relative Complexity**	**Connectivity Type**
ENN	Nearest Neighbor based on simple Euclidean distance	Low	Structural
B0.2	Percentage of buffer 200 m from target fragment consisting of other fragments	Low	Potential
B1.0	Percentage of buffer 1 km from target fragment consisting of other fragments	Low	Potential
B2.0	Percentage of buffer 2 km from target fragment consisting of other fragments.	Low	Potential
EAN	Average Euclidean distance to all adjacent neighbors	Medium	Structural
AEN	Euclidean distance to nearest neighbor weighted by area	Medium	Potential
AAN	Average distance to all adjacent neighbors weighted by area	Medium	Potential
CNN	Cost distance to nearest neighbor	High	Potential
CAN	Average cost distance to all adjacent neighbors	High	Potential
ACN	Cost distance to nearest neighbor weighted by area	High	Potential
ACA	Cost distance to all adjacent neighbors weighted by area	High	Potential
TST	T-statistic: modified Incidence Function Model	High	Potential

Table 2. Cost values used for 30 m resolution cost surface raster for prairie dog movement, calculated with Analytic Heirarchy Process (AHP: Saaty 1980, 1990, 1994). For data on the contents of each feature, see the Methods section.

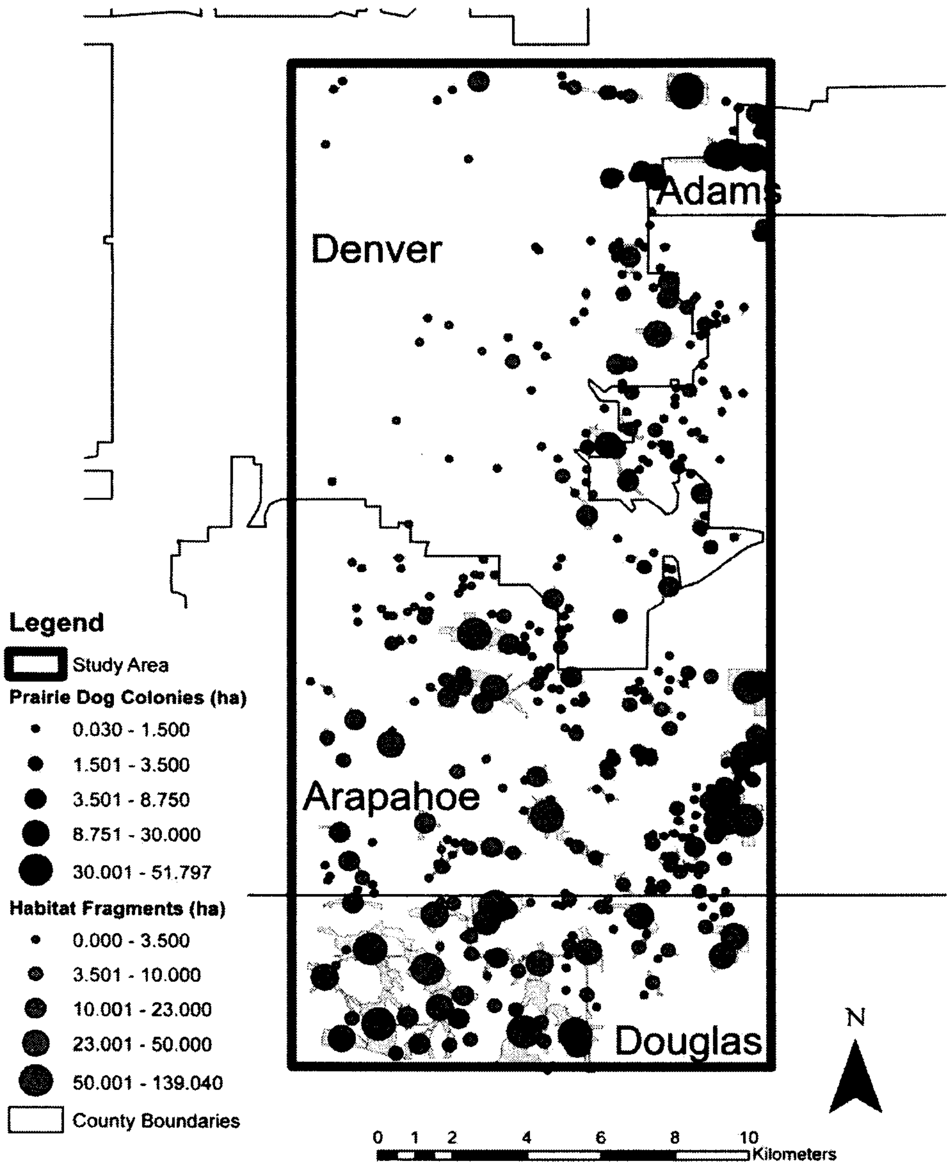
Feature	**Cost**
Water	10.75
Urban	2.14
Agricultural	1.51
Habitat	1.00
Local Roads	3.37
Medium Volume Roads (Arterials and Collectors)	5.90
Highways	10.21
Stream banks	0.71

Table 3. AICc results for tested connectivity metrics in a study of distribution of prairie dogs in urban habitat fragments in the Denver Metropolitan area . Letters in parentheses are the metric acronym referenced in the methods section. The "expected" column describes whether the metric predicted prairie dog occurrence in the expected direction—Y means colonies were more likely to be present in more connected fragments, N means colonies were more likely to be present in more isolated fragments. See text for details of models.

