

# Rangeland dynamics: Investigating vegetation composition and structure of urban and exurban prairie dog habitat

Rebecca Hopson, Paul J. Meiman, Graeme Shannon

Rapid human population growth and habitat modification in the western United States has led to the formation of urban and exurban rangelands. Many of these rangelands are also home to populations of black-tailed prairie dogs (*Cynomys ludovicianus*). Our study aimed to compare the vegetation composition of an urban and exurban rangeland, and explore the role that prairie dogs play in these systems. The percent absolute canopy cover of graminoids (grasses and grass-like), forbs, shrubs, litter, and bare ground were estimated at sampling areas located on and off prairie dog colonies at an urban and an exurban site. Herbaceous forage quality and quantity were determined on plant material collected from exclosure cages located on the colony during the entire growing season. A relative estimate of prairie dog density was calculated using maximum counts. The exurban site had more litter and plant cover and less bare ground than the urban site. Graminoids were the dominant vegetation at the exurban plots. In contrast, mostly introduced forbs were found on the urban prairie dog colony. However, the forage quality and quantity tests demonstrated no difference between the two colonies. The relative prairie dog density was greater at the urban colony, which has the potential to drive greater vegetation utilization and reduced cover. Exurban rangeland showed lower levels of impact, fewer introduced species, and retained all of the plant functional groups both on- and off-colony. These results suggest that activities of prairie dogs might further exacerbate impacts of humans in fragmented urban rangeland habitats. Greater understanding of the drivers of these impacts and the spatial scales at which they occur are likely to prove valuable in the management and conservation of rangelands in and around urban areas.

**1 Rangeland dynamics: Investigating vegetation composition and structure of**  
**2 urban and exurban prairie dog habitat**

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19 **Abstract**

Rapid human population growth and habitat modification in the western United States has led to the formation of urban and exurban rangelands. Many of these rangelands are also home to populations of black-tailed prairie dogs (*Cynomys ludovicianus*). Our study aimed to compare the vegetation composition of an urban and exurban rangeland, and explore the role that prairie dogs play in these systems. The percent absolute canopy cover of graminoids (grasses and grass-like), forbs, shrubs, litter, and bare ground were estimated at sampling areas located on and off prairie dog colonies at an urban and an exurban site. Herbaceous forage quality and quantity were determined on plant material collected from exclosure cages located on the colony during the entire growing season. A relative estimate of prairie dog density was calculated using maximum counts. The exurban site had more litter and plant cover and less bare ground than the urban site. Graminoids were the dominant vegetation at the exurban plots. In contrast, mostly introduced forbs were found on the urban prairie dog colony. However, the forage quality and quantity tests demonstrated no difference between the two colonies. The relative prairie dog density was greater at the urban colony, which has the potential to drive greater vegetation utilization and reduced cover. Exurban rangeland showed lower levels of impact, fewer introduced species, and retained all of the plant functional groups both on- and off-colony. These results suggest that activities of prairie dogs might further exacerbate impacts of humans in fragmented urban rangeland habitats. Greater understanding of the drivers of these impacts and the spatial scales at which they occur are likely to prove valuable in the management and conservation of rangelands in and around urban areas.

## Introduction

The North American Great Plains region is a large dynamic ecosystem that is inhabited by a diverse variety of plants and animals, which have generated a heterogeneous landscape made up

of three major prairie types - shortgrass, mixed, and tallgrass (Lauenroth, Burke & Gutmann 1999). Since European settlement rapidly expanded west during the mid-1800s, large portions of the Great Plains ecosystem have undergone dramatic transformation as a function of human population growth driving agricultural and urban development (Samson & Knopf 1994). These habitats continue to face increasing anthropogenic pressure, with the metropolitan areas of the western United States currently experiencing the greatest rate of growth in the country (Maestas, Knight & Gilgert 2003), forcing many of those cities to further develop open spaces within their city limits. Moreover, increased income, mobility and desirability for rural living has led to the conversion of farm and ranch lands to low-density exurban (rural residential) development (Maestas *et al.* 2003). For example, exurban population growth for the state of Montana from 1980 to 2000 was estimated to be 143% (Theobald 2005).

Rangelands (including prairies) provide a wide range of ecosystem goods and services, which are strongly influenced by the structure, and dynamics of the vegetation (Havstad *et al.* 2007). Often, vegetation structure and dynamics are described using plant functional groups (i.e. plants with morphological and perhaps physiological similarities; Pokorny *et al.* 2005, Peters *et al.* 2006). Remaining prairie habitats located within the boundaries of urban areas and among exurban development face potentially negative impacts associated with land use change and human population growth in surrounding areas. In addition to direct habitat loss and fragmentation, the native plant communities of these habitats can be substantially altered as a result of non-native plant species being introduced (Mack *et al.* 2000). These introductions also contribute to a loss of biodiversity within the rangelands as a result of native species facing competitive exclusion (Maestas *et al.* 2003). These impacts can also extend up the food web, degrading habitat and forage quality for a variety of native wildlife species. One such species that is experiencing severe pressure from development and anthropogenic disturbance is the black-tailed prairie dog (*Cynomys ludovicianus*), which has faced widespread decline across its historic range (Miller, Ceballos & Reading 1994). The decline has been driven by habitat loss, poisoning programs and disease outbreaks (Miller *et al.* 2007). Remaining prairie dog colonies commonly occur in isolated pockets scattered throughout their original range with many of the more dense colonies found in exurban areas surrounding western cities (Armstrong, Fitzgerald & Meaney 2011).

Black-tailed prairie dogs (referred to herein as prairie dogs) are herbivorous, consuming a wide range of available plant material from grasses to prickly pear cactus (Hoogland 1995). They are considered to be keystone species and ecosystem engineers because of their ability to alter the landscape and generate refuges and foraging opportunities for an array of species (Whicker & Detling 1988; Kotliar et al. 2006). For example, in a functional prairie ecosystem, the foraging and burrowing behavior of prairie dogs has been demonstrated to increase biotic diversity (Augustine & Baker 2013) and influence community structure (Van Nimwegen, Kretzer & Cully 2008) in close proximity to the colony, while also playing an important role in ecosystem function (Martinez-Estévez *et al.* 2013). Nevertheless, prairie dogs are also politically controversial. In agricultural areas, prairie dogs are considered to compete directly with livestock for available forage (Vermeire *et al.* 2004; Derner, Detling & Antolin 2006), while colonies in fragmented urban habitats have the potential to negatively impact the ecosystem (e.g. loss of native species, soils and litter) due to elevated densities and restricted movement (Beals *et al.* 2014). There are also public health concerns surrounding the transmission of zoonotic diseases such as the plague (Lowell *et al.* 2005). A number of contentious population control measures have therefore been put in place to reduce prairie dog numbers in areas where they are considered to be a nuisance (Hoogland 1995).

