

# Black-tailed Prairie Dog Colony Expansion and Forage Response to Fire/Grazing Interaction

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**Abstract:** Restoring historic fire/grazing interactions and increasing the population of the black-tailed prairie dog (*Cynomys ludovicianus*), a keystone species, are two management priorities for North America's grasslands. To evaluate the response of prairie dogs to the fire/grazing interaction, 2-ha plots of uncolonized mixed-grass prairie directly adjacent to active prairie dog colonies on Wichita Mountains Wildlife Refuge were burned in 2009 and 2010. Longhorn cattle (*Bos taurus*) and American bison (*Bison bison*) had access to the sites during both years thus replicating historic conditions where herbivores freely chose foraging patches. Prairie dogs responded positively to the fire/grazing interaction treatments by immediately colonizing all burned areas in both years, with the strongest response occurring in 2009 when precipitation during the growing season was lowest. There was no observed attempt to colonize any unburned (control) grasslands. When applied to appropriate sites, it appears that the fire/grazing interaction can create valuable habitat for dispersing prairie dogs which can aid in colony expansion and potentially improve conditions for colony establishment.

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**Key words:** American bison, patch-burning, pyric herbivory, Wichita Mountains

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Black-tailed prairie dogs (*Cynomys ludovicianus*) are a keystone species and an ecosystem engineer (Kotliar et al. 1999). They create and maintain critical habitat for a variety of wildlife, including over 163 vertebrate species. Prairie dog colonies have been shown to host many invertebrate and plant species at higher densities than surrounding uncolonized grasslands (Koford 1958, Wuerthner 1997, Winter et al. 2002). Native fauna which benefit from prairie dog colonies include threatened and endangered species such as the black-footed ferret (*Mustela nigripes*) and swift fox (*Vulpes velox*) (Johnsgard 2005, Hoogland 2006).

Similar to many grassland species, the black-tailed prairie dog has experienced significant rangewide population declines, estimated at rates as high as 98% (Johnsgard 2005). However, because it is often considered a nuisance species, the prairie dog has been subjected not only to habitat loss and degradation but also range-wide poisoning, trapping, sylvatic plague (*Yersinia pestis*), and recreational shooting (Barko 1997, Hoogland 2006). Due to these threats, the species has become functionally extinct in many areas as colonies have become smaller and increasingly isolated (Wuerthner 1997, Lomolino and Smith 2003).

Historically, black-tailed prairie dog colonies interacted as complexes when close to one another (<6.4 km). Restoration of intracolony (i.e., complex) interactions, including dispersal, has been listed as a primary goal of prairie dog conservation (Hoogland 2006). Black-tailed prairie dog dispersal and colony expansion

is concentrated during the growing season following the spring emergence of juveniles from natal burrows (Garrett and Franklin 1988). Dispersing individuals aid in the establishment and expansion of colonies within complexes, creating new family units (i.e., coterries) within the colony, immigrating to neighboring colonies, or leaving to establish new colonies. Prairie dog dispersal distances average 2.4 km with maximum recorded distances of 9.6 km (Hoogland 2006). Dispersal plays an important role in maintaining genetic integrity and stable populations within metapopulations (Garrett and Franklin 1988, Hoogland 2006). It also allows for the repopulation of colonies affected by human activities (trapping or poisoning), disease, or other stochastic events (Hoogland 2006).

Predation, infanticide, and inability to survive the winter are the three primary causes for prairie dog mortalities. Dispersing prairie dogs have a higher risk of predation while dispersing through or colonizing densely vegetated habitat than while on colonies or other areas with short, grazed or burned vegetation (Hoogland 2006). Additionally, infanticide and an inability to survive the winter can be related to overcrowding, which may be partially attributed to unsuitable habitat for colony expansion or establishment of new colonies within dispersal distance of the colony (Hoogland 1995). Conditions favorable for colonization include slopes of less than 6%; deep, well drained, medium textured soils; and low vegetation structure (<15 cm) (Hoogland 1995, Truett et al. 2001, Avila-

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Flores et al. 2010). While the first two characteristics cannot be manipulated, the third can be through the use of mowing, grazing, and/or fire. Northcott et al. (2008) suggest that reducing standing vegetation mimics conditions found on established prairie dog colonies and enhances predator detection and communication between prairie dogs. A site which offers these desired characteristics (soils, slope, and structure) may be more attractive to dispersing prairie dogs than sites with increased vertical structure.