Model	Δ AICc	Model Weight	Sum of Weight	Expected
Area and Cost Weighted Nearest Neighbor (ACN)	0	0.489	0.490	Y
Area and Cost Weighted Adjacent Neighbors (ACA)	0.187	0.446	0.935	Y
Area Weighted Nearest Neighbor (AEN)	4.304	0.057	0.992	Y
T-statistic (modified Incidence Function Model) (TST)	8.792	0.006	0.998	Y
Area Weighted Adjacent Neighbors (AAN)	12.007	0.001	0.999	Y
Cost-Weighted Nearest Neighbor (CNN)	13.903	<0.001	0.999	Y
Null Model (Intercept Only)	18.046	<0.001	0.999	N/A
Euclidean Nearest Neighbor (ENN)	18.539	<0.001	0.999	Y
Proportion of Fragments within 2 km (B2.0)	19.544	<0.001	0.999	Y
Euclidean Distance to Adjacent Neighbors (EAN)	19.885	<0.001	~1	N
Proportion of Fragments within 0.2 km (B0.2)	20.031	<0.001	~1	Y
Proportion of Fragments within 1 km (B1.0)	20.032	<0.001	~1	Y
Cost-Weighted Adjacent Neighbors (CAN)	20.055	<0.001	1	N

Figure 1.

Map of the study area in Metropolitan Denver, Colorado. Symbols do not represent actual fragment or colony dimensions, but rather location and relative size. The four counties included in the study area are labeled.



CHAPTER 4

INVESTIGATING THE DISTRIBUTION OF PRAIRIE DOGS IN AN URBAN LANDSCAPE

Abstract

Habitat fragmentation is one of the prevalent threats to biological diversity. Landscape biogeographic and local habitat characteristics can be important determinants of the distribution of wildlife populations in habitat patches in urban landscapes. However, the specifics of which characteristics are most critical to maintaining wildlife populations are not fully known for prairie ecosystems, especially in fragmented urban habitat. This study focuses on black-tailed prairie dogs along an urban gradient in Denver, Colorado. Prairie dogs have declined precipitously throughout the region and may be an essential part of the prairie ecosystem, making them excellent study subjects. I identified a series of habitat fragments in the fully urbanized areas and south suburbs of Denver, Colorado, both containing and not containing prairie dogs. Landscape characteristics, including fragment size, age and connectivity, and local characteristics, including fragment slope, vegetative cover, height and density, were measured on each fragment. I used likelihood-based methods to explore which variables most accurately predicted prairie dog occurrence within my study area. Slope and percentage cover of litter were the most reliable variables, although all tested predictors had some explanatory power. My study

provides the first attempt to model prairie dog occurrence in highly fragmented urban habitat and has important implications for the management and conservation of prairie dogs.

Introduction

Habitat fragmentation is one of the prevalent threats to biological diversity (Wilcox and Murphy 1985, Wilcove et al. 1998). As human settlements continue to spread throughout the world, the wildlife habitat that remains is diminished and isolated. Many species find refuge in small patches of habitat that remain inside urban environments. Urban fragments serve many important roles (Kellert 1980), including housing rare or endangered species (Bolger et al. 1997, Crooks et al. 2001, Crooks 2002, Crooks et al. 2004), facilitating bird migrations by providing stop-over sites (Stouffer and Bierregaard 1995, Fischer and Lindenmayer 2002), providing wildlife corridors or stepping stones between undeveloped areas (Soulé 1991, Estrada 1993, Turner and Corlett 1996, Gibb and Hochuli 2002), enhancing property values (Correll et al. 1978, Bolitzer and Netusil 2000), and producing aesthetically pleasing landscapes (Smith 1993, Garrod and Willis 1995). In addition, isolated fragments may not be subject to diseases that affect more connected populations (Lomolino and Smith 2003). Frequently the degree of connectivity between these isolated patches is a key driver in determining species persistence and community structure (Soulé et al. 1988, Bolger et al. 1991, Crooks 2002, Crooks et al. 2004, Crooks and Sanjayan 2006). When viewed at a landscape scale, urban habitat fragments can comprise a gradient of patches that represent the full range of effects of urbanization on wildlife communities. Urban gradients are increasingly used in ecological studies, and can produce environmental heterogeneity that is useful in exploring how the effects of human development can influence other species (Matson 1990, McDonnell and Pickett 1990, McDonnell et al. 1993, Crooks et al. 2004).

To adequately protect urban habitat fragments and the wildlife they support, it is essential that we understand the characteristics of these habitat patches and how they impact plant and animal populations. Prairie ecosystems are particularly threatened by habitat fragmentation and are rapidly being converted into urban development (Samson and Knopf 1994, 1996). Throughout prairie ecosystems, the black-tailed prairie dog (*Cynomys ludovicianus*) is one of the most ecologically pivotal and controversial animals. Over the last century, government extermination programs, sylvatic plague (caused by the bacterium *Yersinia pestis*), agricultural expansion, and commercial and residential development have reduced prairie dog populations drastically, to a small fraction of their historic range (Miller et al. 1990, 1994, Kotliar et al. 1999, 2006, but see White et al. 2005). Many of the remaining prairie dog colonies exist in small patches in some urban areas and in rural regions (Lomolino and Smith 2001, 2003, Lomolino et al. 2003, Magle 2003, Johnson and Collinge 2004) and some function as metapopulations (Roach et al. 2001). Prairie dogs influence soil mixing as well as influence primary production of plants and landscape heterogeneity (Holland and Detling 1990, Ceballos et al. 1999, Bangert and Slobodchikoff 2000), and may function as keystone species (Whickler and Detling 1988, Miller et al. 1990, 1994, 2000, Forrest 2005, but see Stapp 1998, Vermeire et al. 2004). Because prairie dogs are heavily impacted by human development, and because they fundamentally alter ecosystems, they are excellent focal species for a fragmentation study.