The aim of our study was to compare the vegetation of black-tailed prairie dog habitat between an urban and an exurban rangeland, to explore whether the associated difference in human disturbance may lead to differences in vegetation abundance and composition on and off prairie dog colonies. The predictions were: 1) The presence of a prairie dog colony would reduce the abundance of vegetation and litter and increase the amount of bare ground at both sites, as a function of prairie dog foraging behavior and burrowing activity. 2) The exurban site would support a greater abundance of graminoids (grasses and grass-like plants) and forbs, and have greater quantities of litter and less bare ground than urban site, due to less human disturbance enabling prairie dog foraging and burrowing to be distributed over a larger area at the exurban site. 3) The urban site would have lower native plant cover due to a greater probability of non-native plant species being introduced from nearby developments. 4) The quantity and quality of forage at the exurban prairie dog colony would be greater than at the urban prairie dog colony. 5) Prairie dog density would be greater at the urban colony compared with the exurban colony due

103 to the limited available range and lack of habitat connectivity for animals to disperse to nearby  
104 rangelands.

## 105 **Methods**

### 106 *Study Sites*

107 The research was conducted in Fort Collins, Colorado from June – August 2013. Two rangeland  
108 study sites (urban and exurban) were selected according to their location relative to the city,  
109 proximity to infrastructure and in conjunction with the definitions of urban and exurban  
110 developments given in Theobald (2005). Colina Mariposa Natural Area was chosen as the urban  
111 site, this rangeland is located in southwestern Fort Collins at the intersection of two busy roads,  
112 with urban neighborhoods on the eastern and western borders (Fig.1). A railroad track bisects the  
113 natural area, with the prairie dog colony predominantly located on the east side of the tracks.  
114 Pineridge Natural Area was selected as the exurban site, being located on the western edge of  
115 Fort Collins in a public open lands district (Fig. 1). It has a reservoir on the northern side, a road  
116 to the northwest, while the western boundary is predominantly natural habitat with sparse houses.  
117 The southern edge and part of the southeastern side adjoins more open space and a community  
118 park, while a small section of the eastern border consists of low-density housing. Both sites were  
119 further evaluated to ensure that they had similar topographical characteristics, represented similar  
120 rangeland ecological sites and that there was sufficient area to collect data on vegetation  
121 abundance and composition, both on and off prairie dog colonies. Fort Collins Natural Areas  
122 provided us with a research permit (#: 296-2012) that stipulated their approval of the proposed  
123 study and the conditions under which we could conduct the work.

124 The vegetation composition varied across the sampling areas (Table 1). Overall, forbs were more  
125 common on-colony and graminoids were more common off-colony. The only species that was  
126 common to multiple sampling areas was western wheatgrass (*Elymus smithii* (Rydb.) Gould). The  
127 species observed on- and off-colony at the urban site were different and there was no overlap in  
128 dominants. There was more similarity in the vegetation on- and off-colony at the exurban site  
129 with two common dominant species; western wheatgrass and Japanese brome (*Bromus japonicus*  
130 Thunb.). There were more introduced species observed at the exurban site than at the urban site.

131 *Data collection*

132 Data were collected on and off of the prairie dog colonies at each of the two study sites. On-  
 133 colony sampling was conducted by locating the approximate center of the colony using prairie  
 134 dog burrow distribution and animal density as indicators. Once the center point was identified, a  
 135 thirty-five meter transect was positioned across the colony, with the center point of the transect  
 136 corresponding to the center of the colony. Two more thirty-five meter transects were established;  
 137 one on each side of the central transect, running parallel and separated by a distance of 15 meters.  
 138 Selection of the off-colony sampling areas was dependent on the absence of burrows and a  
 139 minimum buffer of 20 meters from the nearest observed evidence of prairie dog activity (e.g.  
 140 burrow, trail). Once a suitable area was demarcated, three thirty-five meter transects were laid out  
 141 following the same approach used for the on-colony plots. The methods described above to locate  
 142 transects in the sampling areas resulted in thorough coverage of the prairie dog colonies and  
 143 similar sized neighboring off-colony areas. The data used in the analyses are available in the  
 144 Supplemental Information (Spreadsheet S1).

145 *Cover Estimates*

146 Canopy cover and vegetation composition were determined using an extended Daubenmire frame  
 147 (see Bonham, Mergen & Montoya 2004) placed every 5 meters along each transect for a total of  
 148 7 x 0.5 m<sup>2</sup> frame locations (subsamples) along each transect (transect = observation). Canopy  
 149 cover was estimated once each month during the summer (June – August) to track changes in  
 150 vegetation composition through time. The three data collection periods were classified as early  
 151 summer (June), peak standing crop (July) and late summer (August). Cover was categorized into  
 152 four distinct functional groups: 1) graminoids, 2) forbs, 3) litter, and 4) bare ground. In mid-July,  
 153 the graminoid and forb functional groups were further subdivided according to their duration  
 154 (perennial or annual), origin (native or introduced), and growing season (cool or warm). The mid-  
 155 July sampling was assumed to represent peak standing crop and data were collected in the same  
 156 manner as described above. The graminoids group was subdivided into perennial native cool  
 157 season, perennial native warm season, annual native cool season, perennial introduced cool  
 158 season, and annual introduced cool season graminoids. The forbs group was subdivided into  
 159 perennial native, annual native, biennial native, perennial introduced, annual introduced, and  
 160 biennial introduced forbs.

### Forage Quality and Quantity

The quality and quantity of forage available to the prairie dogs on the colony was estimated from three exclosure cages (dimensions: 30 x 60 x 75 cm) made out of 0.5cm x 0.5cm hardware cloth over wire panels placed on each colony (urban and exurban). The exclosure cages were positioned 15m apart on a line that ran through the center of the sampling area perpendicular to the transects, with the first cage located at the mid-point between transects 1&2. In August, all herbaceous material in each cage was clipped to ground level, bagged and placed in drying ovens at 55°C for one week. The dried material was weighed and then sent for laboratory analysis (Servi-Tech Laboratories, Hastings, Nebraska) to determine the percentage of total digestible nutrients, crude protein, acid detergent fiber, neutral detergent fiber, and a relative feed value index (see Table2).

### Maximum prairie dog counts

A relative measure of prairie dog density was determined using aboveground counts of animals in a demarcated sampling area (100 m<sup>2</sup>). Five repeat counts were performed at each site from the same observation point, which was approximately 150 meters away from the marked area. The data were collected from August 15 to August 31, with a minimum of 24h between repeat counts. The counts were conducted between 7:00am and 11:00am and lasted for 90 minutes with the total number of aboveground animals within the marked observation area recorded every 10 minutes. A standardized settling time of 30 minutes was initiated prior to data collection, allowing the prairie dogs sufficient time to return to their normal behavior after the disturbance of the observer's arrival (Shannon *et al.* 2014). The maximum number of animals observed across the 10 observations per count period was selected, generating five independent measures of relative density at each site following the approach of Menkens & Biggins (1990). Wet overcast weather resulted in the fifth count from the urban site being dropped from the analysis due to unusually low prairie dog activity (max count = ~5 individuals). As the study involved minimally invasive vegetation sampling and behavioral observation, an institutional review of the research was not required.