Previously, prairie dogs were thought to compete with livestock for forage, but studies have shown that prairie dog-cattle relationships can be positive or negative depending on the productivity of the site, stocking rate of livestock, and density of prairie dogs (O'Meilia et al. 1982, Guenther and Detling 2003). Livestock may encourage colony expansion or facilitate colony persistence through grazing and trampling (Coppock et al. 1983b, Wuerthner 1997); however, under typical stocking rates in more productive grasslands, standing vegetation may still be too dense for colonization to occur (Koford 1958, Coppock et al. 1983b).

Recent studies have also found a positive correlation between fire and/or mowing and colonization (Milne-Laux and Sweitzer 2006, Augustine et al. 2007, Ford et al. 2008, Northcott et al. 2008). However, these studies were conducted in shortgrass steppe (Augustine et al. 2007) and desert grassland (Ford et al. 2008, Northcott et al. 2008); less productive grasslands where vegetation is sparser with inherently lower vertical structure. Additionally, some studies only considered colonies that were already expanding (Milne-Laux and Sweitzer 2006), and none considered large herbivore grazing, a common disturbance throughout the black-tailed prairie dog's range. Mowing is not a natural disturbance, and can be cost prohibitive, time consuming, or restricted by terrain or remoteness of a site (Ford et al. 2008). Conversely, fire can be applied on many scales and terrains in a cost and time efficient manner and has many ecological values in fire-dependent grasslands.

North America's grasslands are adapted to fire and grazing. However, today fire suppression and highly altered grazing practices have changed the management of grasslands within the range of the black-tailed prairie dog. Native large herbivores have been largely replaced with domestic livestock, and there exists a great disparity between historic grazing patterns of free-ranging, native herbivores (American bison [*Bison bison*], elk [*Cervus elaphus*], pronghorn [*Antilocapra americana*]) and fenced, domestic cattle (*Bos taurus*) (Coppock et al. 1983b, Hartnett et al. 1997, Steuter and Hiding 1999, Towne et al. 2005).

The application and interaction of fire and grazing, often called "patch burning" or "patch-burn grazing," is becoming increasingly popular among land managers (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). Patch-burn grazing has already been evalu-

ated for many species of plants (Fuhlendorf et al. 2006), grassland birds (Fuhlendorf et al. 2006, Churchwell et al. 2007, Coppedge et al. 2008), invertebrates (Fay 2003), domestic cattle (Vermeire et al. 2004), and bison (Coppedge and Shaw 1998, Biondini et al. 1999). Patch burning increases heterogeneity by performing both spatially and temporally randomized burns where only a portion of a pasture or management area is burned and herbivores are not restricted such that they choose grazing patches within the total area (Fuhlendorf and Engle 2001). Associated effects of patch-burn grazing include increased heterogeneity and increased forage quality (Shaw and Carter 1990, Coppedge and Shaw 1998, Biondini et al. 1999, Fuhlendorf and Engle 2001). Exhaustive evidence has shown that large herbivores such as bison and cattle are attracted to burned sites and that they influence fuel loads and alter the intensity and probability of future fires occurring on a given site (Coppedge and Shaw 1998, Fuhlendorf et al. 2009). It is this mosaic of burned/grazed patches and unburned/ungrazed patches that prairie dogs evolved under. This fire/grazing interaction management style is today largely absent within the range of the black-tailed prairie dog and the effects on prairie dogs is unknown.

