

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

Rapid human population growth and habitat modification in the western United States has led to the formation of fragmented urban and exurban rangelands. Many of these rangelands are also home to populations of black-tailed prairie dogs (*Cynomys ludovicianus*). Our study aimed to explore the effects that fragmentation has had on vegetation composition in an urban and exurban rangeland, and the role that prairie dogs play in these systems. We estimated the percent absolute canopy cover of grasses and grass-like, forbs, shrubs, litter, and bare ground at plots located on and off of prairie dog colonies at the urban and exurban sites. Herbaceous forage quality and quantity were determined on plant material collected from enclosure 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. Grasses and grass-like 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 may drive greater vegetation utilization and reduced cover. At both sites there was evidence of the impact of habitat fragmentation and human disturbance, however, exurban rangeland showed lower levels of impact, fewer introduced species, and retained all of the functional cover groups at both the on- and off-colony plots. These results indicate how small fragmented rangeland habitats can be ecologically degraded from the impacts of human disturbance, which the presence of prairie dogs can further exacerbate. Greater understanding of the drivers of these impacts and the spatial scales at which they occur will prove valuable in the management and conservation of

rangelands in and around urban areas.

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

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27 **Abstract**

28 Rapid human population growth and habitat modification in the western United States  
29 has led to the formation of fragmented urban and exurban rangelands. Many of these  
30 rangelands are also home to populations of black-tailed prairie dogs (*Cynomys*  
31 *ludovicianus*). Our study aimed to explore the effects that fragmentation has had on  
32 vegetation composition in an urban and exurban rangeland, and the role that prairie dogs  
33 play in these systems. We estimated the percent absolute canopy cover of grasses and  
34 grass-likes, forbs, shrubs, litter, and bare ground at plots located on and off of prairie dog  
35 colonies at the urban and exurban sites. Herbaceous forage quality and quantity were  
36 determined on plant material collected from exclosure cages located on the colony during  
37 the entire growing season. A relative estimate of prairie dog density was calculated using  
38 maximum counts. The exurban site had more litter and plant cover and less bare ground  
39 than the urban site. Grasses and grass-likes were the dominant vegetation at the exurban  
40 plots. In contrast, mostly introduced forbs were found on the urban prairie dog colony.  
41 However, the forage quality and quantity tests demonstrated no difference between the  
42 two colonies. The relative prairie dog density was greater at the urban colony, which may  
43 drive greater vegetation utilization and reduced cover. At both sites there was evidence of  
44 the impact of habitat fragmentation and human disturbance, however, exurban rangeland  
45 showed lower levels of impact, fewer introduced species, and retained all of the  
46 functional cover groups at both the on- and off-colony plots. These results indicate how  
47 small fragmented rangeland habitats can be ecologically degraded from the impacts of  
48 human disturbance, which the presence of prairie dogs can further exacerbate. Greater  
49 understanding of the drivers of these impacts and the spatial scales at which they occur  
50 will prove valuable in the management and conservation of rangelands in and around  
51 urban areas.

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## 58 **Introduction**

59 The North American Great Plains region is a large dynamic ecosystem that is inhabited  
60 by a diverse variety of plants and animals, which have generated a heterogeneous  
61 landscape made up of three major prairie types - shortgrass, mixed, and tallgrass  
62 (Lauenroth, Burke & Gutmann 1999). Since European settlement rapidly expanded west  
63 during the mid-1800s, large swathes of the Great Plains ecosystem have undergone  
64 dramatic transformation as a function of human population growth driving agricultural  
65 and urban development (Samson & Knopf 1994). These habitats continue to face  
66 increasing anthropogenic pressure, with the metropolitan areas of the western United  
67 States currently experiencing the greatest rate of growth in the country (Maestas, Knight  
68 & Gilgert 2003), forcing many of those cities to further develop open spaces within their  
69 city limits. Moreover, increased income, mobility and desirability for rural living has led  
70 to the conversion of farm and ranch lands to low-density exurban (rural residential)  
71 development (Maestas *et al.* 2003). For example, exurban population growth for the state  
72 of Montana from 1980 to 2000 was estimated to be 143% (Theobald 2005).

73  
74 Remaining prairie habitats located within the boundaries of urban areas and among  
75 exurban development face potentially negative impacts associated with land use change  
76 and human population growth in surrounding areas. In addition to direct habitat loss and  
77 fragmentation, the native plant communities of these habitats can be substantially altered  
78 as a result of non-native plant species being introduced (Mack *et al.* 2000). These  
79 introductions also contribute to a loss of biodiversity within the rangelands as a result of  
80 native species facing competitive exclusion (Maestas *et al.* 2003). These impacts can also  
81 extend up the food web, degrading habitat and forage quality for a variety of native  
82 wildlife species. One such species that is experiencing severe pressure from development  
83 and anthropogenic disturbance is the black-tailed prairie dog (*Cynomys ludovicianus*),  
84 which has faced widespread decline across its historic range (Miller, Ceballos & Reading  
85 1994). The decline has been driven by habitat fragmentation, poisoning programs and  
86 disease outbreaks (Miller *et al.* 2007). Remaining prairie dog colonies commonly occur  
87 in isolated pockets scattered throughout their original range with many of the more dense

88 colonies found in exurban areas surrounding western cities (Armstrong, Fitzgerald &  
89 Meaney 2011).

90

91 Prairie dogs are considered ecosystem engineers because of their ability to alter the  
92 landscape and generate refuges and foraging opportunities for an array of species  
93 (Whicker & Detling 1988). For example, in a functional prairie ecosystem, the foraging  
94 and burrowing behaviour of prairie dogs has been demonstrated to increase biotic  
95 diversity (Augustine & Baker 2013) and influence community structure (Van Nimwegen,  
96 Kretzer & Cully 2008) in close proximity to the colony, while also playing an important  
97 role in ecosystem function (Martinez-Estévez *et al.* 2013). Nevertheless, prairie dogs are  
98 also politically controversial. In agricultural areas, prairie dogs are considered to compete  
99 directly with livestock for available forage (Vermeire *et al.* 2004; Derner, Detling &  
100 Antolin 2006), while there are public health concerns surrounding the transmission of  
101 zoonotic diseases such as the plague (Lowell *et al.* 2005). A number of contentious  
102 population control measures have therefore been put in place to reduce prairie dog  
103 numbers in areas where they are considered to be a nuisance (Hoogland 1995).

