

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 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. 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.

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

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Abstract

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 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. 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.

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 swathes 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).

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 fragmentation, 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).

Prairie dogs are considered ecosystem engineers because of their ability to alter the landscape and generate refuges and foraging opportunities for an array of species (Whicker & Detling 1988). For example, in a functional prairie ecosystem, the foraging and burrowing behaviour 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 there are 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 in urban and exurban rangeland, to explore whether the associated gradient in human disturbance led to differences in vegetation abundance and composition on and off prairie dog colonies. We predicted that: 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 grasses and grass-like plants and forbs, and have greater quantities of litter and less bare ground than urban site, due to less fragmentation 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 to the limited available range and lack of habitat connectivity for animals to disperse to nearby rangelands.

Methods

Study Sites

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

Data collection

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

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

Cover Estimates

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

Dominant Species

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

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

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). Exclosure cages were positioned at the mid-point between the transects and 7.5 meters into the plot area. 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 m²). Five repeat counts were performed at each site from the same observation point, which was approximately 150 meters away from the marked area. The observations 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). As the study involved minimally invasive vegetation sampling and behavioural 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 an 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. All data presented are original scale.

Results

Cover By Functional Groups

Cover values for the functional groups we sampled 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 significantly 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 consistent at the two sites ($F = 3.07$, $P = 0.093$). 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 significantly more bare ground observed at the on-colony plots compared with the off-colony plots ($F = 47.39$, $P < 0.001$; Fig. 3). The effect of colony on cover of bare ground was consistent across the two sites ($F = 2.33$, $P = 0.140$).

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

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

Cover at Peak Standing Crop

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

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

The abundance of annual native forbs was significantly greater on colony at the urban site compared with all of the other plots, 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 at the urban on colony plot, 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 urban on-colony plot had the greatest percentage of cover by perennial introduced forbs (27%) while cover of this functional group at the exurban on-colony and urban off-colony plots were similar. No perennial introduced forbs were found off-colony at the exurban site. These results reflect the common dominance of field bindweed (*Convolvulus arvensis* L.) at three of the four plots (see Table 1). Cover of annual introduced forbs and biennial introduced forbs accounted for $\leq 1\%$ at each plot and therefore values were too small to detect meaningful differences across either site or in the presence or absence of a prairie dog colony.

Dominant Species

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

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.

Discussion

Our results demonstrated marked differences in vegetation composition between the exurban and urban sites as well as between plots with and without a prairie dog colony. The exurban site had more live plant cover and less bare ground compared to the urban site, and the vegetation composition was similar between plots, with the off-colony predominately comprised of grasses with fewer forbs, while the on-colony plot was a more even mixture of grasses and forbs. The vegetation composition at the urban site varied greatly between plots. The off-colony plot vegetation was a mixture of mostly grasses and grass-like with some forbs, while the on-colony plot vegetation comprised 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).

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 grasses and grass-like, while increasing forb abundance observed in the community (see also Magle & Crooks 2008; Beals *et al.* 2014). Exurban and urban systems are 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.

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 greater density of prairie dogs at the smaller and more fragmented urban site could result in reduced movement and dispersal; processes which appear to be impacted to a lesser extent at the exurban site (Johnson 2004). 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. 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 increases the amount of time prairie dogs spend vigilant while foraging for food (Ramirez & Keller 2010; Shannon *et al.* 2014). Nevertheless, there is evidence to suggest that prairie dogs are able to adapt their foraging behavior and become acclimated to human disturbances near their colonies (Magle & Angeloni 2011). Besides the loss of time foraging, these colonies also have greater risk of disease and faster depletion of resources (Johnson 2004).

Key plant functional groups are absent from the urban site, with the on-colony plots dominated by field bindweed. These results suggest that the presence of prairie dogs are 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). 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 contribute to the retention of their role as ecosystem engineers. The exurban colony also exhibited a greater diversity in dominant species according to the functional groups represented, which is consistent with the suggestion that the presence of a prairie dog colony increases the diversity of the system in this setting (Whicker & Detling 1988). Similar results were reported from a study that was conducted in a protected area (Coppock *et al.* 1983), indicating the exurban site has likely 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. Through the removal of litter and vegetation by the prairie dogs this regime is still somewhat maintained (Baker *et al.* 2013). However, it is important to note that unlike the study of the protected area, 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 grasses, and grass-like 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 urban colony dominant species were made up of three forb species and included one introduced with two native species.