### Data Analysis



Cover data for each functional group were analyzed using a mixed modeling procedure and repeated measures analysis (season) to test for the effects of site, presence or absence of a prairie dog colony, season, and all possible interactions. Peak standing crop cover data were analyzed separately to test for the effects of site, presence or absence of a prairie dog colony, and all possible interactions. The data were analyzed using analysis of variance in SAS 9.3 (PROC mixed SAS Institute, Cary, NC, USA) to determine effects of site, presence or absence of prairie dog colony and all possible interactions. Where F-tests identified significant effects, the means were separated using Fisher's LSD Alpha = 0.05. Data were transformed prior to analysis by calculating the arc-sine square root of the original data to meet assumptions of the analysis. T-tests were used to analyze the peak standing crop data, forage quality and quantity, and the population density indicator estimates. As the study design involved data collected from two sites, it was not possible to replicate the urban versus exurban comparison in our analyses. All data presented are original scale. A complete table of results from the repeated measures analysis is provided in the Supplemental Information (Table S1).

## Results

### *Cover By Functional Groups*

Cover values for the plant functional groups, litter and bare ground were not affected by season ( $F=0.15-2.54$ ,  $P=0.100-0.863$ ), the season by site interaction ( $F=0.04-1.37$ ,  $P=0.272-0.96$ ), the season by colony interaction ( $F=0.16-3.34$ ,  $P=0.053-0.855$ ), or the interaction of all three factors ( $F=0.26-2.47$ ,  $P=0.106-0.7706$ ).

Absolute litter cover was greater at the exurban site than at the urban site ( $F=21.06$ ,  $P<0.001$ ) and also greater off-colony than on-colony ( $F=9.11$ ,  $P=0.006$ ; Fig. 2). The effect of colony on litter cover was not affected by site ( $F=3.07$ ,  $P=0.093$ ). The overall percentage of bare ground was greater at the urban site compared to the exurban site ( $F=48.37$ ,  $P<0.001$ ; Fig. 3). There was also more bare ground observed on-colony plots compared to off-colony ( $F=47.39$ ,  $P<0.001$ ; Fig. 3). The effect of colony on cover of bare ground was not affected by site ( $F=2.33$ ,  $P=0.140$ ).

216 Absolute cover of graminoids was affected by site ( $F = 94.64$ ,  $P < 0.001$ ), presence of a prairie  
 217 dog colony ( $F = 135.72$ ,  $P < 0.001$ ), and the two factors simultaneously ( $F = 15.46$ ,  $P < 0.0001$ ).  
 218 The absolute cover of graminoids ranged from 46% off-colony at the exurban site to 0% on-  
 219 colony at the urban site, while cover values off-colony at the urban site and on-colony at the  
 220 exurban site were similar and around 25% (Fig. 4).

221 Forb cover was not affected by site ( $F = 3.39$ ,  $P = 0.078$ ), but was affected by the presence of a  
 222 prairie dog colony ( $F = 63.04$ ,  $P < 0.001$ ), and the two factors simultaneously ( $F = 26.03$ ,  
 223  $P < 0.001$ ). Absolute forb cover was greatest (40%) on-colony at the urban site and least (5%) off-  
 224 colony at the urban site (Fig. 5). Absolute cover values of forbs on- and off-colony at the exurban  
 225 site were similar to one another (18% and 11% respectively), less than the value at the on-colony  
 226 urban site and greater than the value at the off-colony urban site (Fig. 5).

#### 227 *Cover at Peak Standing Crop*

228 Perennial native warm season graminoids were not affected by site ( $F = 0.79$ ,  $P = 0.399$ ), but had  
 229 lower cover values on prairie dog colonies compared to off ( $F = 15.43$ ,  $P = 0.004$ ). The interaction  
 230 between colony and site was not significant ( $F = 0.11$ ,  $P = 0.7525$ ). Cover of perennial native cool  
 231 season graminoids was affected by a significant interaction between site and presence of a prairie  
 232 dog colony ( $F = 51.90$ ,  $P < 0.001$ ; Fig. 6), a result that was driven by the fact that no graminoids  
 233 were observed throughout the entire growing season on-colony at the urban site (see Fig. 4).  
 234 However, there were no differences in the abundance of perennial native cool season graminoids  
 235 among the other sampling areas (Fig. 6).

236 Annual introduced cool season graminoids were only found at the exurban site ( $F = 10.32$ ,  $P$   
 237  $= 0.012$ ), while the presence of a prairie dog colony did not affect cover ( $F = 0.01$ ,  $P = 0.909$ ) nor  
 238 did the two factors interact ( $F = 0.2511$ ,  $P = 0.6298$ ). Perennial introduced cool season  
 239 graminoids were affected by the two-way interaction between site and colony ( $F = 131.29$ ,  $P$   
 240  $< 0.001$ ; Fig. 6). The greatest percent cover by perennial introduced cool season graminoids was  
 241 observed off-colony at the exurban site (31%), which was mostly *Poa pratensis* L. (see Table 1).

At all of the other plots, there was little to no perennial introduced cool season graminoid cover (Fig. 6).

Perennial native forb species cover did not vary significantly by site ( $F = 3.47$ ,  $P = 0.10$ ) or the presence or absence of a prairie dog colony ( $F = 1.01$ ,  $P = 0.344$ ). The interaction between site and colony was also non-significant ( $F = 0.39$ ,  $P = 0.549$ ). Biennial native forbs were only observed off-colony at the urban site.

The abundance of annual native forbs was significantly greater on-colony at the urban site compared with all of the other areas, resulting in a significant two-way interaction between site and presence or absence of a prairie dog colony ( $F = 16.80$ ,  $P = 0.003$ ; Fig. 7). Annual native forbs accounted for 13% cover on-colony at the urban site, reflecting the abundance of two of the three dominant species (see Table 1).

Absolute (%) cover of perennial introduced forbs was not affected by site ( $F = 0.49$ ,  $P = 0.502$ ) but was affected by the presence of a prairie dog colony ( $F = 34.73$ ,  $P = 0.001$ ). The interaction between site and colony was also significant ( $F = 11.40$ ,  $P = 0.01$ ) (Fig. 7). The greatest percent cover by perennial introduced forbs (27%) occurred on-colony at the urban site while cover of this functional group on-colony at the exurban site and off-colony at the urban site were similar. Perennial introduced forb canopy cover was least off-colony at the exurban site. These results reflect the dominance of field bindweed (*Convolvulus arvensis* L.) at three of the four sampled areas (see Table 1). Cover of annual introduced forbs and biennial introduced forbs accounted for  $\leq 1\%$  across the study areas and therefore values were too small to detect meaningful differences across either site or in the presence or absence of a prairie dog colony.

#### *On-Colony Forage*

The forage testing analysis and data gathered from weighing the dried biomass revealed no significance differences between sites for the six measures of forage quality and quantity (see Table 2).

#### *Prairie Dog Density Estimate*

The prairie dog population observations taken from each colony indicated that the relative measures of prairie dog densities differed significantly between the exurban and urban colonies ( $F=10.20$ ,  $P=0.02$ ). The mean relative density of prairie dogs at the exurban colony was  $14 (\pm 2 \text{ SE})$  individuals per hectare, while the density at the urban colony was  $19 (\pm 3 \text{ SE})$  individuals per hectare. The dataset comprised nine separate counts, so caution is required with the interpretation of the results.