104

105 The aim of our study was to compare the vegetation of black-tailed prairie dog habitat in  
106 urban and exurban rangeland, to explore whether the associated gradient in human  
107 disturbance led to differences in vegetation abundance and composition on and off prairie  
108 dog colonies. We predicted that: 1) The presence of a prairie dog colony would reduce  
109 the abundance of vegetation and litter and increase the amount of bare ground at both  
110 sites, as a function of prairie dog foraging behavior and burrowing activity. 2) The  
111 exurban site would support a greater abundance of grasses and grass-like plants and forbs,  
112 and have greater quantities of litter and less bare ground than urban site, due to less  
113 fragmentation enabling prairie dog foraging and burrowing to be distributed over a larger  
114 area at the exurban site. 3) The urban site would have lower native plant cover due to a  
115 greater probability of non-native plant species being introduced from nearby  
116 developments. 4) The quantity and quality of forage at the exurban prairie dog colony  
117 would be greater than at the urban prairie dog colony. 5) Prairie dog density would be

118 greater at the urban colony compared with the exurban colony due to the limited available  
119 range and lack of habitat connectivity for animals to disperse to nearby rangelands.

120

## 121 **Methods**

### 122 *Study Sites*

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

141

### 142 *Data collection*

143 Two study plots were established at each site. The on-colony sampling plots were  
144 determined by locating the approximate center of the colony using prairie dog burrow  
145 distribution and animal density as indicators. Once the center point was identified, a  
146 thirty-five meter transect was positioned across the colony, with the center point of the  
147 transect corresponding to the center of the colony. Two more thirty-five meter transects  
148 were established; one on each side of the central transect, running parallel and separated

149 by a distance of 15 meters. Selection of the off-colony plots was dependent on the  
150 absence of burrows and a minimum buffer of 20 meters from the nearest observed  
151 evidence of prairie dog activity (e.g. burrow, trail). Once a suitable area was demarcated,  
152 three thirty-five meter transects were laid out following the same approach used for the  
153 on-colony plots.

154

#### 155 *Cover Estimates*

156 Canopy cover and vegetation composition were determined using an extended  
157 Daubenmire frame (see Bonham, Mergen & Montoya 2004) placed every 5 meters along  
158 each transect, with a total of 21 frame observations at each plot (7 frame locations per  
159 transect and 3 transects per plot). These cover observations were conducted once each  
160 month during the summer (June – August) to track changes in vegetation composition  
161 through time. Cover was categorized into four distinct categories: 1) grasses and grass-  
162 likes, 2) forbs, 3) litter, and 4) bare ground. In mid-July, the grasses and grass-likes and  
163 forb cover classes were further subdivided according to their duration (perennial or  
164 annual), origin (native or introduced), and growing season (cool or warm). The mid-July  
165 sampling was assumed to represent peak standing crop, and data were collected in the  
166 same manner as described above. The grasses and grass-likes group was subdivided into  
167 perennial native cool season, perennial native warm season, annual native cool season,  
168 perennial introduced cool season, and annual introduced cool season grasses and grass-  
169 likes. The forbs group was subdivided into perennial native, annual native, biennial  
170 native, perennial introduced, annual introduced, and biennial introduced forbs.

171

#### 172 *Dominant Species*

173 The dominant plant species at each plot were documented during the June sampling  
174 period. These species were determined by recording the number of times along each  
175 transect that the eight most common plant species occurred. The mean number of times  
176 each species was observed was calculated for each plot. The most common plant species  
177 were selected on the basis that mean frequency was equal to, or greater than three  
178 sightings per transect. The percent absolute canopy cover of each of those species was

179 then estimated using the extended Daubenmire frame during July observations (at peak  
180 standing crop).

181

### 182 *Forage Quality and Quantity*

183 The quality and quantity of forage available to the prairie dogs on the colony was  
184 estimated from three exclosure cages (dimensions: 30 x 60 x 75 cm) made out of 0.5cm x  
185 0.5cm hardware cloth over wire panels placed on each colony (urban and exurban).  
186 Exclosure cages were positioned at the mid-point between the transects and 7.5 meters  
187 into the plot area. In August, all herbaceous material in each cage was clipped to ground  
188 level, bagged and placed in drying ovens at 55°C for one week. The dried material was  
189 weighed and then sent for laboratory analysis (Servi-Tech Laboratories, Hastings,  
190 Nebraska) to determine the percentage of total digestible nutrients, crude protein, acid  
191 detergent fiber, neutral detergent fiber, and a relative feed value index (see Table2).

192

### 193 *Maximum prairie dog counts*

194 A relative measure of prairie dog density was determined using aboveground counts of  
195 animals in a demarcated sampling area (100 m<sup>2</sup>). Five repeat counts were performed at  
196 each site from the same observation point, which was approximately 150 meters away  
197 from the marked area. The observations were conducted between 7:00am and 11:00am  
198 and lasted for 90 minutes with the total number of aboveground animals within the  
199 marked observation area recorded every 10 minutes. A standardized settling time of 30  
200 minutes was initiated prior to data collection, allowing the prairie dogs sufficient time to  
201 return to their normal behavior after the disturbance of the observer's arrival (Shannon *et*  
202 *al.* 2014). As the study involved minimally invasive vegetation sampling and behavioural  
203 observation, an institutional review of the research was not required.

204

### 205 *Data Analysis*

206 Cover data for each functional group were analyzed using a mixed modeling procedure  
207 and repeated measures analysis (season) to test for the effects of site, presence or absence  
208 of a prairie dog colony, season, and all possible interactions. Peak standing crop cover  
209 data were analyzed separately to test for the effects of site, presence or absence of a

210 prairie dog colony, and all possible interactions. The data were analyzed using an  
211 analysis of variance in SAS 9.3 (PROC mixed SAS Institute, Cary, NC, USA) to  
212 determine effects of site, presence or absence of prairie dog colony and all possible  
213 interactions. Where F-tests identified significant effects, the means were separated using  
214 Fisher's LSD Alpha = 0.05. Data were transformed prior to analysis by calculating the  
215 arc-sine square root of the original data to meet assumptions of the analysis. T-tests were  
216 used to analyze the peak standing crop data, forage quality and quantity, and the  
217 population density indicator estimates. All data presented are original scale.