Growing interest in restoring functioning metapopulations and complexes and managing existing colonies of prairie dogs warrants further study of habitat management methods. By applying prescribed burns adjacent to colonies in the spring prior to dispersal, habitat suitable for colonization may be provided for dispersing prairie dogs. We sought to examine the combined effects of prescribed fire and grazing by large herbivores (Texas longhorn cattle and American bison), as compared to the more common management practice of grazing large herbivores without fire, on colony expansion rates of black-tailed prairie dogs to provide guidance on habitat management for this keystone species. While fire and grazing independently will undoubtedly have varying effects, such studies have been exhaustively conducted for many systems and species. Further, separating these disturbances is not ecologically appropriate and inhibits an understanding of historic conditions and how to mimic them at present.

## Study Area

Three study sites were located on the U.S. Fish and Wildlife Service's (USFWS) Wichita Mountains Wildlife Refuge (WMWR) in Comanche County in southwest Oklahoma. The refuge is 23,885 ha of mixed-grass prairie, short-grass prairie, and crosstember forest (USFWS 2002). WMWR was established for the preservation of the American bison and Texas longhorn cattle. Large patches of the refuge are burned on a rotational basis to create a landscape of diverse habitat conditions for wildlife. Livestock are not excluded from any burned areas. Animals may freely move across the landscape and

choose forage patches. Thus, the refuge mimics the historic disturbance patterns that the Great Plains flora and fauna evolved with.

Precipitation is highly variable between years, but averages 79 cm, occurring on an average of 61 days per year. The annual average temperature is 17 C with average highs and lows of 36 and -3 C, respectively. Growing seasons are typically 218 days (OCS 2010).

The refuge has a total of 11 soil types. Several soils supporting grasslands have clay pans which inhibit prairie dog colonization. Still, most of the grasslands are on silty loam to silty clay soils with slopes between zero and 5% (Crockett 1964). Black-tailed prairie dogs historically occurred scattered in suitable soils throughout most of the WMWR, but were removed in the 1920s (P.J. Depuy, Bureau of Biological Survey, unpublished report; A.A. Putnam, Bureau of Biological Survey, unpublished report). Black-tailed prairie dog colonies were reestablished with translocated prairie dogs beginning in 1991 (W. Munsterman, U.S. Fish and Wildlife Service, personal communication). When this study was initiated, three prairie dog colonies occupied approximately 26 ha.

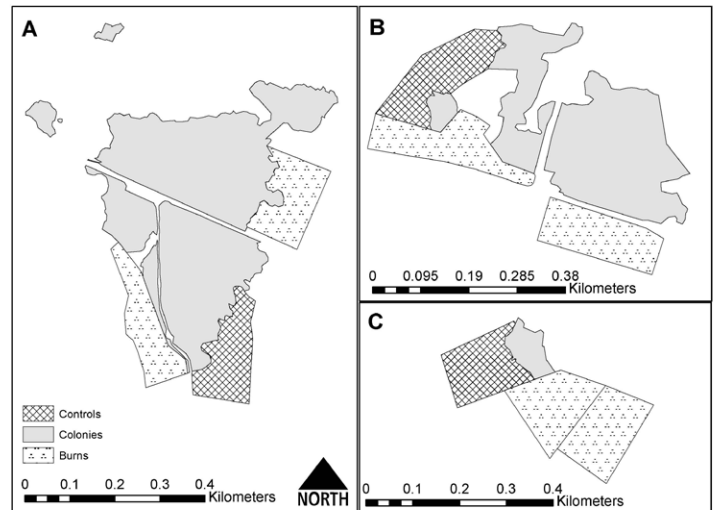
The three prairie dog colonies monitored in our study were Turkey Creek colony, Holy City colony, and Quanah Parker colony. These three colonies ranged in size from 0.70 to 15 ha with well-drained deep loam to clay loam soils with 25% to 70% granite cobblestones and scattered boulders.

## Methods

### Prescribed Fire and Grazing Treatments

On 23 and 24 March 2009, prior to juvenile emergence and yearling dispersal, 2-ha treatment plots were burned adjacent to each prairie dog colony. On 29 March 2010, new 2-ha plots were established and likewise burned adjacent to each colony. Thus, each colony had an adjacent burned (treatment) plot each year. Additionally, 2-ha unburned (control) plots of native grassland were established directly adjacent to each colony at the beginning of the study (Figure 1). Control plot locations were the same in both years of study. Where possible, control and treatment plots were adjacent to one another in order to have the most uniform conditions. Control and treatment plots had comparable vegetation structure, slope, and soil types at each site that were sufficient to allow prairie dog excavation of new burrows. Additionally, no prairie dogs or active burrows were detected within control and treatment plots at the initiation of the study.