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

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References

- Armstrong, D.M., Fitzgerald, J.P. & Meaney, C.A. (2011) Mammals of Colorado. University Press of Colorado.
- Augustine, D.J. & Baker, B.W. (2013) Associations of Grassland Bird Communities with Black-Tailed Prairie Dogs in the North American Great Plains. *Conservation Biology*, 27, 324-334.
- Baker, B.W., Augustine, D.J., Sedgwick, J.A. & Lubow, B.C. (2013) Ecosystem engineering varies spatially: a test of the vegetation modification paradigm for prairie dogs. *Ecography*, 36, 230-239.
- Beals, S.C., Hartley, L.M., Prev  y, J.S. & Seastedt, T.R. (2014) The effects of black-tailed prairie dogs on plant communities within a complex urban landscape: an ecological surprise? *Ecology*, 95, 1349-1359.
- Bonham, C.D., Mergen, D.E. & Montoya, S. (2004) Plant cover estimation: a contiguous Daubenmire frame. *Rangelands*, 26, 17-22.
- Coppock, D.L., Detling, J.K., Ellis, J.E. & Dyer, M.I. (1983) Plant-herbivore interactions in a North American mixed-grass prairie. *Oecologia*, 56, 1-9.
- Derner, J.D., Detling, J.K. & Antolin, M.F. (2006) Are livestock weight gains affected by black-tailed prairie dogs? *Frontiers in Ecology and the Environment*, 4, 459-464.
- Hoogland, J.L. (1995) The Black-Tailed Prairie Dog: Social Life of a Burrowing Mammal. University of Chicago Press.
- Johnson, W. (2004) Landscape effects on black-tailed prairie dog colonies. *Biological Conservation*, 115, 487-497.
- Lauenroth, W., Burke, I.C. & Gutmann, M.P. (1999) The structure and function of ecosystems in the central North American grassland region. *Great Plains Research*, 9, 223-259.
- Lomolino, M.V. & Smith, G.A. (2003) Prairie dog towns as islands: applications of island biogeography and landscape ecology for conserving nonvolant terrestrial vertebrates. *Global Ecology and Biogeography*, 12, 275-286.
- Lowell, J.L., Wagner, D.M., Atshabar, B., Antolin, M.F., Vogler, A.J., Keim, P., Chu, M.C. & Gage, K.L. (2005) Identifying Sources of Human Exposure to Plague. *Journal of Clinical Microbiology*, 43, 650-656.
- Mack, R.N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *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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Table 1 Dominant species observed at each plot during peak standing crop observations in mid July at the urban and exurban sites both on and off the prairie dog 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.) 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

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Table 2

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).

Feed Test Results	Urban (mean)	Exurban (mean)	T-statistic	P-value
Biomass (grams/m ²)	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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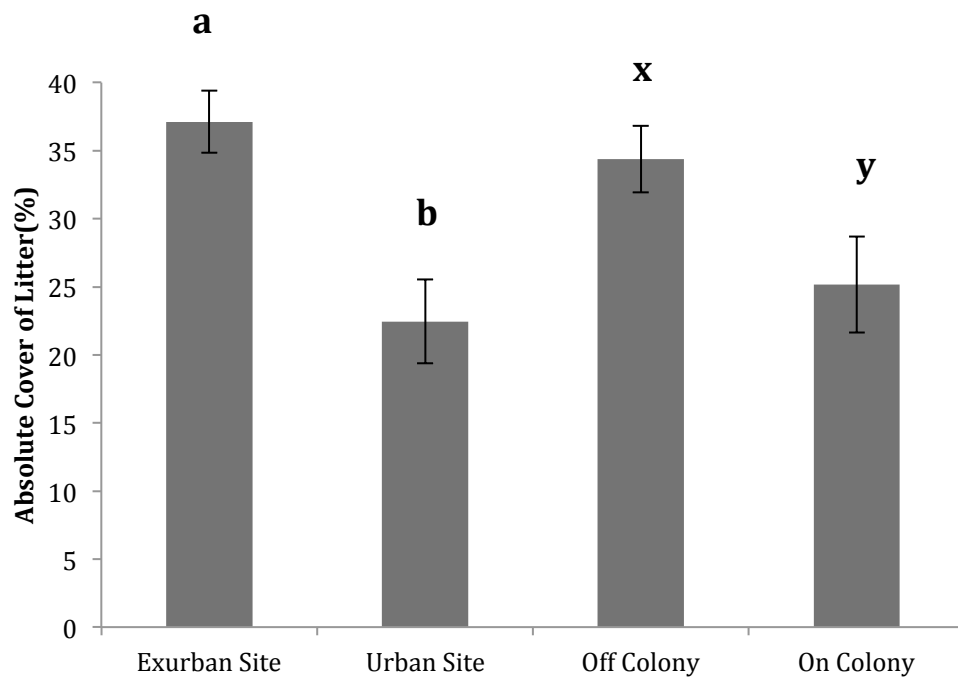