## Discussion

Our results demonstrated marked differences in vegetation composition between the exurban and urban rangeland sites studied, as well as between areas sampled on and off of a prairie dog colony. The exurban site had more live plant cover and less bare ground compared with the urban site, and the vegetation composition was similar between sampling areas, with the off-colony vegetation predominately comprised of graminoids with fewer forbs, while the on-colony vegetation was a more even mixture of graminoids and forbs. The vegetation composition off-colony at the urban site was a mixture of mostly graminoids with some forbs, while on-colony vegetation was comprised of only forbs with field bindweed the most abundant species, concurring with recent research on prairie dogs in urban habitats (Magle & Crooks 2008; Beals *et al.* 2014). The abundance of bindweed at the urban site is a common feature of disturbed urban and exurban rangeland systems (Whitson *et al.* 1998). Indeed, the success of this plant in colonizing highly disturbed areas suggests that the foraging and burrowing activities of prairie dogs on the urban colony is enabling its propagation (Magle & Crooks 2008; Beals *et al.* 2014). It is important to note at the outset that our study involves the comparison of two distinct rangeland sites, and while these were chosen for their contrasting locations with regard to urban infrastructure and human disturbance, we acknowledge that the lack of site replication limits the inference of our results.

The on-colony data also indicates that prairie dog activity drives the occurrence of bare ground, however this effect is more pronounced at the urban site. Besides initiating changes in the amount of bare ground, the prairie dog colonies also changed the vegetation structure by decreasing the abundance of graminoids, while increasing forb abundance observed in the community (see also Magle & Crooks 2008; Beals *et al.* 2014). These changes in vegetation structure have also been

documented in natural prairie dog habitat and underpin the ecosystem-engineering role of the species (Whicker & Detling 1988; Baker *et al.* 2013). However if the optimal level of disturbance is exceeded, over grazing can occur, which has the potential to amplify negative ecological impacts, particularly in prairie habitats that are already impacted by human disturbance (Beals *et al.* 2014). Furthermore, exurban and urban systems are also susceptible to the introduction of non-native species due to their fragmented state and proximity to human activity (Magle *et al.* 2010). There was at least one introduced dominant plant species at all plots, with the exception of the urban off-colony plot where interestingly all four dominants were native. The introduced species varied according to plot, species, and growth form; with field bindweed the most commonly observed introduced forb at both on-colony plots. Non-native species are likely to vary in terms of their impacts on prairie habitat, with many species being relatively benign. Bindweed, however, has the potential to be a pervasive weed that can spread rapidly due to the root system being capable of vegetative reproduction, while the plant produces large numbers of long-lived seeds (Jacobs 2007). This can result in vast, dense and tangled vine mats that outcompete and ultimately exclude native plant species, particularly in altered or disturbed habitats (Jacobs 2007).

Interestingly there was no evidence of a significant difference in forage quality or quantity between the urban and exurban site. The abundance of field bindweed at the urban on-colony site is likely to generate significant plant biomass and relatively high values for many of the forage quality measures, rivaling that of the exurban site. Nevertheless, bindweed contains tropane; a potentially toxic alkaloid that led to high levels of mortality in mice that were fed concentrated diets of bindweed (Schultheiss *et al.* 1995). These findings demonstrate that secondary compounds are also crucial when assessing forage quality. Moreover, a greater sample size, and determinations of forage quality at multiple times throughout the growing season would need to be collected to increase the accuracy of the analysis on forage quality before firm conclusions can be drawn.

The exurban population density indicator estimated fewer prairie dogs per hectare than at the urban site, which along with the greater size of the exurban site may result in an intermediate disturbance regime, enabling the retention of their role as ecosystem engineers. Indeed the

disturbance from prairie dogs foraging and burrowing at the larger exurban site is distributed over a greater area, so impact on vegetation is lessened and allows for greater recovery periods for many of the native plants. Whereas elevated densities and reduced dispersal typical of fragmented and disturbed habitats (Johnson & Collinge 2004; Magle *et al.* 2008) can ultimately lead to overgrazing and a loss in vegetation cover, diversity and richness (Beals *et al.* 2014). However, it is worth noting that relative aboveground prairie dog densities of 5 individuals per hectare were documented at an undisturbed colony 40km from Fort Collins (Shannon *et al.* 2014), significantly lower than those measured at either of the colonies used in this study. In addition to the elevated prairie dog densities that can impact native vegetation cover and species persistence, habitat fragmentation and human disturbance has the potential to affect prairie dog fitness by altering behavior at both the urban and exurban study sites. The close proximity to human disturbances can increase the amount of time prairie dogs spend vigilant while foraging for food (Ramirez & Keller 2010; Shannon *et al.* 2014).

Native annual forbs and perennial native cool season graminoids are absent on-colony at the urban site. Instead, the on-colony sampling area at the urban site was dominated by field bindweed. These results suggest that the presence of prairie dogs is contributing to the relatively disturbed state of the vegetation, which is further compounded by site history, the proximity of the site to agricultural fields and a suburban neighborhood (Beals *et al.* 2014). However, the dominant species on-colony at the exurban site represented three functional groups compared with only two functional groups at the on-colony urban site, which is consistent with the suggestion that the presence of a prairie dog colony can increase the heterogeneity and biotic diversity in more natural prairie habitats (Coppock *et al.* 1983; Whicker & Detling 1988; Kotliar *et al.* 2006; Baker *et al.* 2013). Our findings indicate that the exurban site may have retained a number of its functions as a grassland ecosystem. For example, the only native dominant plant species of the four observed at the exurban sites is western wheatgrass, a cool season grass that has adapted to a grazing disturbance dynamic. Nonetheless, it is important to note that unlike the study of the protected area (Coppock *et al.* 1983), the other three of the four dominant species at the exurban colony were introduced species (see Table 1). Furthermore, the relationship between the diversity of forb and graminoid species at the exurban site also remained significantly lower than that of the protected natural prairie in Wind Cave National Park (Coppock *et al.* 1983). The

356 urban colony dominant species were made up of three forb species and included one introduced  
357 with two native species.

358 The results we present are from a comparison of two sites and the limitations on inference could  
359 be greatly improved by conducting a larger scale study that selected multiple urban and exurban  
360 field sites. Such an approach would provide more data and valuable replicates to aid in  
361 establishing concrete patterns in the effects of urbanization on habitat fragmentation and the role  
362 that prairie dogs play in these altered rangeland systems. Nevertheless, our study demonstrated a  
363 marked difference in vegetation composition and habitat disturbance between an exurban and  
364 urban rangeland with prairie dogs present. The exurban site retained greater litter cover and less  
365 bare ground than the urban site, greater abundance of native cool season graminoids on-colony,  
366 while the most abundant plant on-colony at the urban site was an introduced, invasive forb.  
367 Habitat disturbance and fragmentation also have implications for prairie dogs, which face a  
368 greater risk of extinction, loss of immigration and emigration routes, and reduction in genetic  
369 variability. Although prairie dog colonies provide a suite of ecosystem services such as improved  
370 quality of forage on their colonies for other herbivores, increased turnover of soil nutrients, and  
371 decreased soil compaction (Martinez-Estévez *et al.* 2013), these processes may well be  
372 compromised in disturbed and fragmented rangeland habitats. A situation that can result in prairie  
373 dog colonies exacerbating the impacts associated with human disturbance and environmental  
374 change (Beals *et al.* 2014). Based on our initial results, we recommend that the scale-dependent  
375 interactions between prairie dogs and vegetation composition be further researched, particularly  
376 with regard to their keystone role (see also Lomolino & Smith 2003; Magle & Crooks 2008;  
377 Beals *et al.* 2014). Indeed, a greater understanding of these factors will aid effective conservation  
378 and management of prairie dog habitats and the integrity of U.S. rangelands, particularly in the  
379 face of expanding urban growth.