The goal of my study was to evaluate which factors most strongly influence the distribution of a potential keystone species, the black-tailed prairie dog, along a gradient of urbanization in shortgrass prairie fragments in the rapidly developing landscape of the Colorado Front Range. Landscape biogeographic and local habitat characteristics can be important predictors of wildlife populations in habitat patches in urban landscapes (Bolger et al. 1997, Crooks et al. 2001, Crooks 2002); however, little is known about the combined effects of landscape and local variables on the distribution of urban prairie dogs. Following predictions of island biogeography theory (MacArthur and Wilson 1967) as applied to habitat fragments (Diamond 1975, Soule et al. 1988, Bolger et al. 1991, Lomolino and Smith 2003), I hypothesized that landscape variables would be important determinants of prairie dog occurrence, with fragment size and degree of connectivity positively related to prairie dog presence, and fragment age negatively related to their occurrence. In addition, local habitat variables may be strongly associated with prairie dog distribution because prairie dogs significantly influence vegetative communities (Whicker and Detling 1988, Holland and Detling 1990, Chapter 1), and because slope and floral attributes are known to be important determinants of prairie dog occupancy in natural areas (Reading et al. 1989, Detling 1998, Proctor et al. 1998). Following these prior studies, I predicted that graminoid and forb coverage and amount of bare ground would be positively related to prairie dog presence, and coverage of litter, fragment slope, and vegetative height and density would be negatively related to prairie dog occurence in urban fragments. The ability to relate prairie dog distribution to measurable landscape and local features will be critical to conservation and management efforts directed towards prairie dogs in fragmented systems.

Methods

Identifying fragments

In the summer of 2002 I used aerial photography maps to identify a section of the greater Denver metropolitan area (13 x 29 km, ~374 km^2) spanning from downtown Denver south through Highlands Ranch (a southern suburb of Denver), isolating a gradient of increasing urbanization south to north (Figure 1). At the time of the survey, the southern boundary represented the outer edge of urban development. I performed a census that identified 387 habitat fragments within this study area. A fragment was defined as any plot of undeveloped land with an area of at least 0.25 ha that was not regularly landscaped or manicured by humans, and that was embedded in a dissimilar, less-hospitable, human-modified matrix. Highway embankments were omitted due to inaccessibility. All fragments were verified via field reconnaissance, and characterized as colonized or not colonized by prairie dogs. Fifty-four of the fragments contained colonies in summer of 2002. Because prairie dog colonies are diurnal and conspicuous (Hoogland 1995), terrain was reasonably flat, and surveys were thorough, I am confident that colonization status of all fragments was accurately assessed.

Measuring landscape and local variables

Landscape variables were calculated for each fragment in the study area as follows: All fragments were digitized in ArcGIS 9.1 (ESRI, Inc.), and area of each patch (ha) was calculated. Age of fragments (time since complete isolation by urban development) was determined from review of parcel data from Denver, Adams, Arapahoe and Douglas county assessors that indicated the year developments were constructed. I determined the number of years since development for each parcel adjacent to a habitat fragment, and used the largest value as a surrogate for age; if bias is present the analysis is likely biased towards a conservative overestimate of age. To quantify patch isolation or connectivity, I used an area- and cost-weighted distance to nearest neighbor connectivity metric described in Chapter 3. This metric was the strongest predictor of prairie dog distribution in this area based on their comparison of 12 connectivity metrics spanning a range of complexity.

As a first step in calculating this metric, I created a cost surface raster for the study area (Chapter 3). A cost surface is a raster layer where each cell is parameterized with a cost value representing how difficult it may be for an organism to move across. Thus, the "cost" for an organism to move from one patch to another is the least cost of possible pathways, represented as the sum of the costs of each cell that must be traversed. My cost surface raster was created beginning with land cover data from the Colorado Vegetation Model (CVM) dataset, which has 30 m resolution (Theobald et al. 2004). I grouped values from this raster as follows: residential, commercial, industrial, and bare rock/sand/clay layers were grouped as "urban"; pasture/hay, row crops, small grains, fallow land, and urban/recreational grasses were combined as "agricultural"; and foothills, woodland, shrubs, and prairie were grouped as "habitat". Then, I added the following features over the underlying land cover value: road and highway data from the Colorado Department of Transportation (1:100000 scale) starting with local roads, then medium volume roads (collectors and arterials), and ending with highways. Next, I overlaid hydrologic features (streams and water bodies) from the National Hydrography Dataset (1:24000 scale) obtained from the United States Geological Survey. I finished by buffering these hydrologic features by one cell (30 m) and designating this buffer "stream banks". This step differentiated land adjacent to water due to the finding of Roach et al. (2001) that prairie dogs frequently disperse along drainages. Most water features in this study area represented agricultural drainages that were dry most of the year, and were thus comparable to previous findings (Roach et al. 2001). Features added later overrode the previous value for a given cell.

Because information regarding the permeability of various terrain for prairie dogs and their habitat selection in urban environments was highly limited (but see Roach et al. 2001), I estimated cost values based on my knowledge of movement behavior. I assigned cost values for landscape features using Analytic Hierarchy Process (AHP: Saaty 1980, 1990, 1994). For this process, pairwise comparisons of each possible pair of habitat features were quantified using my expert opinion on a -9 to 9 scale based on their relative impermeability to prairie dog movement. AHP provides a derived relative cost for each feature based on the provided relative values. For more details on cost surface determination, see Chapter 3.

The connectivity metric calculated used a modification of the proximity index (Gustafson and Parker 1992, Moilanen and Nieminen 2002, Bender et al. 2003) where I summed the area of each patch (in hectares) in a pair of neighbors and divided this sum by the edge-to-edge cost-weighted distance (calculated as above) between the patches. This is a potential connectivity metric (Fagan and Calabrese 2006) because it implicitly models the interaction of organisms and habitat. Based on findings that species frequently respond in a non-linear fashion to changes in habitat area or isolation (Kerkhoff et al. 2000, Brown et al. 2002), I raised the product of the area terms to the 0.7

power and raised the edge-to-edge distance between the patches to the 1.7 power before performing calculations (Theobald 2006), thus the final metric is represented by:

$$C = (A_i A_j)^{0.7} / d_{ij}^{1.7} \qquad (1.0)$$

This equation relates connectance (C) of two neighboring patches (*i* and *j*) to the area of each patch in a neighboring pair (*Aj* and *Ai*) and the cost-weighted distance between them (d_{ij}). The values 0.7 and 1.7 were used based on their superior performance in simulated studies where they exhibited stable behavior over a wider range of areas and distance than traditionally used scaling metrics such as 0.5 and 1.5 (B. Milne, personal communication). Measures of connectivity not only frequently have explanatory power for species distribution, but inclusion of these terms in multivariate models has been found to control for spatial autocorrelation in prairie dog spatial data (M. Antolin, unpublished data).