Figure 2. Absolute cover of litter observed from June-August at the urban and exurban sites both on and off the prairie dog colonies. Means with the same letter are not significantly different, Fishers LSD $\alpha=0.05$.

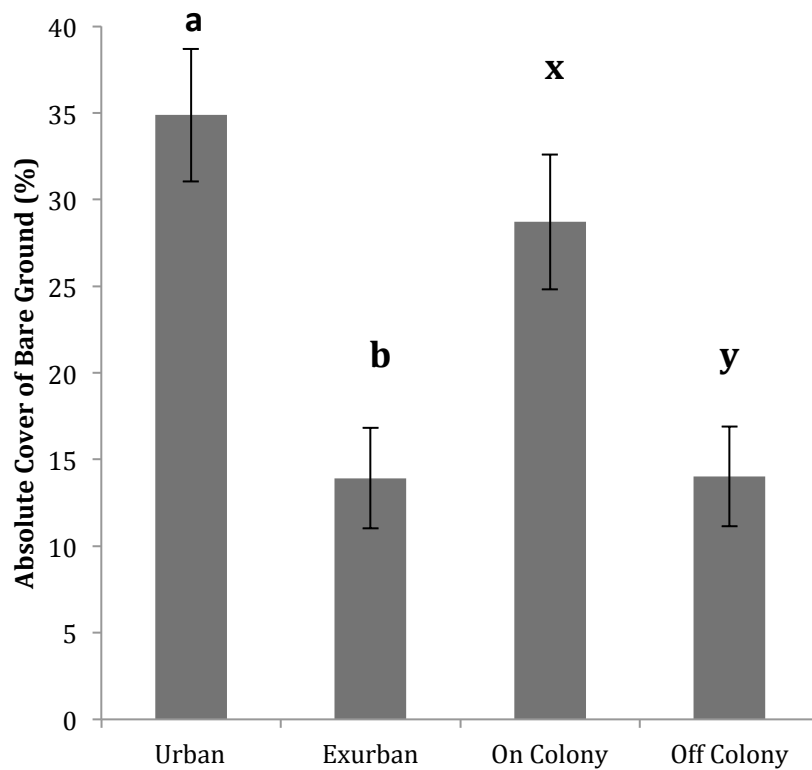


Figure 3. Absolute cover of bare ground observed from June-August at the urban and exurban sites both on and off the prairie dog colonies. Means with the same letter are not significantly different, Fishers LSD, $\alpha=0.05$.