American bison and Texas longhorn cattle had equal and continuous access to all plots in both years of study. The refuge maintains herds of 650 bison and 280 cattle; however, these numbers will vary throughout the year due to reproduction. The timing of our study coincided with the calving season (April and May; Meagher 1986), and therefore densities may have been slightly el-

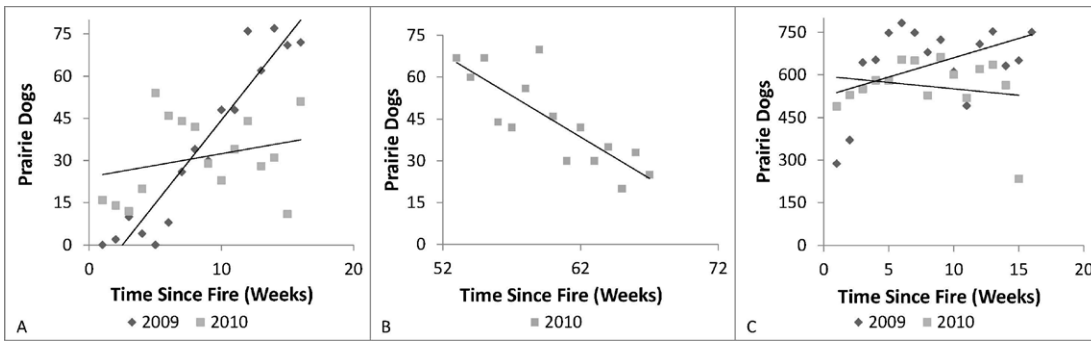


**Figure 1.** Location of Holy City (a), Turkey Creek (b), and Quanah Parker (c) black-tailed prairie dog colonies, control plots, and fire-grazing interaction treatment plots at the Wichita Mountains Wildlife Refuge, Lawton, Oklahoma, for 2009 and 2010.

evated. Thus, estimated stocking densities of <37 ha per bison, <85 ha per head of cattle are likely conservative. As the purpose of this study was to mimic historic grazing conditions where herbivores freely choose grazing patches on large landscapes, grazers were not artificially concentrated or excluded and were free to graze at will during the study period. We only report stocking densities and species of grazers to acknowledge that a fire-grazing interaction occurred.

### Population Assessment and Observations

Following the application of all prescribed fire treatments, weekly counts of prairie dogs were completed at each site for colony, treatment, and control plots to detect colony expansion into plots. Colonization was defined as any excavation and habitation of new burrows in the treatment and control plots. Surveys were conducted from 3 April to 30 July 2009 and 6 April to 20 July 2010. Maximum counts were recorded using alternating 15-minute count and rest intervals totaling three counts and two rests. Additionally, the total number of prairie dogs observed foraging during each survey period was recorded as a measure of activity among plot types (control, treatment, and colony). Counts were conducted following the survey protocol described by Menkens and Anderson (1993) and Milne-Laux and Sweitzer (2006). All observations were made from an elevated location with a spotting scope (15x–45x, Denali by Eagle Optics, Middleton, Wisconsin) and binoculars (10x42, Crossfire by Vortex Optics, Middleton, Wisconsin) as appropriate.



**Figure 2.** Black-tailed prairie dog abundance on burn treatments <1 year old (a; 2009:  $t_1 = 11.84, r^2 = 0.91, \beta = 5.93, P < 0.001$ ; 2010:  $t_1 = 1.06, r^2 = 0.075, \beta = 0.83, P = 0.31$ ), burn treatments >1 year old (b; 2010:  $t_1 = -5.15, r^2 = 0.67, \beta = -2.97, P < 0.001$ ), and prairie dog colonies (c; 2009:  $t_1 = 1.92, r^2 = 0.21, \beta = 13.61, P = 0.075$ ; 2010:  $t_1 = -0.7, r^2 = 0.037; \beta = -4.51, P = 0.49$ ) at the Wichita Mountains Wildlife Refuge, Lawton, Oklahoma for 2009 and 2010.