Local habitat variables were measured (Table 1) between 1 July and 22 August, 2002 on all fragments colonized by prairie dogs where permission to sample was granted (40); sizes of colonized fragments that were surveyed (mean = 24.5 ha, se = 5.74, n = 40) did not differ (t = 1.39; p = 0.17) from sizes of occupied fragments where habitat surveys could not be conducted (mean = 14.7 ha, se = 3.64, n = 14) 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 on average were larger (t = 2.51, p = 0.015) than surveyed unoccupied fragments (mean = 9.0 ha, se = 2.84, n = 54).

When measuring local variables, 3 random transects were chosen, each parallel to the long axis of the colony or fragment and a minimum of 10 meters apart. Transects were either 100 m long or the length of the colony/fragment, whichever was shorter. At 10 m intervals along each transect, I measured slope, vegetative cover, and vegetative height and density (Chapter 1). If a fragment both contained a prairie dog colony and had an uncolonized portion, 3 transects were placed on both the colonized and uncolonized portions, for a total of 6 transects on the fragment. These data were later averaged to provide a fragment-wide estimate of local variables. I estimated vegetative cover in classes of graminoid (grasses, sedges, and rushes), forb, litter, and bare ground with methods modified from Daubenmire (1959). Height and density of vegetation was measured using the Robel method (Robel et al. 1970). Data on slope were derived using an inclinometer, with slope measurements placed into one of 6 categories (following Proctor et al. 1998). For more explicit details of local variable sampling, see Magle and Crooks (Chapter 1). The mean number of measurements of local variables on prairie dog colonies was 26.4 (se = 1.01). Of the 40 measured fragments containing prairie dog colonies, 29 had a large enough uncolonized portion to sample. The mean number of measurements taken on these uncolonized portions was 28.4 (se = 0.84). On each of the 54 uncolonized fragments, I took an average of 28.6 measurements (se = 0.42).

Statistical analysis

Data from this study were analyzed in a likelihood-based framework. I first tested the data by conducting simple logistic regressions with each of the measured local and landscape variables as a predictor variable, and presence of prairie dogs (0/1) as the response variable. This analysis had a sample size of 94, the number of fragments where local variables could be measured. Because I used model selection protocols to determine the relative impact of each variable, a small set of predictor variables was desirable. Thus, I decided not to include local variables that were highly correlated based on Pearson's correlation coefficient, retaining only the one with the lowest -2 log likelihood. Limiting a set of predictor variables based on apparent explanatory power prior to model selection is commonly done (e.g., Apps et al. 2004, Fisher et al. 2004, Smith et al. 2004, Seiler 2005).

To determine the best model comprised of landscape and/or local variables that predicted the presence of prairie dogs in individual habitat patches, I used AIC (Akaike's Information Criterion, Akaike 1973, Burnham and Anderson 2002), based on likelihood values derived from logistic regression. AIC is not based on acceptance or rejection of null models or arbitrary significance levels (e.g. 0.05). Instead, it is used to determine the relative ability of tested models to predict observed patterns. AIC determines the most parsimonious model by inducing a penalty on models proportional to the number of parameters they contain. I used the version of AIC corrected for low sample size (AIC_c) (Burnham and Anderson 2002). The model with the lowest relative AIC_c value is the model that most parsimoniously explains the observed data. Models are compared using ΔAIC_c values, which are the difference in AIC_c values between a given model and the "best" (lowest AIC_c) model. Thus, the top model has a ΔAIC_c value of 0. Models were also assigned Akaike weights, which are measures of the relative likelihood of each model. Akaike weights allow inference from more than one model based on the relative strength of each rather than using only the top model, which may not be overwhelmingly superior to others. I also calculated variable importance weights, which are sums of the AIC_c weights of models that contain each variable. These variable importance weights can provide insight into which variables are the strongest predictors of the dependent variable (Burnham and Anderson 2002).

Results

Correlations

Among my local variables, litter coverage was highly correlated (Table 2) to both forb coverage ($r = -0.447$, $p < 0.001$) and bare ground coverage ($r = -0.790$, $p < 0.001$), and had the lowest -2 log likelihood of the three variables based on logistic regressions (litter: $\chi^2 = 19.70$, $\beta = -0.069$, -2 log likelihood = 108.52, $p = 0.005$, forb: $\chi^2 = 4.69$, $\beta = 0.050$, -2 log likelihood = 123.52, $p = 0.030$, bare: $\chi^2 = 4.17$, $\beta = 0.030$, -2 log likelihood = 124.05, $p = 0.041$), so to reduce the number of local variables in the analysis I removed forb coverage and bare coverage from the analysis. Litter coverage was not significantly correlated with graminoid coverage, vegetative height/density, or slope ($p > 0.05$). There was no significant correlation between graminoid coverage and vegetative height/density or slope ($p > 0.05$). The Robel index of vegetative height and density was correlated with slope ($r = 0.487$, $p < 0.001$), but these terms were both retained since vegetation height and density and slope are biologically disparate features. All three landscape variables were highly correlated (area and age: $r = -0.275$, $p = 0.007$; area and connectivity $r = 0.701$, $p < 0.001$; age and connectivity $r = -0.237$, $p = 0.027$). The observed correlation between area and connectivity is expected, since my connectivity metric is based in part on fragment area. However, I chose to retain both because I was interested in the relative and separate impacts of area and connectivity on prairie dog distribution. Correlated variables should not cause problems in my analysis since AICc model selection will penalize models with redundant variables (Burnham and Anderson 2002).