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**Table 1** (on next page)

Dominant species based on observations along transects established in each sampling area (urban and exurban sites both on and off the prairie dog colonies).

Dominant species were considered as those, which occurred in 9 or more of 21, 0.5m<sup>2</sup> quadrats in each sampling area.

Sampling Area	Species	Common Name	Growth Form	Duration	Growing Season	Origin
Urban Off-Colony	<i>Elymus smithii</i> (Rydb.) Gould	western wheatgrass	grass	perennial	cool	native
	<i>Hesperostipa comata</i> (Trin. & Rupr.) Barkworth	needle and thread	grass	perennial	cool	native
	<i>Carex filifolia</i> Nutt.	threadleaf sedge	grass-like	perennial	cool	native
	<i>Eriogonum annuum</i> Nutt.	annual buckwheat	forb	biennial	cool	native
	<i>Artemisia dracuncululus</i> L.	tarragon	shrub	perennial	warm	native
Urban On-Colony	<i>Convolvulus arvensis</i> L.	field bindweed	forb	perennial	cool	introduced
	<i>Chenopodium incanum</i> (S. Watson) A. Heller	mealy goosefoot	forb	annual	warm	native
	<i>Dyssodia papposa</i> (Vent.) Hitchc.	fetid marigold	forb	annual	warm	native
Exurban Off-Colony	<i>Elymus smithii</i> (Rydb.) Gould	western wheatgrass	grass	perennial	cool	native
	<i>Poa pratensis</i> L.	Kentucky bluegrass	grass	perennial	cool	introduced
	<i>Bromus japonicus</i> Thunb.	Japanese Brome	grass	annual	cool	introduced
	<i>Psoraleidum tenuiflorum</i> (Pursh) Rdydb.	slimflower scurfpea	forb	perennial	warm	native
Exurban On-Colony	<i>Elymus smithii</i> (Rydb.) Gould	western wheatgrass	grass	perennial	cool	native
	<i>Bromus japonicus</i> Thunb.	Japanese Brome	grass	annual	cool	introduced
	<i>Convolvulus arvensis</i> L.	field bindweed	forb	perennial	cool	introduced
	<i>Linaria dalmatica</i> (L.) Mill.	dalmation toadflax	forb	perennial	cool	introduced

**Table 2**(on next page)

A comparison of forage quantity and quality using ANOVA.

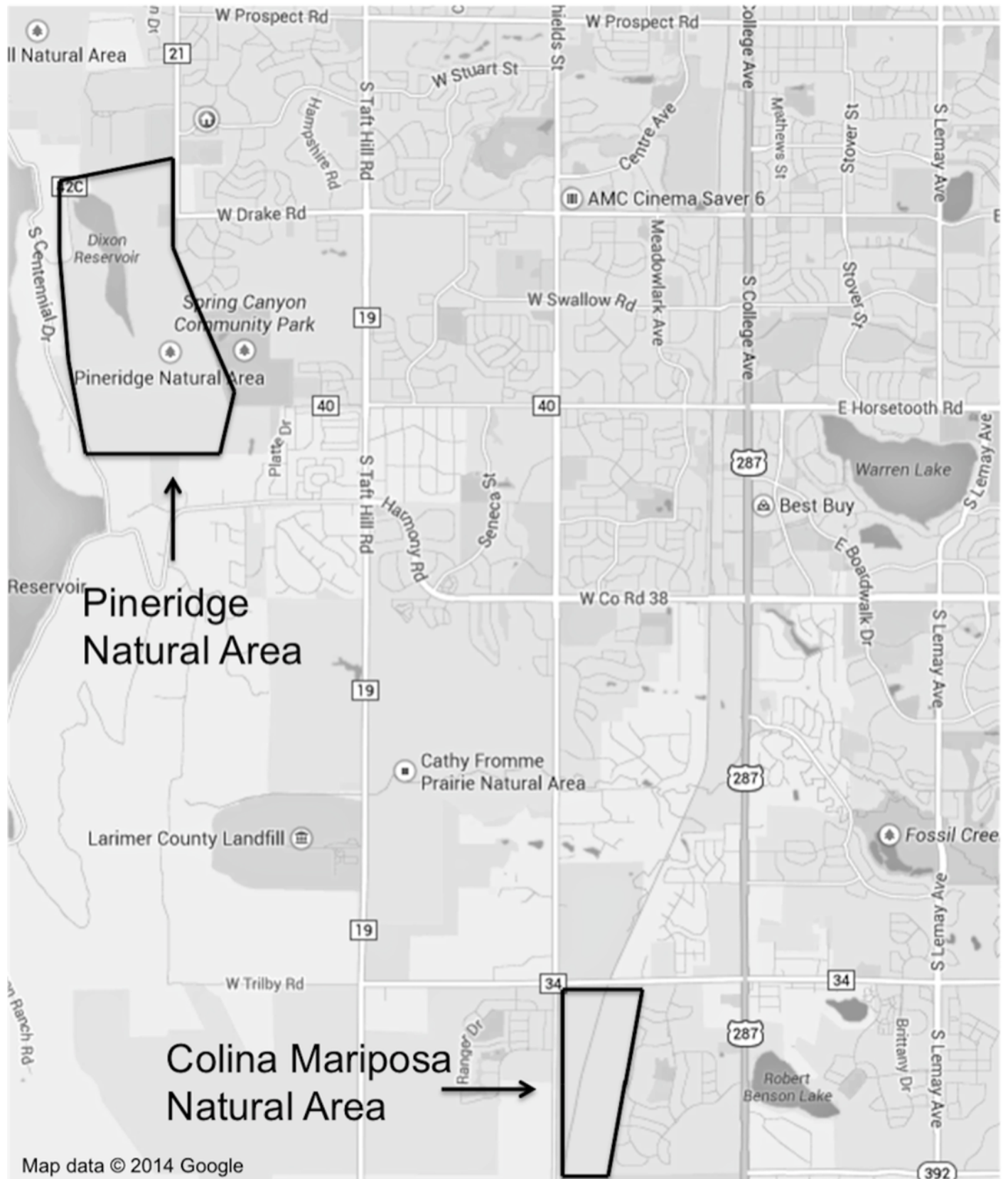
Data were collected in August from the three exclosure cages located on both Exurban and Urban prairie dog colonies (see methods).

<b>Feed Test Results</b>	<b>Urban (mean)</b>	<b>Exurban (mean)</b>	<b>T-statistic</b>	<b>P-value</b>
Biomass (grams/m <sup>2</sup> )	139.72	174.33	-0.520	0.642
Digestible nutrients (%)	63.0	64.5	-0.334	0.755
Crude Protein (%)	11.53	9.40	1.250	0.320
Acid Detergent Fiber (%)	35.40	34.07	0.336	0.755
Neutral Detergent Fiber (%)	45.20	56.23	-2.431	0.075
Relative Feed Value	127.67	104.33	1.497	0.213

# 1

A map of Fort Collins with the locations and extent of the two study sites outlined.