218

## 219 **Results**

### 220 *Cover By Functional Groups*

221 Cover values for the functional groups we sampled were not affected by season ( $F = 0.15-$   
222  $2.54$ ,  $P = 0.100-0.863$ ), the season by site interaction ( $F = 0.04-1.37$ ,  $P = 0.272-0.96$ ), the  
223 season by colony interaction ( $F = 0.16-3.34$ ,  $P = 0.053-0.855$ ), or the interaction of all  
224 three factors ( $F = 0.26-2.47$ ,  $P = 0.106-0.7706$ ).

225

226 Absolute litter cover was significantly greater at the exurban site than at the urban site ( $F$   
227  $= 21.06$ ,  $P < 0.001$ ) and also greater off-colony than on colony ( $F = 9.11$ ,  $P = 0.006$ ; Fig.  
228 2). The effect of colony on litter cover was consistent at the two sites ( $F = 3.07$ ,  $P = 0.093$ ).  
229 The overall percentage of bare ground was greater at the urban site compared to the  
230 exurban site ( $F = 48.37$ ,  $P < 0.001$ ; Fig. 3). There was also significantly more bare ground  
231 observed at the on-colony plots compared with the off-colony plots ( $F = 47.39$ ,  $P < 0.001$ ;  
232 Fig. 3). The effect of colony on cover of bare ground was consistent across the two sites  
233 ( $F = 2.33$ ,  $P = 0.140$ ).

234

235 Absolute cover of grasses and grass-likes was affected by site ( $F = 94.64$ ,  $P < 0.001$ ),  
236 presence of a prairie dog colony ( $F = 135.72$ ,  $P < 0.001$ ), and the two factors  
237 simultaneously ( $F = 15.46$ ,  $P = 0.001$ ). The absolute cover of grasses and grass-like  
238 species ranged from 46% at the off-colony exurban plot to 0% at the on-colony urban  
239 plot, while cover values at the urban off colony and exurban on colony plots were similar  
240 and around 25% (Fig. 4).

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

248

#### 249 *Cover at Peak Standing Crop*

250 Perennial native warm season grasses and grass-likes were not affected by site ( $F = 0.79$ ,  
251  $P = 0.399$ ), but had lower cover values on prairie dog colonies compared to off ( $F = 15.43$ ,  
252  $P = 0.004$ ). The interaction between colony and site was not significant ( $F = 0.11$ ,  
253  $P = 0.7525$ ). Cover of perennial native cool season grasses and grass-likes was affected by  
254 a significant interaction between site and presence of a prairie dog colony in the plot ( $F$   
255  $= 51.90$ ,  $P < 0.001$ ; Fig. 6), a result that was driven by the fact that no grasses were  
256 observed throughout the entire growing season at the urban on-colony plot (see Fig. 4).  
257 However, there was no significant difference in the abundance of perennial native cool  
258 season grasses and grass-likes between the exurban on colony, exurban off colony, and  
259 urban off colony plots (Fig. 6).

260

261 Annual introduced cool season grasses were only found at the exurban site ( $F = 10.32$ ,  $P$   
262  $= 0.012$ ), while the presence of a prairie dog colony did not affect cover ( $F = 0.01$ ,  $P$   
263  $= 0.909$ ). Perennial introduced cool season grasses and grass-likes were affected by the  
264 two-way interaction between site and colony ( $F = 131.29$ ,  $P < 0.001$ ; Fig. 6). The greatest  
265 percentage of cover by perennial introduced cool season grasses and grass-likes was  
266 observed off colony at the exurban site (31%), which was mostly *Poa pratensis* L. (see  
267 Table 1). At all of the other plots, there were little to no perennial introduced cool season  
268 grasses observed (Fig. 6).

269

270 Perennial native forb species cover did not vary significantly by site ( $F = 3.47$ ,  $P = 0.10$ )  
271 or the presence or absence of a prairie dog colony ( $F = 1.01$ ,  $P = 0.344$ ). The interaction

272 between site and colony was also non-significant ( $F = 0.39$ ,  $P = 0.549$ ). Biennial native  
273 forbs were only observed at the urban off colony plot.

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

279 Absolute (%) cover of perennial introduced forbs was not affected by site ( $F = 0.49$ ,  $P$   
280  $= 0.502$ ) but was affected by the presence of a prairie dog colony ( $F = 34.73$ ,  $P = 0.001$ ).  
281 The interaction between site and colony was also significant ( $F = 11.40$ ,  $P = 0.01$ ) (Fig. 7).  
282 The urban on-colony plot had the greatest percentage of cover by perennial introduced  
283 forbs (27%) while cover of this functional group at the exurban on-colony and urban off-  
284 colony plots were similar. No perennial introduced forbs were found off-colony at the  
285 exurban site. These results reflect the common dominance of field bindweed  
286 (*Convolvulus arvensis* L.) at three of the four plots (see Table 1). Cover of annual  
287 introduced forbs and biennial introduced forbs accounted for  $\leq 1\%$  at each plot and  
288 therefore values were too small to detect meaningful differences across either site or in  
289 the presence or absence of a prairie dog colony.

290

### 291 *Dominant Species*

292 The dominant plant species were mostly site specific. Overall, the on-colony plots were  
293 dominated by more forb species than the off-colony plots where more grasses and grass-  
294 like species were present (see Table 1). The only species that was common at multiple  
295 plots was western wheatgrass (*Elymus smithii* (Rydb.) Gould), which was found at three  
296 of the four plots. The species observed at the urban on-and off-colony plots were  
297 different and there was no overlap in dominants. However, at the exurban on- and off-  
298 colony plots, there was more similarity in the vegetation with two common dominant  
299 species, western wheatgrass and Japanese brome (*Bromus japonicas* Thunb.). There were  
300 more introduced species observed at the exurban site than at the urban site.

301

302 *On Colony Forage*

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

306

307 *Prairie Dog Density Estimate*

308 The prairie dog population observations taken from each colony indicated that the  
309 relative measures of prairie dog densities differed significantly between the exurban and  
310 urban colonies ( $F=10.20$ ,  $P=0.02$ ). The mean relative density of prairie dogs at the  
311 exurban colony was 14 ( $\pm 2$  SE) individuals per hectare, while the density at the urban  
312 colony was 19 ( $\pm 3$  SE) individuals per hectare.