Logistic Regressions

Simple logistic regressions of each variable on prairie dog presence revealed a positive relationship with fragment area ($\chi^2 = 7.73$, $\beta = 0.928$, -2 log likelihood = 120.49, $p = 0.005$) and connectivity ($\chi^2 = 4.715$, $\beta = 0.30$, -2 log likelihood = 123.50, $p = 0.029$), and a trend towards a negative relationship with fragment age ($\chi^2 = 3.61$, $\beta = -0.01$, -2 log likelihood = 124.61, $p = 0.057$). Percent cover of graminoids was positively related to prairie dog presence ($\chi^2 = 5.92$, $\beta = 0.08$, -2 log likelihood = 122.30, $p = 0.015$), while litter coverage was negatively related to prairie dog presence ($\chi^2 = 19.70$, $\beta = -0.07$, -2 log likelihood = 108.52, $p < 0.001$), as was slope ($\chi^2 = 11.96$, $\beta = -1.75$, -2 log likelihood = 116.26, $p < 0.001$), and vegetative height and density ($\chi^2 = 10.05$, $\beta = -2.05$, -2 log likelihood = 118.17, $p = 0.002$).

Prairie Dog Distribution Modeling

With 7 explanatory variables in the global analysis, combinations of variables yielded 128 potential models (2^7). Because this was not greatly larger than the number of observations (94), I tested all potential models containing these 7 variables. When the number of explanatory variables is small, this type of model selection is unlikely to lead to spurious relationships or other statistical problems (K.P. Burnham, personal communication).

The top model contained the variables for fragment area, litter coverage, graminoid coverage, vegetative height and density, and slope (Table 3). This model held only 20.3% of the total model weight, so multi-model inference was appropriate. Based on the variable importance weights, litter coverage and slope appeared to be the most important explanatory variables, followed by graminoid coverage, vegetative height and density, fragment area, fragment age, and connectivity (Table 4). All variables in this global model set had variable importance weights > 0.35, indicating that each may be useful in explaining prairie dog presence (Burnham and Anderson 2002).

To illustrate the magnitude and direction of these impacts on prairie dog presence, I also provide parameter estimates for the top model, and the global model (Table 5). Presenting the global model allows us to demonstrate the strength and direction of the effects of all independent variables on the dependent variable (prairie dog presence). As predicted, fragment age, litter coverage, slope, and vegetative height and density were negatively related to the distribution of prairie dogs, while fragment area, connectivity and graminoid coverage were positively related to prairie dog colony presence.

Discussion

Landscape Factors

Although landscape factors had lower predictive power in this study compared to the local variables, fragment area had the highest relative weight among the landscape variables. The positive correlation between presence of prairie dogs in urban systems and the area of the fragment is consistent with predictions derived from the theory of island biogeography (MacArthur and Wilson 1967, Soulé et al. 1988, Bolger et al. 1991). However, the interpretation of this theory should be used with caution in this case, since the "islands", or fragments may not be in equilibrium, but rather in a state of faunal collapse, which is not predicted by the island biogeography theory (MacArthur and Wilson 1967, Soulé et al. 1988, Bolger et al. 1997, 2000, Crooks and Soulé 1999, Crooks et al. 2001). While monitoring fragments in this study area between 2002 and 2006, I documented 19 local extinction events compared to only 13 colonization events, providing further evidence for faunal collapse. Nine of these extinctions were determined to be caused directly by urban development, and another 8 appeared to be the result of poisoning. The cause of the remaining 2 extinction events was not determined, and plague cannot be ruled out. Local extinctions may also be caused by genetic factors or stochastic events following isolation. It should be noted that while larger patches are expected to be more likely to house species based on habitat relationships and island biogeography theory, larger areas also might be more likely to contain prairie dog colonies by random chance, simply because they encompass more space. Thus, this effect may be partially an artifact of sampling (Bolger et al. 1991). However, previous prairie dog mapping attempts for this area (EDAW 2000) indicate that a minimum of 6.1% of the unoccupied fragmented habitat in this study area previously contained prairie dog colonies, providing more evidence that local extinctions are at least partially responsible for the patterns observed.

Though the age term was not one of the most important variables in terms of ranking, it still had a variable importance weight of 0.509, indicating that older fragments are somewhat less likely to contain prairie dogs, perhaps due to local extinctions that occur over time. Area and age were negatively related in this study area, indicating that the larger fragments were less likely to have been isolated for long periods of time. Age was also negatively correlated with connectivity, so the younger fragments were more connected. The correlation of age with fragment area and connectivity is a natural result of the pattern of urban growth—the newer subdevelopments are conserving more open space, and in larger, more connected blocks. Age was also negatively correlated with graminoid coverage and slope. This indicates that the older fragments tended to have less graminoid coverage (probably because of incursion by invasive forbs) and were flatter on average. It is conceivable that extinctions on older fragments occur due to a reduction in the graminoid layer leading to inadequate forage.

Connectivity (the inverse of isolation) had the lowest relative importance among the variables I considered. However, with a variable importance weight of 0.376, it may still have non-redundant explanatory power (Burnham and Anderson 2002). Even when predictive power is low, it may be important to include connectivity variables in multivariate analyses to control for spatial autocorrelation (M. Antolin, unpublished data). The strong correlation between connectivity and area of patches is expected because my connectivity term is partially based on fragment area. It is possible that the relatively low variables weights found for both connectivity and area relative to local variables result because the two measures are somewhat redundant predictors. Isolation should be particularly important in systems with low to moderate movement among fragments (Crooks et al. 2001, Crooks 2002), but it is possible that movement among urban patches is rare enough to produce low explanatory power for connectivity measures

(Magle and Crooks in submission). However, colonization events do occur in this system (Magle unpublished data). The relationship observed between connectivity and prairie dog distribution may arise because isolated populations are at risk from genetic problems such as inbreeding, as well as stochastic events that can cause local extinctions in the absence of dispersal (Hanski and Gaggiotti 2004).