The latitude and longitude are given below for the center point of the Pineridge Natural Area transects (on-colony: 40.542850, -105.139589 and off-colony: 40.544677, -105.141220) and the Colina Mariposa Natural Area transects (on-colony: 40.483427, -105.093809 and off-colony: 40.485108, -105.091277).

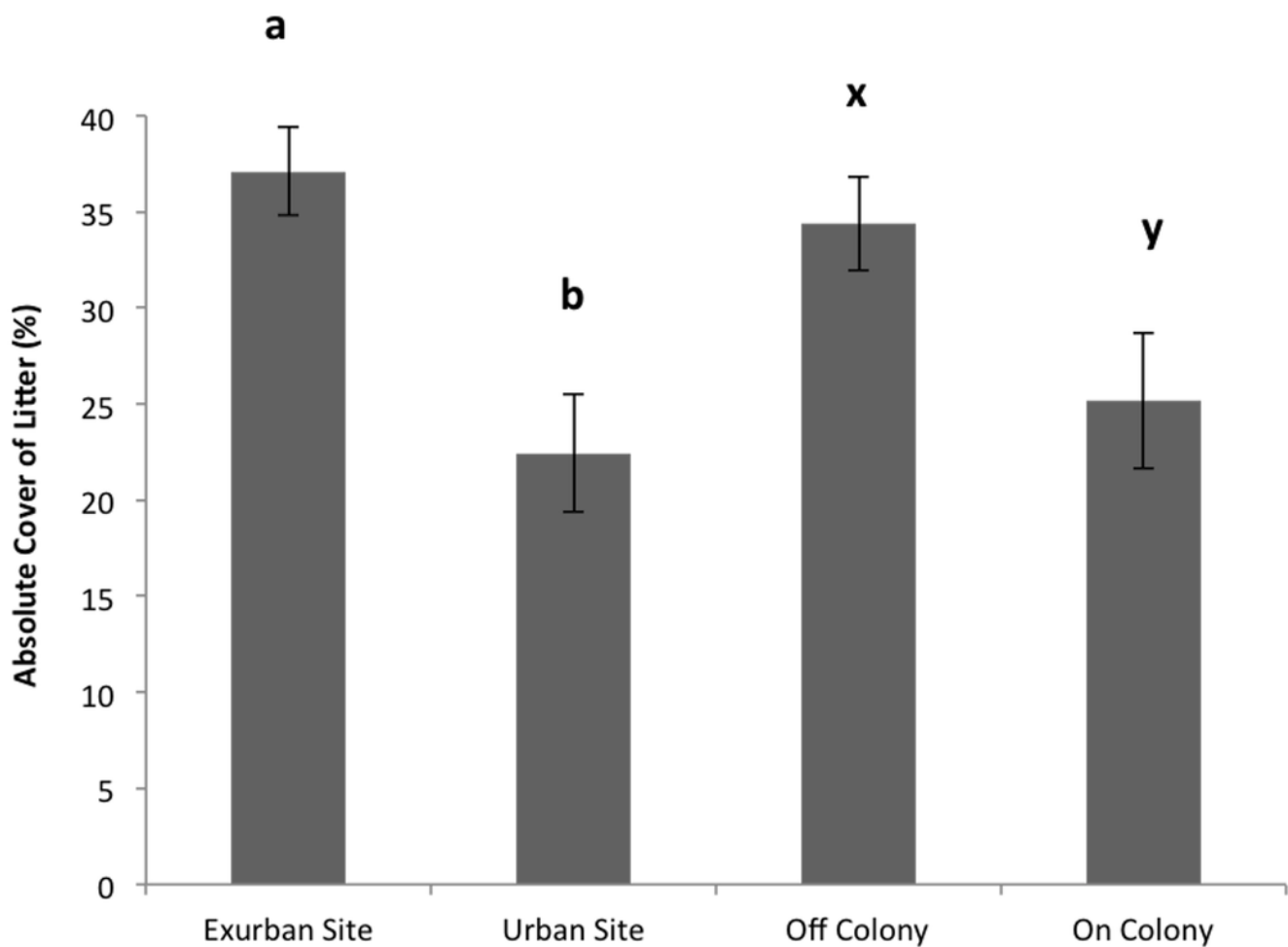




## 2

Absolute cover of litter observed from June-August at the urban and exurban sites both on and off the prairie dog colonies.

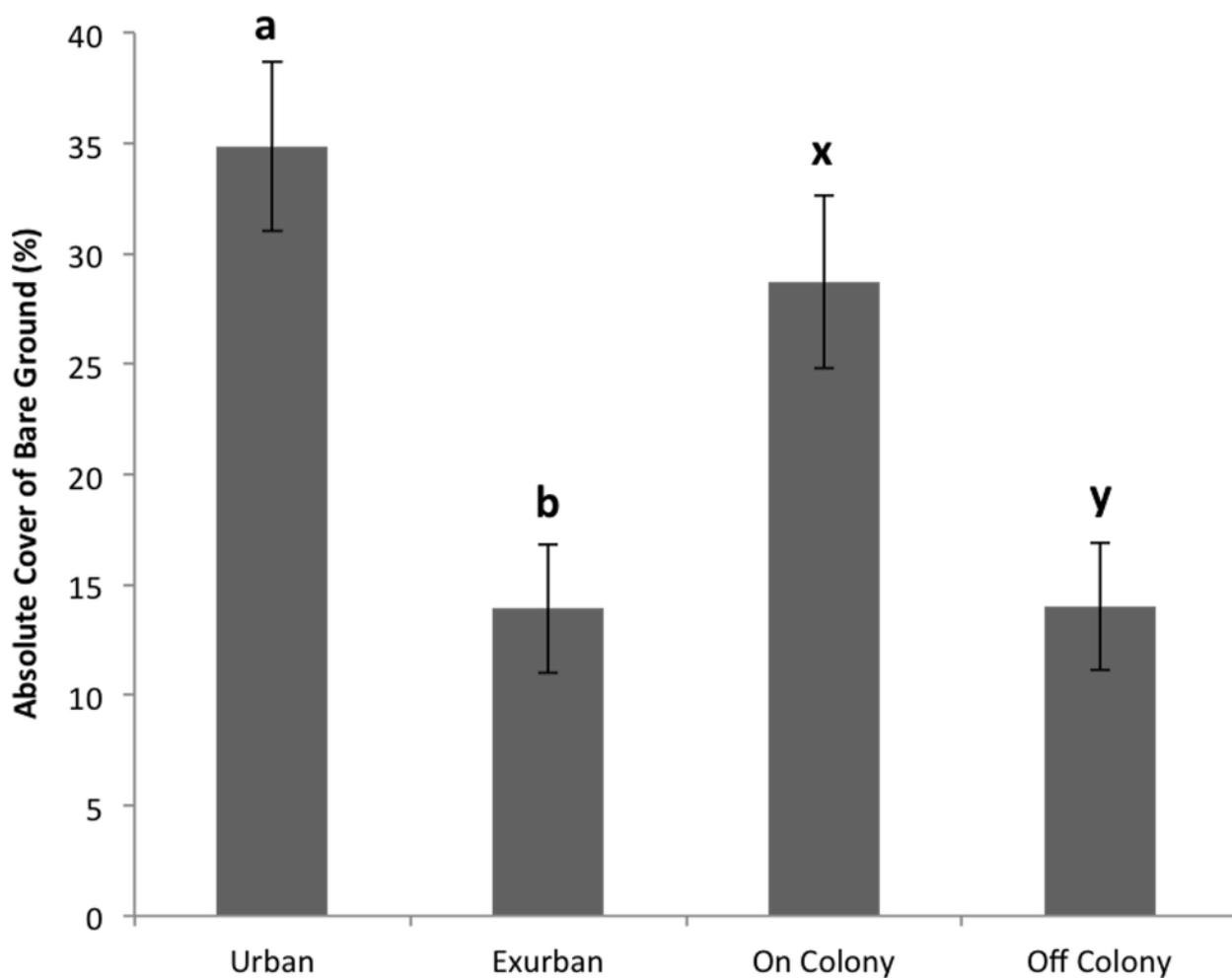
Means with the same letter (a-b for site and x-y for colony) are not significantly different, Fishers LSD  $\alpha=0.05$ .