313

314 **Discussion**

315 Our results demonstrated marked differences in vegetation composition between the  
316 exurban and urban sites as well as between plots with and without a prairie dog colony.  
317 The exurban site had more live plant cover and less bare ground compared to the urban  
318 site, and the vegetation composition was similar between plots, with the off-colony  
319 predominately comprised of grasses with fewer forbs, while the on-colony plot was a  
320 more even mixture of grasses and forbs. The vegetation composition at the urban site  
321 varied greatly between plots. The off-colony plot vegetation was a mixture of mostly  
322 grasses and grass-like with some forbs, while the on-colony plot vegetation comprised  
323 only forbs with field bindweed the most abundant species, concurring with recent  
324 research on prairie dogs in urban habitats (Magle & Crooks 2008; Beals *et al.* 2014). The  
325 abundance of bindweed at the urban site is a common feature of disturbed urban and  
326 exurban rangeland systems (Whitson *et al.* 1998). Indeed, the success of this plant in  
327 colonizing highly disturbed areas suggests that the foraging and burrowing activities of  
328 prairie dogs on the urban colony is enabling its propagation (Magle & Crooks 2008;  
329 Beals *et al.* 2014).

330

331 The on-colony data also indicates that prairie dog activity drives the occurrence of bare  
332 ground, however this effect is more pronounced at the urban site. Besides initiating

333 changes in the amount of bare ground, the prairie dog colonies also changed the  
334 vegetation structure by decreasing the abundance of grasses and grass-likes, while  
335 increasing forb abundance observed in the community (see also Magle & Crooks 2008;  
336 Beals *et al.* 2014). Exurban and urban systems are susceptible to the introduction of non-  
337 native species due to their fragmented state and proximity to human activity (Magle *et al.*  
338 2010). There was at least one introduced dominant plant species at all plots, with the  
339 exception of the urban off-colony plot where interestingly all four dominants were native.  
340 The introduced species varied according to plot, species, and growth form; with field  
341 bindweed the most commonly observed introduced forb at both on-colony plots.

342

343 Interestingly there was no evidence of a significant difference in forage quality or  
344 quantity between the urban and exurban site. The abundance of field bindweed at the  
345 urban on colony site is likely to generate significant plant biomass and relatively high  
346 values for many of the forage quality measures, rivaling that of the exurban site.  
347 Nevertheless, bindweed contains tropane; a potentially toxic alkaloid that led to high  
348 levels of mortality in mice that were fed concentrated diets of bindweed (Schultheiss *et al.*  
349 1995). These findings demonstrate that secondary compounds are also crucial when  
350 assessing forage quality. Moreover, a greater sample size, and determinations of forage  
351 quality at multiple times throughout the growing season would need to be collected to  
352 increase the accuracy of the analysis on forage quality before firm conclusions can be  
353 drawn.

354

355 The greater density of prairie dogs at the smaller and more fragmented urban site could  
356 result in reduced movement and dispersal; processes which appear to be impacted to a  
357 lesser extent at the exurban site (Johnson 2004). Indeed, the disturbance from prairie  
358 dogs foraging and burrowing at the larger exurban site is distributed over a greater area,  
359 so impact on vegetation is lessened and allows for greater recovery periods for many of  
360 the native plants. However, it is worth noting that relative aboveground prairie dog  
361 densities of 5 individuals per hectare were documented at an undisturbed colony 40km  
362 from Fort Collins (Shannon *et al.* 2014), significantly lower than those measured at either  
363 of the colonies used in this study. In addition to the elevated prairie dog densities that can

364 impact native vegetation cover and species persistence, habitat fragmentation and human  
365 disturbance has the potential to affect prairie dog fitness by altering behavior at both the  
366 urban and exurban study sites. The close proximity to human disturbances increases the  
367 amount of time prairie dogs spend vigilant while foraging for food (Ramirez & Keller  
368 2010; Shannon *et al.* 2014). Nevertheless, there is evidence to suggest that prairie dogs  
369 are able to adapt their foraging behavior and become acclimated to human disturbances  
370 near their colonies (Magle & Angeloni 2011). Besides the loss of time foraging, these  
371 colonies also have greater risk of disease and faster depletion of resources (Johnson  
372 2004).

373

374 Key plant functional groups are absent from the urban site, with the on-colony plots  
375 dominated by field bindweed. These results suggest that the presence of prairie dogs are  
376 contributing to the relatively disturbed state of the vegetation, which is further  
377 compounded by site history, the proximity of the site to agricultural fields and a suburban  
378 neighborhood (Beals *et al.* 2014). The exurban population density indicator estimated  
379 fewer prairie dogs per hectare than at the urban site, which along with the greater size of  
380 the exurban site may contribute to the retention of their role as ecosystem engineers. The  
381 exurban colony also exhibited a greater diversity in dominant species according to the  
382 functional groups represented, which is consistent with the suggestion that the presence  
383 of a prairie dog colony increases the diversity of the system in this setting (Whicker &  
384 Detling 1988). Similar results were reported from a study that was conducted in a  
385 protected area (Coppock *et al.* 1983), indicating the exurban site has likely retained a  
386 number of its functions as a grassland ecosystem. For example, the only native dominant  
387 plant species of the four observed at the exurban sites is western wheatgrass, a cool  
388 season grass that has adapted to a grazing disturbance dynamic. Through the removal of  
389 litter and vegetation by the prairie dogs this regime is still somewhat maintained (Baker  
390 *et al.* 2013). However, it is important to note that unlike the study of the protected area,  
391 the other three of the four dominant species at the exurban colony were introduced  
392 species (see Table 1). Furthermore, the relationship between the diversity of forb and  
393 grasses, and grass-like species at the exurban site also remained significantly lower than  
394 that of the protected natural prairie in Wind Cave National Park (Coppock *et al.* 1983).

395 The urban colony dominant species were made up of three forb species and included one  
396 introduced with two native species.

397

398 Our study demonstrated a gradient in the level of habitat disturbance between an exurban  
399 and urban rangeland with prairie dogs present. The exurban site retained a greater number  
400 of plant functional groups, while the urban on-colony plot was dominated by a single  
401 introduced species and bare ground. Habitat disturbance and fragmentation also have  
402 implications for prairie dogs, which face a greater risk of extinction, loss of immigration  
403 and emigration routes, and reduction in genetic variability. Although prairie dog colonies  
404 provide a suite of ecosystem services such as improved quality of forage on their colonies  
405 for other herbivores, increased turnover of soil nutrients, and decreased soil compaction  
406 (Martinez-Estévez *et al.* 2013), these processes may well be compromised in fragmented  
407 rangeland habitats. A situation that can result in prairie dog colonies exacerbating the  
408 impacts associated with human disturbance and environmental change (Beals *et al.* 2014).  
409 All of these factors point toward the need for effective conservation and management of  
410 prairie dog habitats in order to preserve the integrity of U.S. rangelands, particularly in  
411 the face of expanding urban growth (Miller *et al.* 1994). Based on our results, we  
412 recommend that the scale-dependent interactions between prairie dogs and vegetation  
413 composition be further researched, particularly with regard to their keystone role (see  
414 also Lomolino & Smith 2003; Magle & Crooks 2008; Beals *et al.* 2014). A comparison  
415 of multiple study sites would provide more data to aid in establishing concrete trends in  
416 the effects of urbanization on habitat fragmentation and the role that prairie dogs play in  
417 these altered rangeland systems.