Previous work from other urban systems indicates that highly isolated urban patches are seldom visited by mammalian carnivores such as bobcats (*Lynx rufus*) or coyotes (*Canis latrans*) (Crooks 2002). In addition, some researchers have speculated that less connected fragments are probably not subject to repeated sylvatic plague outbreaks (Lomolino and Smith 2001, Lomolino et al. 2003), which regularly decimate prairie dogs in natural settings (Hoogland 1995, Cully and Williams 2001). However, other researchers found no relationship between colony isolation and plague (Stapp et al. 2004). Though plague was never directly observed in this study area, it cannot be ruled out as a cause of extinction of two colonies, and plague events did occur in colonies just outside the urban area during the duration of the study. However, my more isolated fragments (those with low connectivity) were less likely to contain prairie dog colonies, perhaps indicating that even the potential reduction of predation or disease was insufficient to counter the negative effects of isolation on prairie dog populations.

I used an area and cost-weighted connectivity metric based on distance to habitat fragments because it demonstrated superior performance in previous studies (Chapter 3). However, researchers have previously found connectivity metrics based on distance to prairie dog colonies (rather than fragments) to be reliable predictors of colony presence in agricultural landscapes (Lomolino and Smith 2001, Lomolino et al. 2003), and to predict prairie dog abundance in Boulder, Colorado (Johnson and Collinge 2004). I declined to test metrics based on distance to colonies because my dependent variable was presence or absence of prairie dogs, and predicting wildlife distribution using pre-existing data on that distribution would be uninformative. However, simple clustering statistics demonstrate that colonies are spatially clustered on this landscape (Chapter 3), which could be a result of historical distribution or patterns of human control. A preliminary analysis indicated that colony-based connectivity measures are much stronger predictors than the fragment-based metric I used, due to the clustered nature of these colonies (Chapter 3), despite being inappropriate predictive variables in this study. Although I find a limited role of connectivity in this model selection process, I caution researchers to bear in mind that the clustered nature of colonies does suggest that urban colonies persist when located near other colonies, which could facilitate demographic and genetic flow and metapopulation dynamics (e.g. Roach et al. 2001).

Local factors

Local variables were strongly related to the probability of prairie dogs occupying fragments. Significant predictors included percentage of litter coverage, graminoid coverage, vegetative height and density, and slope. Litter coverage was substantially lower on prairie dog colonies. Percent coverage of forb and bare ground were not included because they were negatively correlated with litter coverage, thus the litter term used in my model selection could be considered to stand as a proxy for these other vegetative variables as well—low levels of litter usually indicate high forb coverage and amount of bare ground. Typically prairie dogs decimate the graminoid layer on their colonies, allowing forbs to flourish (Bonham and Lerwick 1976, Coppock et al. 1983, Cid et al. 1991, Detling 1998). Although graminoid cover was higher overall on colonized fragments compared to uncolonized ones, this was because prairie dogs tend to be present on fragments with high graminoid cover, even though that cover was reduced in the immediate vicinity of their colonies (Chapter 1). Prairie dogs tended to be present on sites with low vegetative height and density, probably due to grazing and clipping vegetation. My Robel index of vegetative height and density was positively correlated with slope, indicating that the sites with shorter, less dense vegetation were also more flat. Prairie dogs were more likely to occur on flatter fragments (as in Proctor et al. 1998). Age was negatively correlated with slope, so the flatter fragments tended to be older. These findings are largely consistent with data from unfragmented systems (Whicker and Detling 1988, Holland and Detling 1990, Reading and Matchett 1997, Detling 1998, Proctor et al. 1998, Chapter 1). The majority of plant species on prairie dog colonies in this system were non-native, and included field bindweed (Convolvulus arvensis) and smooth brome (Bromus inermis) (Chapter 1). The causality of relating prairie dog presence to vegetative factors is unclear, since prairie dogs directly impact vegetative cover (Hoogland 1995, Detling 1998). The power of local variables to predict prairie dog distributions 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. In the case of vegetative coverage (graminoid, forb, litter, and bare ground) and height/density, direct alterations through grazing are the most likely explanation for the patterns observed.

Conclusions

My results show that multiple factors influence the distribution of prairie dogs in urban settings. Thus, efforts to manage or preserve prairie dogs should explicitly consider the spatial context of colonies as well as their local characteristics. Litter coverage was the strongest predictor based on variable importance weight, and this variable is strongly related to other local vegetative measures such as forb and bare ground coverage. However, landscape variables such as area, age, and connectivity of fragments were also related to prairie dog distribution. Large fragments, flat areas, and those with high graminoid coverage should also be priority habitat for those interested in conservation or management of prairie dogs in fragmented settings. The fact that age of fragments was negatively related to prairie dog presence may indicate that colonies are being lost to stochastic events over time, and perhaps that there is an "extinction debt" (Tilman et al. 1994) in place in this system. If we consider these prairie dogs to be functioning as a potential metapopulation, as other prairie dogs appear to (Roach et al. 2001), this relationship could indicate that dispersal is insufficient to counteract local extinctions of prairie dogs in these habitat patches. However, prairie dog metapopulation dynamics are frequently driven by plague (Roach et al. 2001), which was either rare or not present in this study area, and more precise estimates of movement between patches would be necessary to denote these populations as metapopulations. Genetic sampling may provide an efficient means of estimating movement rates (Roach et al. 2001).

Burnham and Anderson (2002) suggest that variables with a variable importance weight higher than 0.31 may have important explanatory power, and all of my variables had variable importance weights >0.35. It may seem surprising that all of my tested variables had explanatory power for prairie dog presence in this study system. Typically, during AIC model selection, some variables (which have low variable importance weight) are dropped from all high ranking models as unimportant (Burnham and Anderson 2002). However, I put consideration into the biological meaning of all variables considered, and to maintain a small candidate model set I omitted some variables from the model selection process based on preliminary analysis. AIC and other likelihood-based model selection and multi-model inference techniques function optimally when substantial *a priori* thought is put into considered variables (Burnham and Anderson 2002).