**Spatial Data**

A Garmin eTrex Vista HCx (Olathe, Kansas) global positioning system was used to record treatment boundaries and census active burrows (Augustine et al. 2007). Colony boundaries, which are quite distinct, were determined using vegetation height and burrow distribution (Magle et al. 2007). Burrow counts were conducted during periods of stable weather at the beginning, middle, and end of each field growing season (or April, May, and August), using the presence of fresh scat, fresh digging, or visual observation of use to determine whether a burrow was active (Severson and Plumb 1998, Augustine et al. 2007).

**Data Analysis**

Prairie dog observation data were analyzed using simple linear regression (PROC REG), plotting the change in number of prairie dogs (y) across time (x; weeks) (SAS 2003). Data were analyzed separately for 2009 and 2010 due to significant differences in precipitation patterns and prairie dog responses between years. Plots of residuals were examined to ensure that regression assumptions of normality were met for data. A Chi-square test was used to compare foraging effort (i.e., proportion of foraging prairie dogs) between controls, colonies, and burned treatments (Zar 1999, SAS 2003). All inferential tests with  $P < 0.05$  were considered significant. Burrow counts were summarized and are presented as supplementary information as an indication and validation of prairie dog colony expansion rather than foraging activity alone. However, due to the highly correlated nature of burrow density and prairie dog density, we do not include inferential test results for burrows.

**Results**

**Populations**

Pretreatment black-tailed prairie dog populations were zero on all treatment and control plots in both years. Prairie dogs colonized

all burned treatments in both years; there was no prairie dog colonization of controls during the entire study period. There was a significant increase in the number of prairie dogs within all burn treatments in 2009 (Figure 2a). This was true when sites were analyzed separately or collectively (i.e., all colonies combined; Table 1). Maximum prairie dog counts within treatment plots were 17 (HC), 58 (TC), and 36 (QP) animals during 2009. Populations on the source colonies increased throughout the 2009 growing season (Figure 2c); however, this was only significant on HC colony (Table 1).

Similarly in 2010, black-tailed prairie dog populations increased within all treatment plots that were less than 12 months old (i.e., 2010 treatments; Figure 2a), but this was only significant at QP colony (Table 2). Maximum populations within 2010 treatment plots were 14 (HC), 32 (TC), and 19 (QP) prairie dogs. There were no significant changes in the source colony populations and population growth was variable between colonies in 2010 (Figure 2c; Table 2).

In 2010, black-tailed prairie dog counts significantly declined within the 2009 burn treatments at two of the three sites (Turkey Creek and Quanah Parker; Figure 2b, Table 2). Although prairie dog abundance did decrease over time, all three 2009 burn treat-

**Table 1.** Simple linear regression of black-tailed prairie dog populations in 2009 on 2-ha burns <1 year time since fire (<1Y TSF) and colonies (COL) at Holy City (HC), Turkey Creek (TC), Quanah Parker (QP), and all three sites combined (TOTAL) at the Wichita Mountains Wildlife Refuge, Lawton, Oklahoma.

Site	Plot	$t_1$	$r^2$	$\beta$	$P$
HC	<1Y TSF	6.95	0.78	1.05	<0.001
TC	<1Y TSF	5.69	0.70	3.31	<0.001
QP	<1Y TSF	3.95	0.53	1.56	0.002
TOTAL	<1Y TSF	11.84	0.91	5.93	<0.001
HC	COL	4.22	0.56	7.7	<0.001
TC	COL	1.19	0.091	5.73	0.26
QP	COL	3.95	0.0018	0.18	0.88
TOTAL	COL	1.92	0.21	13.61	0.075

**Table 2.** Simple linear regression of black-tailed prairie dog populations in 2010 on 2-ha burns <1 year time since fire (<1YTSF), 2-ha burns >1 year time since fire (>1YTSF), and colonies (COL) at Holy City (HC), Turkey Creek (TC), Quana Parker (QP), and all three sites combined (TOTAL) at the Wichita Mountains Wildlife Refuge, Lawton, Oklahoma.