418

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426 **References**

427

428 Armstrong, D.M., Fitzgerald, J.P. & Meaney, C.A. (2011) *Mammals of Colorado*.  
429 University Press of Colorado.

430 Augustine, D.J. & Baker, B.W. (2013) Associations of Grassland Bird Communities with  
431 Black-Tailed Prairie Dogs in the North American Great Plains. *Conservation Biology*,  
432 27, 324-334.

433 Baker, B.W., Augustine, D.J., Sedgwick, J.A. & Lubow, B.C. (2013) Ecosystem  
434 engineering varies spatially: a test of the vegetation modification paradigm for prairie  
435 dogs. *Ecography*, 36, 230–239.

436 Beals, S.C., Hartley, L.M., Prev y, J.S. & Seastedt, T.R. (2014) The effects of black-  
437 tailed prairie dogs on plant communities within a complex urban landscape: an  
438 ecological surprise? *Ecology*, 95, 1349–1359.

439 Bonham, C.D., Mergen, D.E. & Montoya, S. (2004) Plant cover estimation: a contiguous  
440 Daubenmire frame. *Rangelands*, 26, 17–22.

441 Coppock, D.L., Detling, J.K., Ellis, J.E. & Dyer, M.I. (1983) Plant-herbivore interactions  
442 in a North American mixed-grass prairie. *Oecologia*, 56, 1–9.

443 Derner, J.D., Detling, J.K. & Antolin, M.F. (2006) Are livestock weight gains affected by  
444 black-tailed prairie dogs? *Frontiers in Ecology and the Environment*, 4, 459–464.

445 Hoogland, J.L. (1995) *The Black-Tailed Prairie Dog: Social Life of a Burrowing*  
446 *Mammal*. University of Chicago Press.

447 Johnson, W. (2004) Landscape effects on black-tailed prairie dog colonies. *Biological*  
448 *Conservation*, 115, 487–497.

449 Lauenroth, W., Burke, I.C. & Gutmann, M.P. (1999) The structure and function of  
450 ecosystems in the central North American grassland region. *Great Plains Research*, 9,  
451 223–259.

452 Lomolino, M.V. & Smith, G.A. (2003) Prairie dog towns as islands: applications of  
453 island biogeography and landscape ecology for conserving nonvolant terrestrial  
454 vertebrates. *Global Ecology and Biogeography*, 12, 275–286.

455 Lowell, J.L., Wagner, D.M., Atshabar, B., Antolin, M.F., Vogler, A.J., Keim, P., Chu,  
456 M.C. & Gage, K.L. (2005) Identifying Sources of Human Exposure to Plague.  
457 *Journal of Clinical Microbiology*, 43, 650–656.

458 Mack, R.N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M. & Bazzaz, F.A.  
459 (2000) Biotic invasions: causes, epidemiology, global consequences, and control.  
460 *Ecological Applications*, 10, 689–710.

- 461 Maestas, J.D., Knight, R.L. & Gilgert, W.C. (2003) Biodiversity across a Rural Land-Use  
462 Gradient. *Conservation Biology*, 17, 1425–1434.
- 463 Magle, S.B. & Angeloni, L.M. (2011) Effects of urbanization on the behaviour of a  
464 keystone species. *Behaviour*, 148, 31–54.
- 465 Magle, S.B. & Crooks, K.R. (2008) Interactions between black-tailed prairie dogs  
466 (*Cynomys ludovicianus*) and vegetation in habitat fragmented by urbanization.  
467 *Journal of Arid Environments*, 72, 238–246.
- 468 Magle, S.B., Reyes, P., Zhu, J. & Crooks, K.R. (2010) Biological Conservation.  
469 *Biological Conservation*, 143, 2146–2155.
- 470 Martinez-Estévez, L., Balvanera, P., Pacheco, J. & Ceballos, G. (2013) Prairie Dog  
471 Decline Reduces the Supply of Ecosystem Services and Leads to Desertification of  
472 Semiarid Grasslands (ed A Janke). *PloS one*, 8, e75229.
- 473 Miller, B.J., Reading, R.P., Biggins, D.E., Detling, J.K., Forrest, S.C., Hoogland, J.L.,  
474 Javersak, J., Miller, S.D., Proctor, J., Truett, J. & Uresk, D.W. (2007) Prairie Dogs:  
475 An Ecological Review and Current Biopolitics. *Journal of Wildlife Management*, 71,  
476 2801–2810.
- 477 Miller, B., Ceballos, G. & Reading, R. (1994) The prairie dog and biotic diversity.  
478 *Conservation Biology*, 8, 677–681.
- 479 Ramirez, J.E. & Keller, G.S. (2010) Effects of Landscape on Behavior of Black-Tailed  
480 Prairie Dogs (*Cynomys ludovicianus*) in Rural and Urban Habitats. *The*  
481 *Southwestern Naturalist*, 55, 167–171.
- 482 Samson, F. & Knopf, F. (1994) Prairie conservation in north america. *BioScience*, 44,  
483 418–421.
- 484 Schultheiss, P.C., Knight, A.P., Traub-Dargatz, J.L., Todd, F.G. & Stermitz, F.R. (1995)  
485 Toxicity of field bindweed (*Convolvulus arvensis*) to mice. *Veterinary and human*  
486 *toxicology*, 37, 452–454.
- 487 Shannon, G., Angeloni, L.M., Wittemyer, G., Fristrup, K.M. & Crooks, K.R. (2014)  
488 *Animal Behaviour*. *Animal Behaviour*, 94, 135–141.
- 489 Theobald, D.M. (2005) Landscape Patterns of Exurban Growth in the USA from 1980 to.  
490 *Ecology and Society*, 10, 32.
- 491 Van Nimwegen, R.E., Kretzer, J. & Cully, J.F., Jr. (2008) Ecosystem engineering by a  
492 colonial mammal: how prairie dogs structure rodent communities. *Ecology*, 89,  
493 3298–3305.
- 494 Vermeire, L.T., Heitschmidt, R.K., Johnson, P.S. & Sowell, B.F. (2004) The prairie dog  
495 story: do we have it right? *BioScience*, 54, 689–695.