### 3

Absolute cover of bare ground observed from June-August at the urban and exurban sites both on and off the prairie dog colonies.

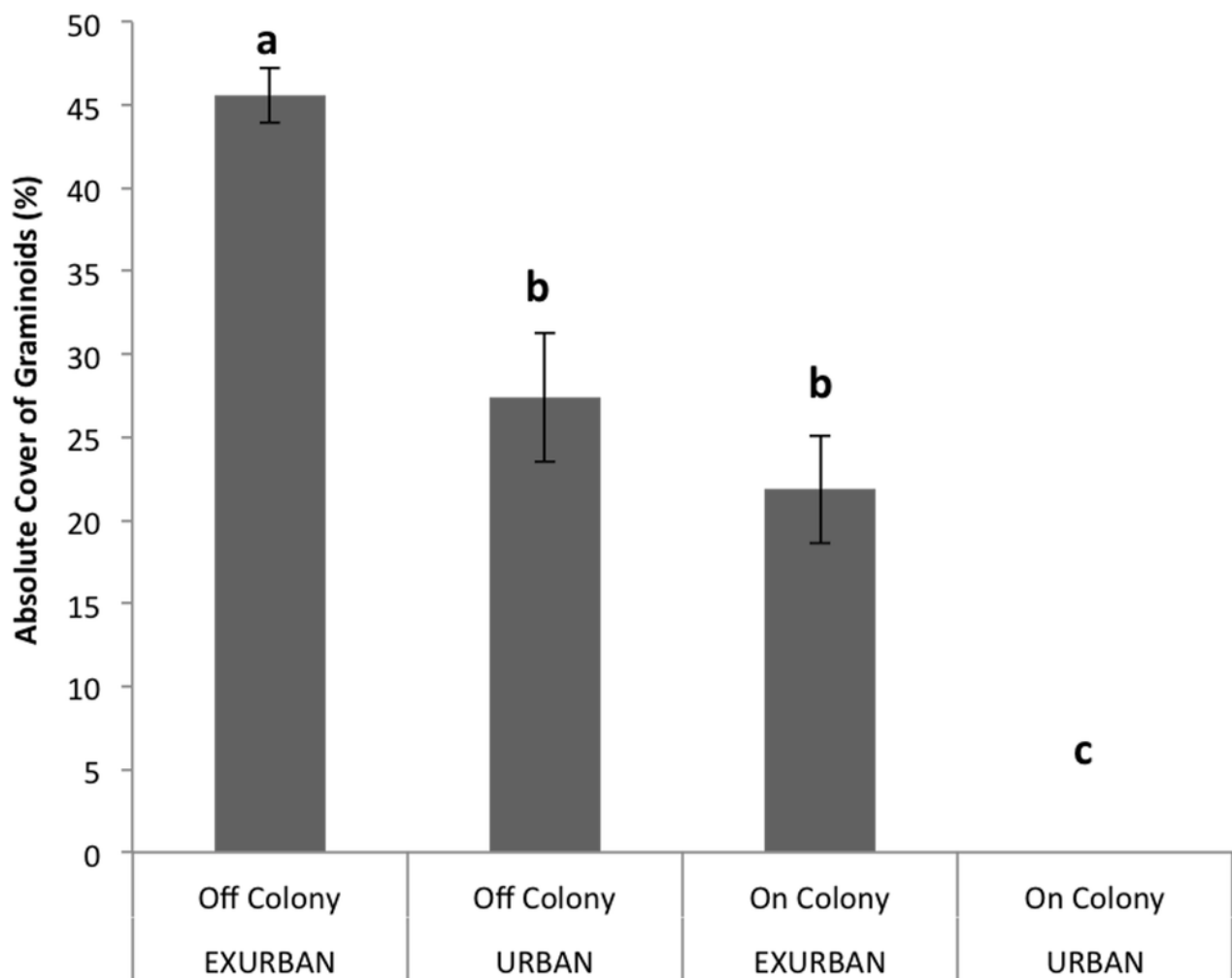
Means with the same letter (a-b for site and x-y for colony) are not significantly different, Fishers LSD,  $\alpha=0.05$ .



# 4

Absolute cover of graminoid species observed from June-August at the urban and exurban sites both on and off the prairie dog colonies.