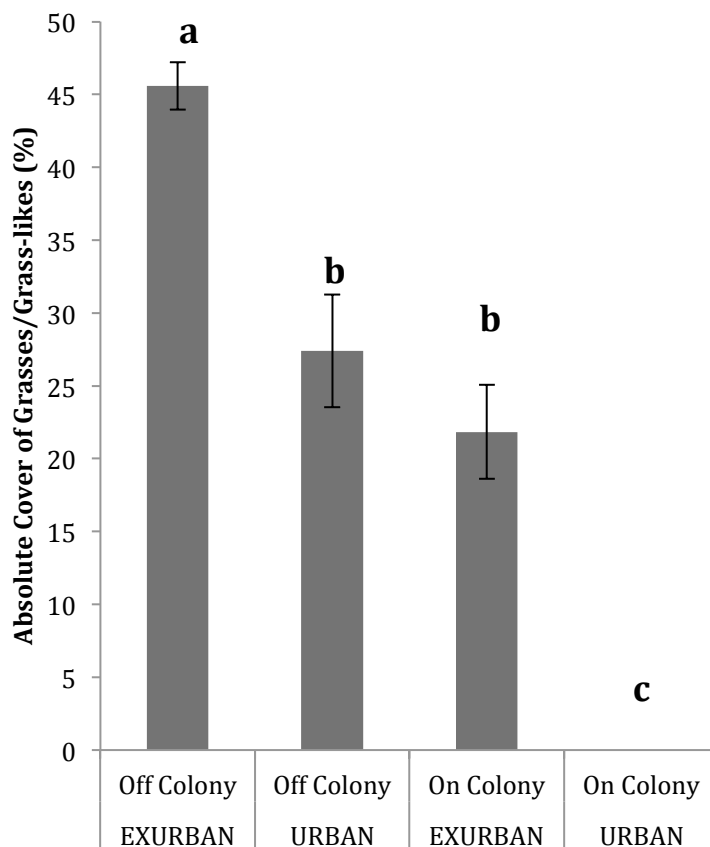


Figure 4. Absolute cover of grasses and grass-like species observed from June-August at the urban and exurban sites both on and off the prairie dog colonies. Means with the same letter are not significantly different, Fishers LSD, $\alpha=0.05$.

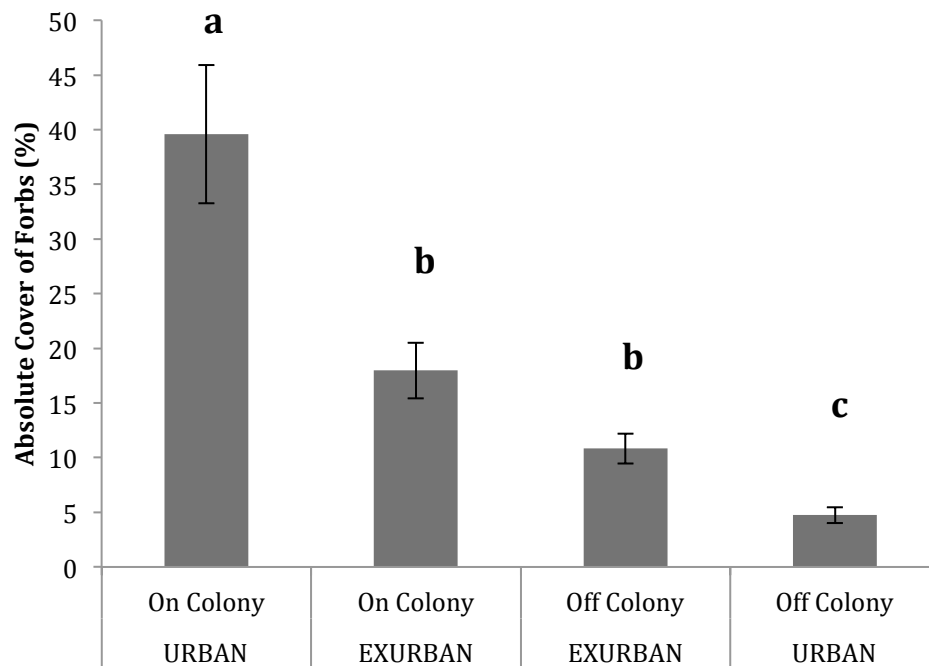


Figure 5. Absolute cover of forb species observed from June-August at the urban and exurban sites both on and off the prairie dog colonies. Means with the same letter are not significantly different, Fishers LSD, $\alpha=0.05$.