496 Whicker, A.D. & Detling, J.K. (1988) Ecological consequences of prairie dog  
497 disturbances. *BioScience*, 38, 778–785.

498 Whitson, T.D., Burrill, L.C., Dewey, S.A., Nelson, B.E., Cudney, D.W., Lee, R.D. &  
499 Parker, R. (1998) *Weeds of the West*. Diane Publishing Company.

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525 **Table 1** Dominant species observed at each plot during peak standing crop  
 526 observations in mid July at the urban and exurban sites both on and off the prairie dog  
 527 colonies.

Plot	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 dracunculus</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.) Hitche.	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

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532 **Table 2**

533 A comparison of forage quantity and quality using ANOVA. Data were collected in  
534 August from the three enclosure cages located on both Exurban and Urban prairie dog  
535 colonies (see methods).

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<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

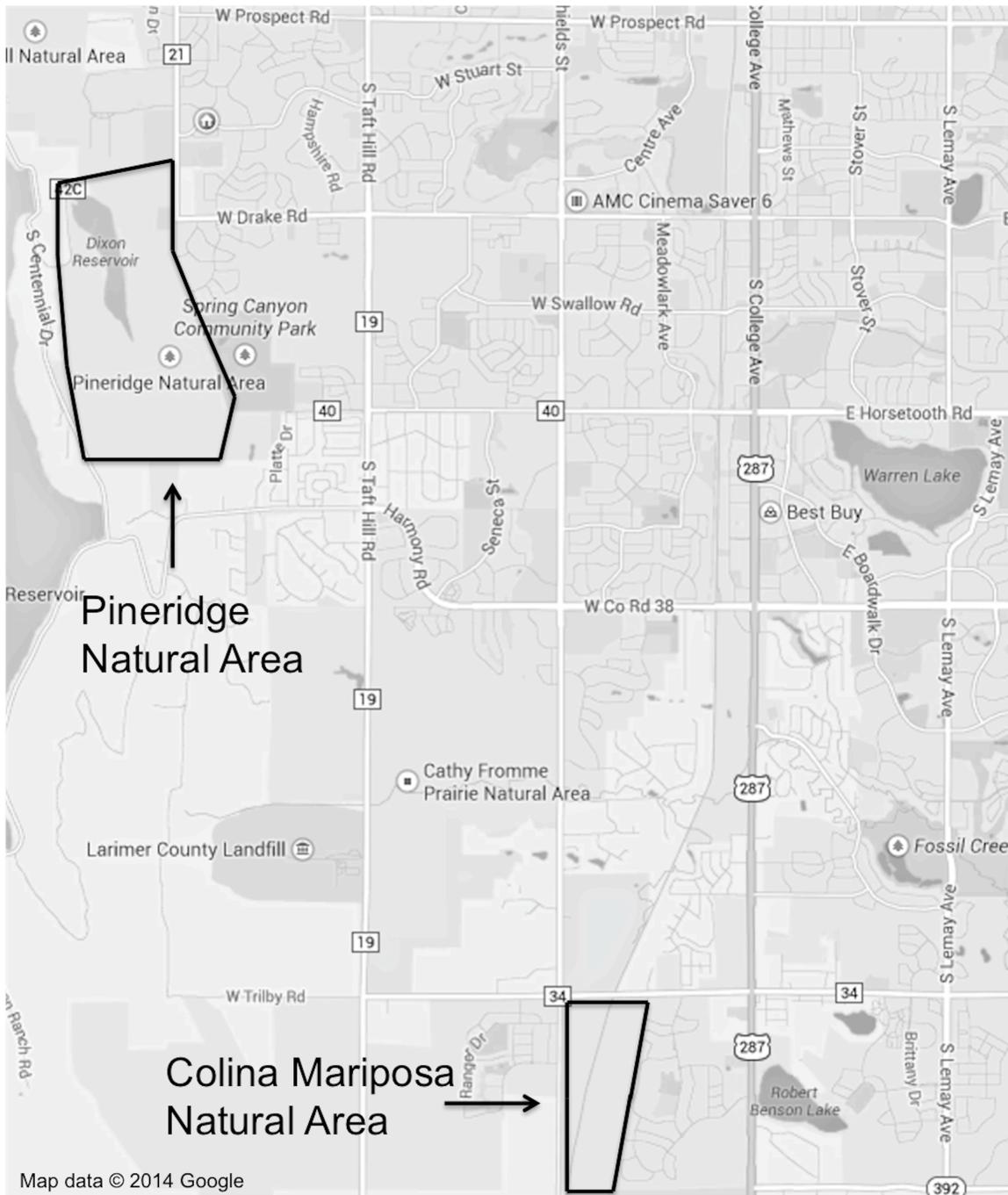
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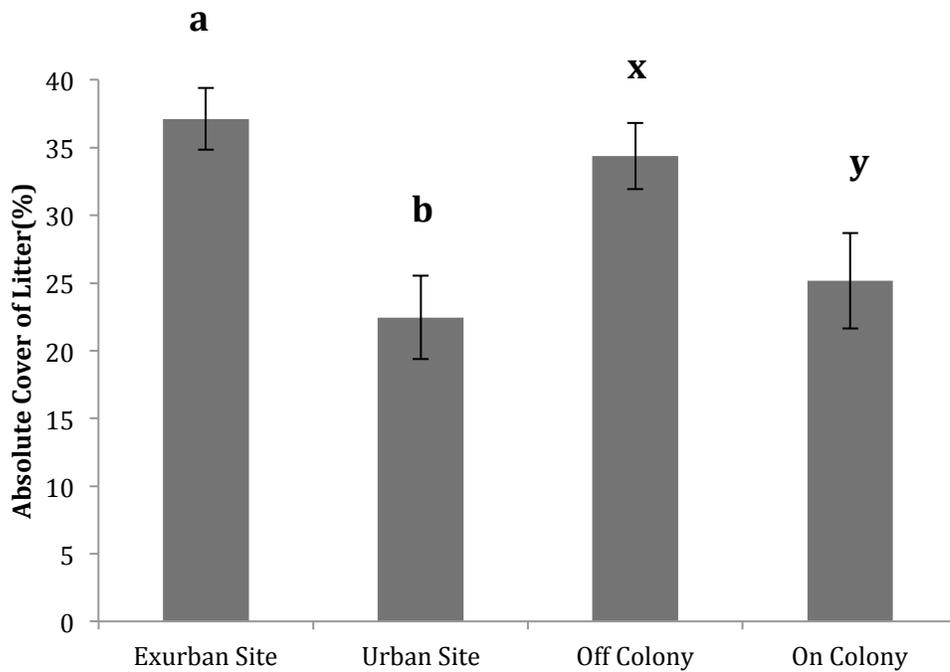
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**Figure 1.** A map of Fort Collins with the locations and extent of the two study sites outlined.