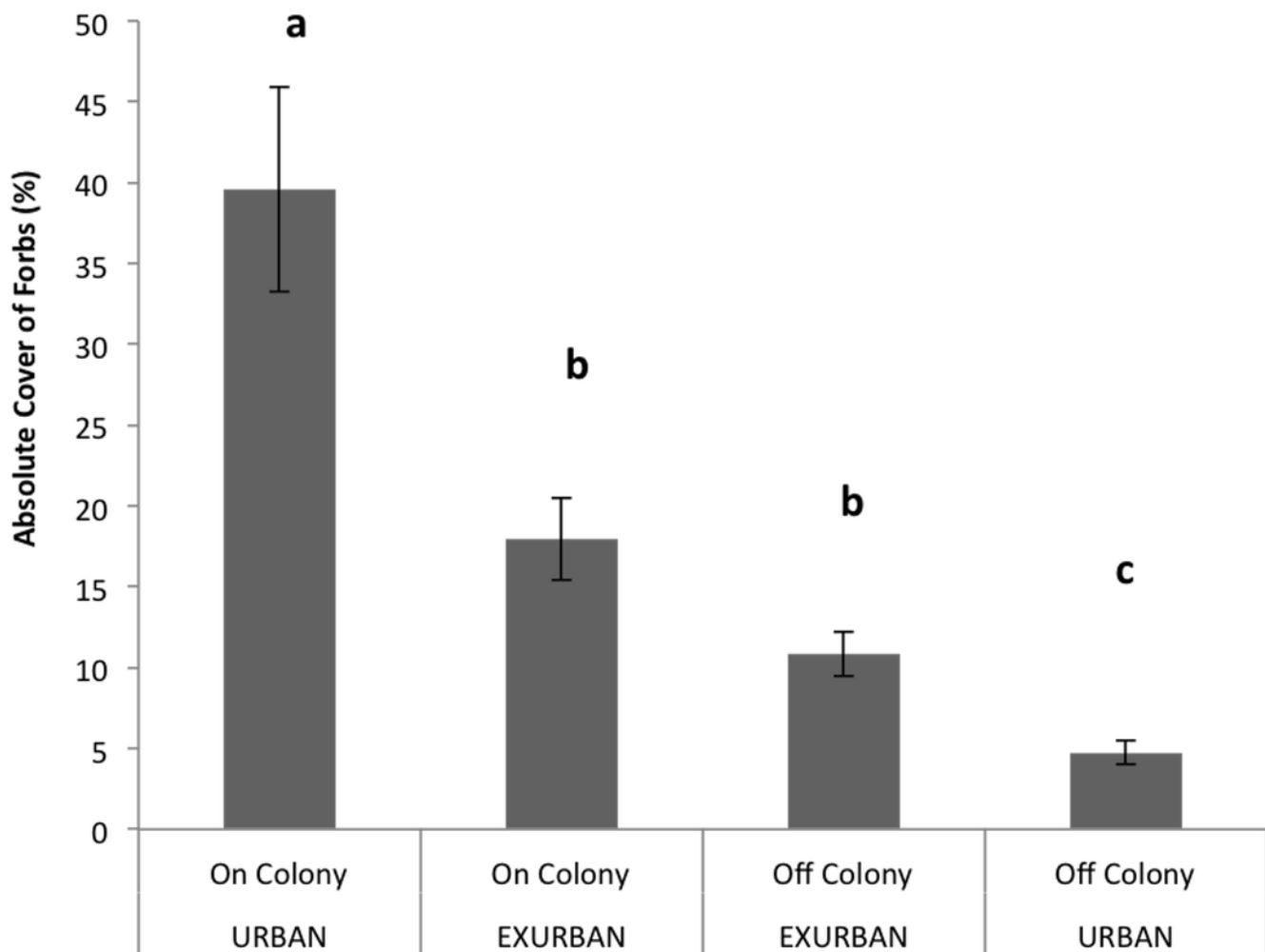
Means with the same letter are not significantly different, Fishers LSD,  $\alpha=0.05$ .



# 5

Absolute cover of forb species observed from June-August at the urban and exurban sites both on and off the prairie dog colonies.

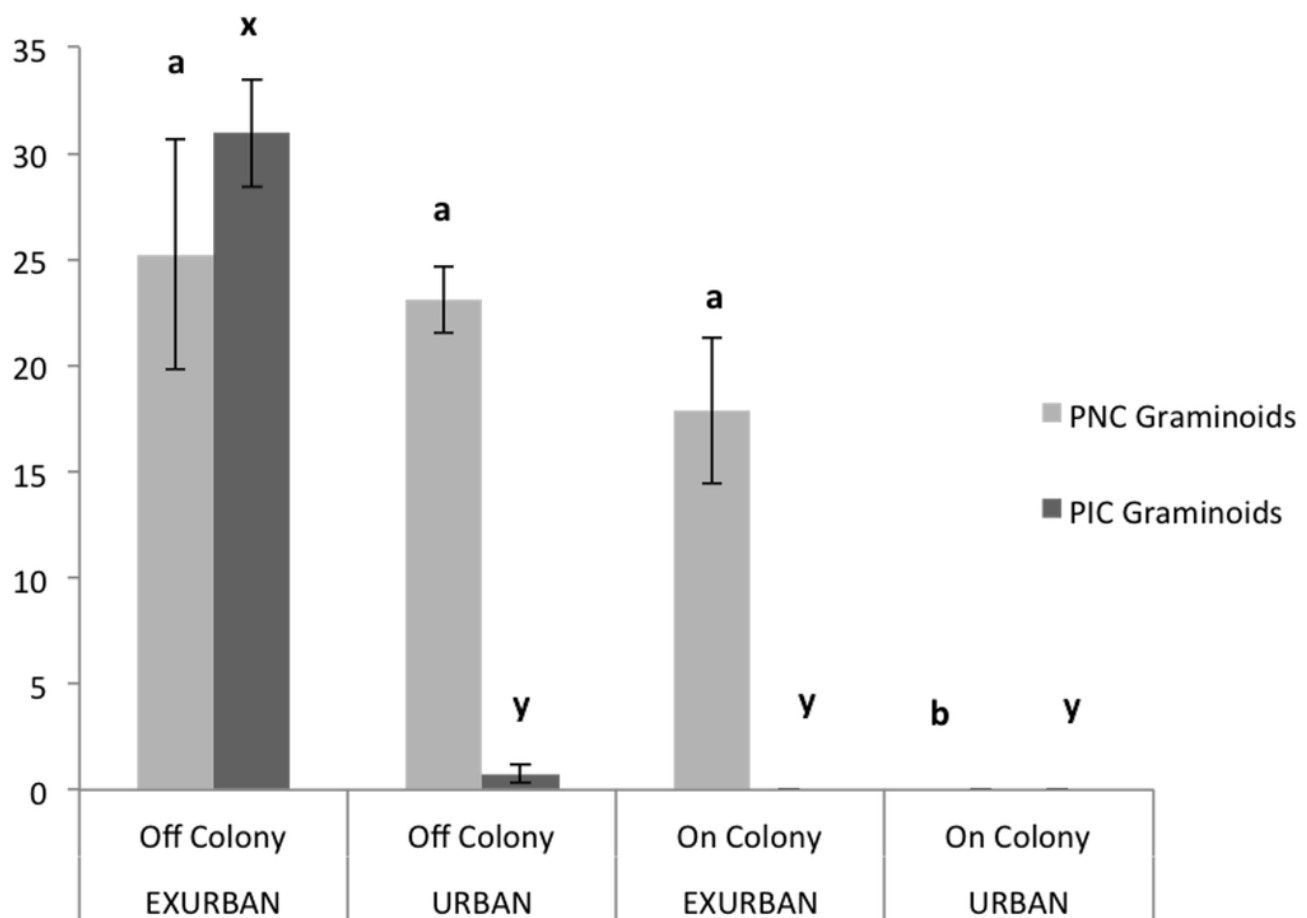
Means with the same letter are not significantly different, Fishers LSD,  $\alpha=0.05$ .



# 6

Absolute cover of perennial native cool season (PNC) and perennial introduced cool season (PIC) graminoids.

Observations were conducted in mid July at peak standing crop at the urban and exurban sites both on and off the prairie dog colonies. Means with the same letter (a and b for PNC graminoids; x and y for PIC graminoids) are not significantly different, Fishers LSD,  $\alpha=0.05$ .



# 7

Absolute cover of perennial introduced forbs (PI Forbs) and annual native forbs (AN Forbs).

Observations were conducted in mid-July at peak standing crop at the urban and exurban sites both on and off the prairie dog colonies. Means with the same letter (a through c for PI Forbs; x and y for AN Forbs) are not different, Fishers LSD,  $\alpha=0.05$ .