Because prairie dogs interact so strongly with other organisms (Agnew et al. 1986, Ceballos et al. 1999, Lomolino and Smith 2003, Reading et al. 1989, Whicker and Detling 1988), and may in fact function as keystone (Forrest 2005, Kotliar et al. 1999, 2006, Kotliar 2000, Miller et al. 1990, 1994, but see Stapp 1998, Vermeire et al. 2004), or highly interactive (Soulé et al., 2003, 2005) species, my findings related to prairie dog distribution may have implications for greater wildlife communities as well, though future work will be needed to clarify if these relationships are maintained in fragmented urban systems (Lomolino and Smith 2003). The fact that a species as important to prairie ecosystems as the prairie dog can persist in urban habitat refugia further supports the contention that there can be tremendous potential for conservation in such areas.

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Figure 1. Map of the study area and sampled study colonies in Metropolitan Denver, Colorado.

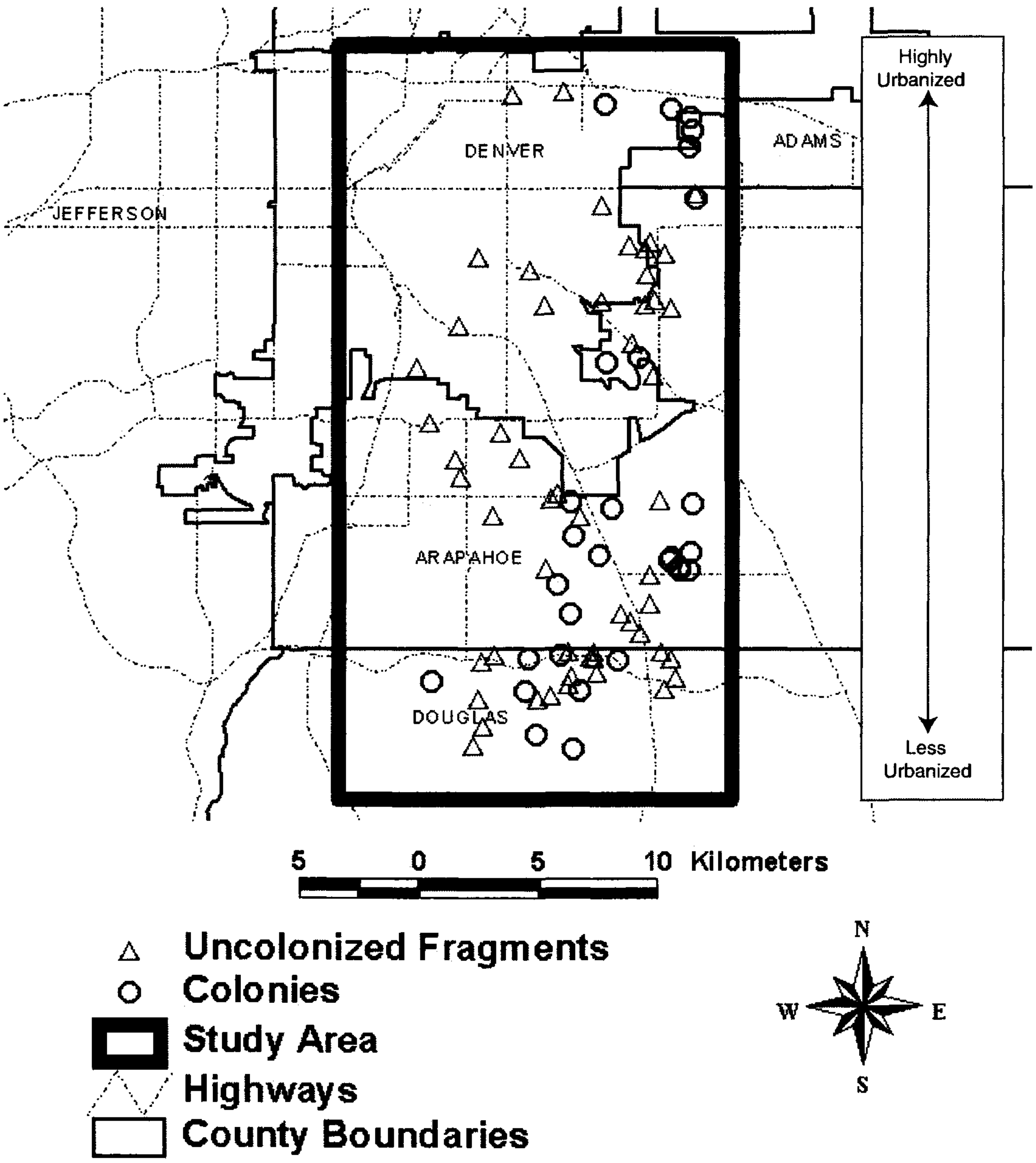

Table 1. Summary of local and landscape variables measured on study fragments in Denver, Colorado. Connectivity refers the proportion of the landscape within 2 km of a fragment comprised of prairie dog colonies. "Conn" refers to the connectivity of fragments, represented by a log-transformed area and cost-weighted metric (see methods). "Robel" is the Robel index of vegetative height and density. Sample size throughout was 54 uncolonized fragments, and 40 colonized fragments, for a total of 94. SE is the standard error of the mean.