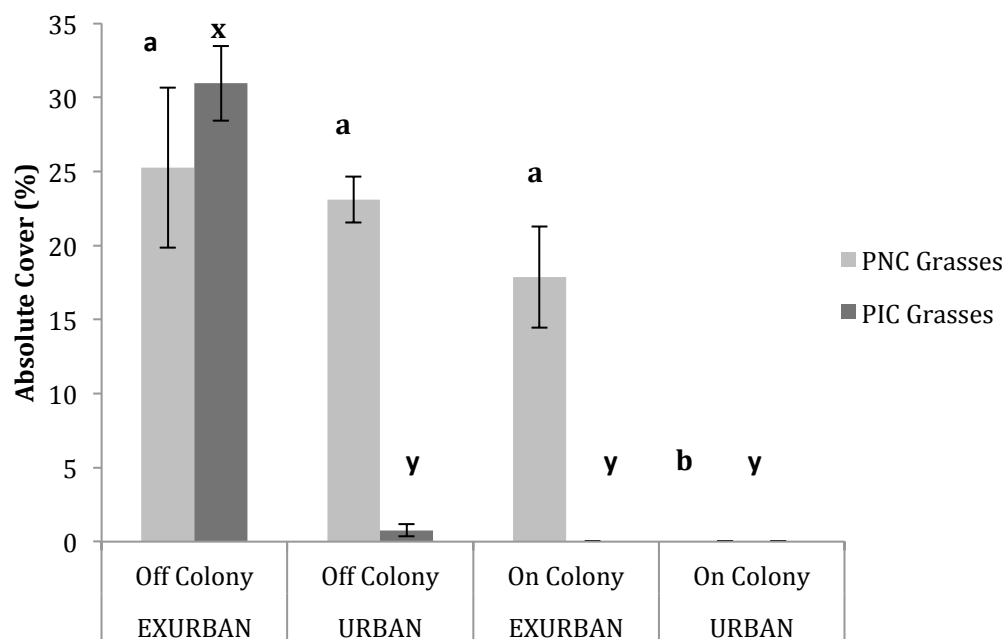


Figure 6. Absolute cover of perennial native cool season (PNC grasses) and perennial introduced cool season (PIC grasses) grasses and grass-likes observed in mid July at peak standing crop at the urban and exurban sites both on and off the prairie dog colonies. Means with the same letter (a and b for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

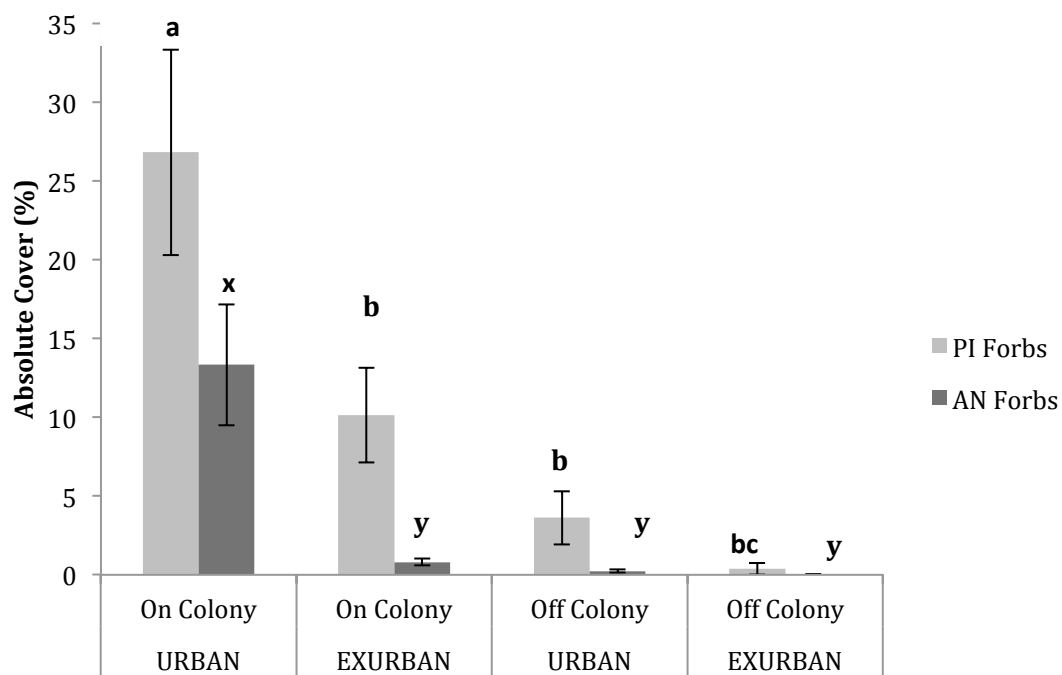


Figure 7 Absolute cover of perennial introduced forbs (PI Forbs) and annual native forbs (AN Forbs) observed in mid-July at peak standing crop at the urban and exurban sites both on and off the prairie dog colonies. Means with the same letter (a through c for PI Forbs; x and y for AN Forbs) are not different,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