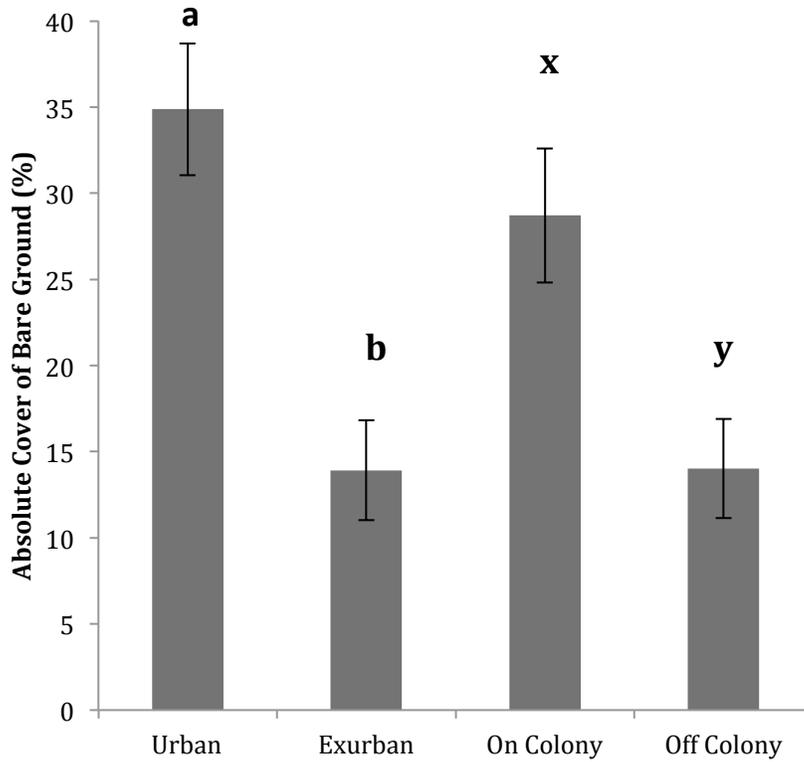
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549 **Figure 2.** Absolute cover of litter observed from June-August at the urban and exurban  
550 sites both on and off the prairie dog colonies. Means with the same letter are not  
551 significantly different, Fishers LSD  $\alpha=0.05$ .

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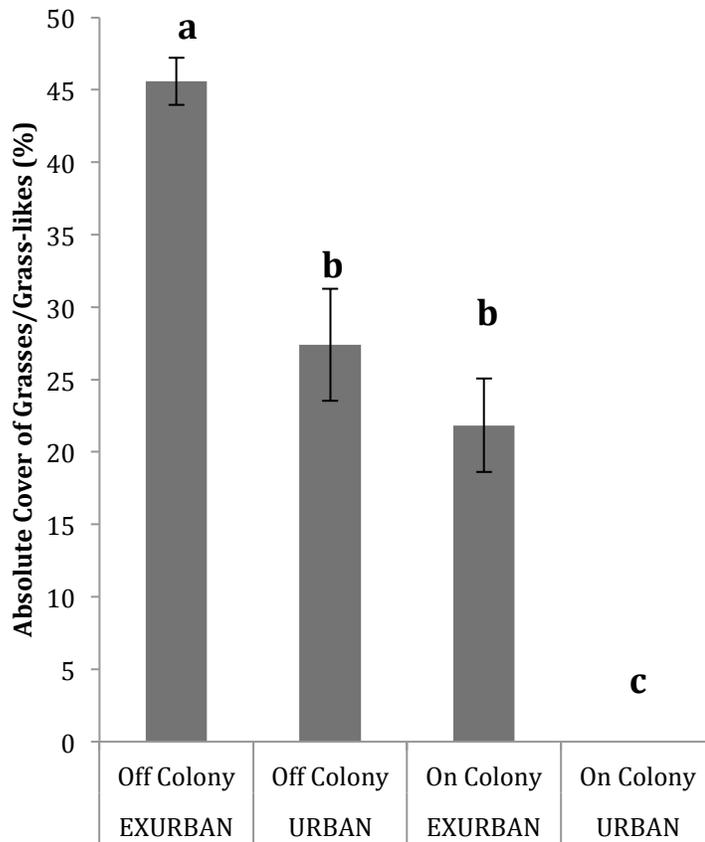
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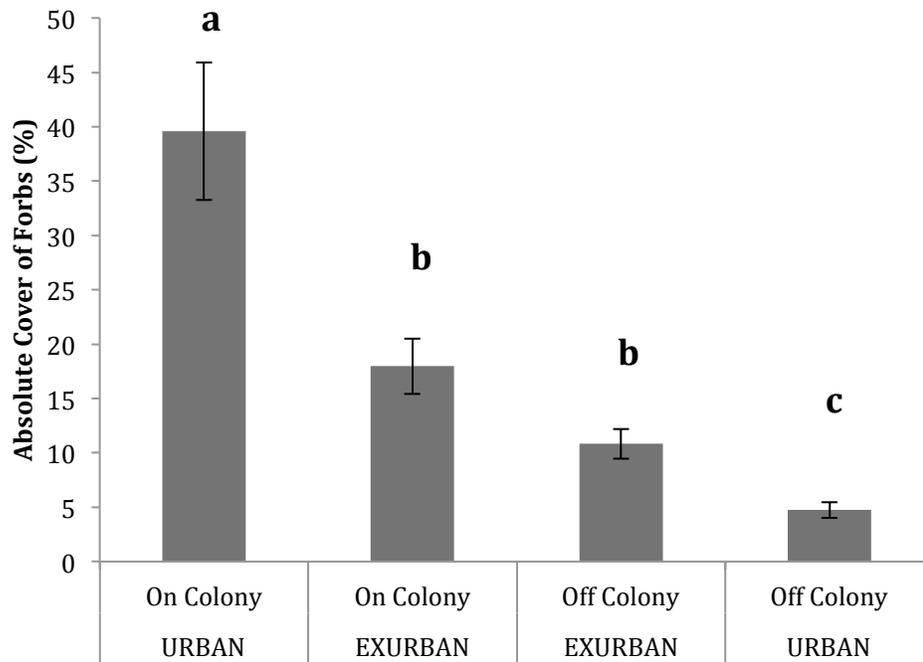
**Figure 3.** Absolute cover of bare ground observed from June-August at the urban and exurban sites both on and off the prairie dog colonies. Means with the same letter are not significantly different, Fishers LSD,  $\alpha=0.05$ .