	Entire Study Area			*Colonized Fragments*			*Uncolonized Fragments*		
Variable	**Mean**	**Range**	**SE**	**Mean**	**Range**	**SE**	**Mean**	**Range**	**SE**
Area (ha)	7.86	0.25 – 139.04	0.88	21.77	0.25 – 139.04	4.45	5.63	0.86 – 123.74	0.65
Age (yrs)	37.24	1 – 134	1.35	33.66	5 – 117	3.11	37.82	1 – 134	1.49
Conn	5.21	-0.16 – 6.49	0.08	5.33	1.03 – 6.49	0.91	5.09	-0.16 – 6.49	0.77
Graminoid	9.07	0 – 25.4	0.65	10.88	0 – 25.42	1.09	7.73	0.67 – 22.83	0.75
Litter	47.21	6.4 – 75.5	1.59	39.38	7.47 – 62.81	2.04	53.02	64.40 – 75.50	1.98
Robel	1.36	1 – 3.13	0.04	1.22	1 – 2.02	0.04	1.46	1 – 3.13	0.47
Slope	1.89	1.1 – 3.47	0.05	1.70	1.10 – 2.20	0.04	2.02	1.13 – 3.47	0.07

Table 2. Correlation matrix for all local and landscape variables considered as predictors of prairie dog presence. The first value in each cell is the Pearson's correlation coefficient r, the second is the p-value. Asterisks indicate a p-value below 0.05. Connectivity refers to the connectivity of fragments, represented by a log-transformed area and cost-weighted metric (see methods). "Robel" is the Robel (1970) index for vegetative height and density.

	Area	**Age**	**Connectivity**	**% Litter**	**% Grass**	**Robel**
Age	-0.275 0.007*					
Connectivity	0.701 <0.001*	-0.237 0.021*				
% Litter	-0.087 0.404	0.069 0.506	0.035 0.740			
% Graminoid	0.183 0.077	-0.288 0.005*	0.150 0.149	0.015 0.889		
Robel	0.108 0.299	-0.103 0.321	0.118 0.257	0.185 0.075	0.163 0.116	
Slope	-0.030 0.772	-0.314 0.002*	0.127 0.224	0.182 0.079	0.142 0.173	0.487 <0.001*

Table 3. AICc model selection for local and landscape variables used to explain presence of prairie dogs in habitat fragments in the Denver area. Represented are the top 25 models (out of 128) that cumulatively hold > 95% of the model weight. K refers to the number of parameters in the model. "Conn" refers to the connectivity of fragments, represented by a log-transformed area and cost-weighted metric (see methods), and "gram" refers to the percent coverage of graminoid species. "Robel" is the Robel (1970) index of vegetative height and density.

Model Variables	**K**	**ΔAIC_c**	**Model Weight (w_i)**
Area, Grass, Litter, Robel, Slope	6	0.000	0.203
Area, Age, Grass, Litter, Robel, Slope	7	0.877	0.131
Conn, Grass, Litter, Robel, Slope	6	1.735	0.085
Area, Conn, Grass, Litter, Robel, Slope	7	2.426	0.060
Age, Grass, Litter, Robel, Slope	6	2.470	0.059
Area, Age, Grass, Litter, Slope	6	2.564	0.056
Age, Conn, Grass, Litter, Robel, Slope	7	2.650	0.054
Age, Grass, Litter, Slope	5	3.059	0.044
Area, Age, Conn, Grass, Litter, Robel, Slope	8	3.089	0.043
Area, Grass, Litter, Robel	5	3.692	0.032
Age, Conn, Grass, Litter, Slope	6	3.991	0.028
Area, Grass, Litter, Slope	5	4.532	0.021
Conn, Grass, Litter, Slope	5	4.681	0.020
Area, Age, Grass, Litter, Robel	6	5.219	0.015
Area, Age, Litter, Robel, Slope	6	5.297	0.014
Area, Age, Conn, Grass, Litter, Slope	7	5.534	0.013
Grass, Litter, Robel, Slope	5	5.805	0.011
Area, Conn, Grass, Litter, Robel	6	5.854	0.011
Area, Age, Litter, Slope	5	6.426	0.008
Area, Conn, Grass, Litter, Slope	6	6.537	0.008
Age, Conn, Litter, Robel, Slope	6	6.625	0.007
Conn, Litter, Robel, Slope	5	6.729	0.007
Area, Age, Conn, Litter, Robel, Slope	7	6.961	0.006
Area, Conn, Litter, Robel, Slope	6	7.155	0.006
Conn, Grass, Litter, Robel	5	7.415	0.005

Table 4. Variable importance weights for the variables used to explain the occurence of prairie dogs in habitat fragments in the Denver area. Provided are the variable importance weights for the combined model set (landscape and local) as well as those from the model sets restricted to landscape and local variables respectively. Connectivity refers to the connectivity of fragments, represented by a log-transformed area and cost-weighted metric (see methods).

Variable	Weight
Full Model (Landscape and Local)	
Litter	0.988
Slope	0.924
Graminoid	0.923
Vegetative Height/Density	0.781
Area	0.649
Age	0.509
Connectivity	0.376

Table 5. Parameter estimates for the top models, as selected by AIC_c model selection from all 128 possible combinations of local and landscape variables that predict the presence of prairie dogs in habitat fragments in the Denver area, and from the global model that uses all 7 variables. SE = standard error. Lower/Upper 95% CI are lower and upper 95% confidence intervals. Connectivity refers to the connectivity of fragments, represented by a log-transformed area and cost-weighted metric (see methods). Robel is the Robel (1970) index of vegetative height and density.

Model	**Variable**	**Estimate (β)**	**SE**	**Lower 95% CI**	**Upper 95% CI**
Top Model	Intercept	1.3745	2.5768	-3.7463	6.4952
	Area	1.2881	0.5326	0.2297	2.3464
	Graminoid	0.1371	0.0514	0.0350	0.2392
	Litter	-0.06050	0.01882	-0.09790	-0.02311
	Robel	-2.61268	1.05884	-4.71691	-0.50846
	Slope	-1.54530	0.76282	-3.06126	-0.02935
Global Model	Intercept	4.07	3.13	-2.16	10.30
	Area	0.9326	0.6779	-0.4151	2.2802
	Age	-0.02291	0.01864	-0.05995	0.01414
	Connectivity	0.1307	0.3084	-0.4824	0.7438
	Graminoid	0.1215	0.0523	0.0175	0.2256
	Litter	-0.05634	0.01893	-0.09397	-0.01872
	Robel	-2.27212	1.09011	-4.43918	-0.10507
	Slope	-2.22166	0.89868	-4.00819	-0.43514