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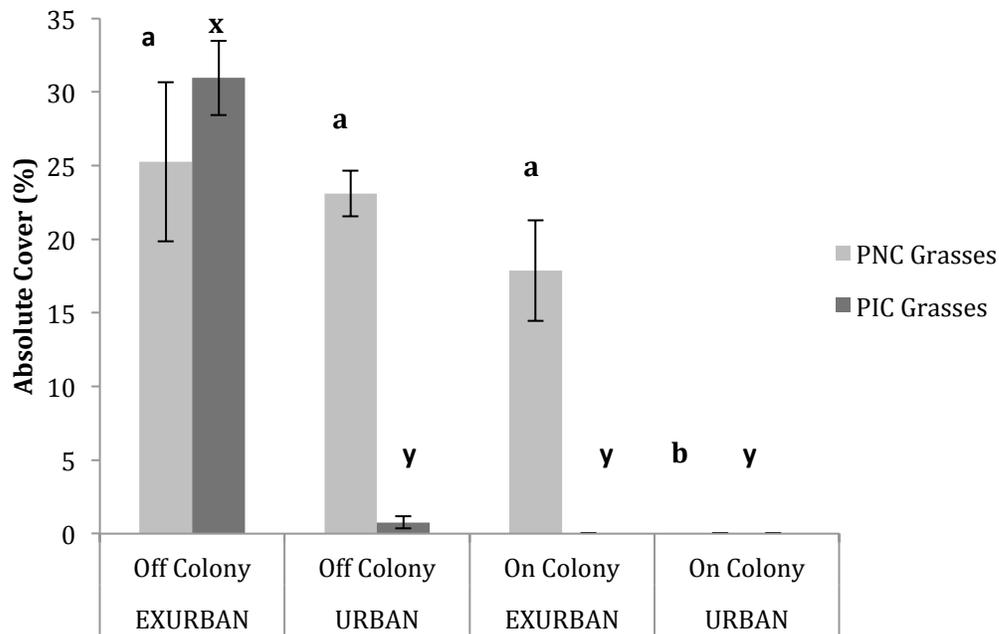
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561 **Figure 4.** Absolute cover of grasses and grass-like species observed from June-August at  
562 the urban and exurban sites both on and off the prairie dog colonies. Means with the same  
563 letter are not significantly different, Fishers LSD,  $\alpha=0.05$ .



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565 **Figure 5.** Absolute cover of forb species observed from June-August at the urban and  
566 exurban sites both on and off the prairie dog colonies. Means with the same letter are not  
567 significantly different, Fishers LSD,  $\alpha=0.05$ .



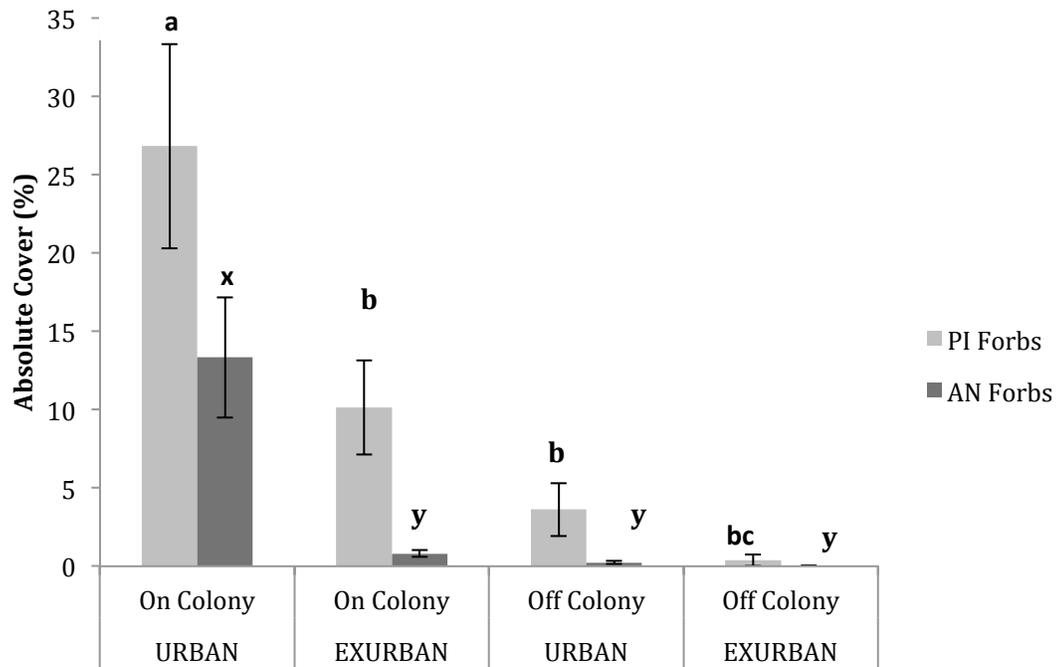
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569 **Figure 6.** Absolute cover of perennial native cool season (PNC grasses) and perennial  
 570 introduced cool season (PIC grasses) grasses and grass-likes observed in mid July at peak  
 571 standing crop at the urban and exurban sites both on and off the prairie dog colonies.  
 572 Means with the same letter (a and b for PNC grasses; x and y for PIC grasses) are not  
 573 significantly different, Fishers LSD,  $\alpha=0.05$ .

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578 **Figure 7** Absolute cover of perennial introduced forbs (PI Forbs) and annual native  
 579 forbs (AN Forbs) observed in mid-July at peak standing crop at the urban and exurban  
 580 sites both on and off the prairie dog colonies. Means with the same letter (a through c for  
 581 PI Forbs; x and y for AN Forbs) are not different, Fishers LSD,  $\alpha=0.05$ .

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