Site	Plot	$t_i$	$r^2$	$\beta$	$P$
HC	<1YTSF	0.38	0.011	0.12	0.71
TC	<1YTSF	0.36	0.009	0.76	0.73
QP	<1YTSF	2.20	0.26	0.66	0.045
TOTAL	<1YTSF	1.06	0.075	0.83	0.31
HC	COL	1.17	0.095	1.86	0.26
TC	COL	1.02	0.080	2.69	0.33
QP	COL	-0.59	0.024	-0.43	0.056
TOTAL	COL	-0.70	0.037	-4.51	0.49
HC	>1YTSF	-0.36	0.0098	-0.06	0.73
TC	>1YTSF	-7.66	0.81	-2.04	0.001
QP	>1YTSF	-2.53	0.31	-0.78	0.024
TOTAL	>1YTSF	-5.15	0.67	-2.97	0.001

ments remained colonized throughout the study period with minimum and maximum counts of 4 and 14 (HC), 5 and 39 (TC), and 5 and 30 (QP) animals, respectively.

### Burrows

As with black-tailed prairie dog abundance, pretreatment burrow densities were zero within all control and treatment plots. Additionally, no prairie dog burrows were detected within controls at any time during the study period. However, similar to prairie dog abundance, burrows increased within all treatment plots in 2009 with maximum burrow counts of 19 (HC), 34 (TC), and 55 (QP). Burrows within source colonies declined or remained stable throughout the 2009 growing season. Further, in 2010 burrows increased within treatment plots <12 months old (i.e., 2010 treatments) to maximums of 35 (HC), 62 (TC), 24 (QP) burrows. However, burrows decreased following exceptional precipitation events in June and July 2010 which led to significant flooding of prairie dog burrows. Burrows decreased within treatment plots >12 months old (i.e., 2009 treatments) during 2010. Source colony burrow counts remained stable or declined, depending on colony, throughout the 2010 growing season. Colonies had maximum active burrow counts of 1225 (HC), 1738 (TC), and 103 (QP) in 2009 and 872 (HC), 1433 (TC), and 111 (QP) in 2010.

### Foraging

Black-tailed prairie dog foraging effort was not significantly different between colonies and treatment plots ( $\chi^2 = 5.99$ ,  $P = 0.995$ ). As no prairie dogs were ever observed in control plots, there was no foraging detected. The total average proportion of animals foraging (all areas combined) was  $72 \pm 0.03\%$  on colonies,  $68 \pm 0.38\%$

on treated plots <12 months old, and  $66 \pm 0.04\%$  on treated plots >12 months old. Colonies, treatments plots, and control plots did not show differences within plot type, thus summary data is reported for between plot type only.

### Discussion

Black-tailed prairie dogs responded to changes in site conditions following the application of the fire/grazing interaction in both years of study. Although only significant in 2009, combination of treatment plots sharply contrasted controls in both years, with consistent lack of prairie dog colonization of controls throughout the study. Thus, colony expansion differed within mixed-grass prairie managed with fire/grazing interaction versus grazing alone.

The affinity of prairie dogs for burned treatments has been explained by reductions in standing vegetation (Augustine et al. 2007, Northcott et al. 2008, Ford et al. 2008). The maximum height of vegetation in mixed-grass prairie controls exceeded 80 cm in some areas (A. Breland, Oklahoma State University, unpublished data) and far surpassed maximum heights of vegetation on established colonies (5–10 cm; Whicker and Detling 1988, Guenther and Detling 2003) and the suggested maximum height for sites suitable for future colonization (20–30 cm; Knowles et al. 2002). In the absence of large grazers, prairie dogs might not be expected to colonize burns as readily in productive grasslands.

The decreased numbers of prairie dogs within burn units in year 2 is not surprising as previous research indicates that increased plant height and decreased plant palatability results in less herbivore attraction (Biondini et al. 1999). Focal grazing by large ungulates is important in the mediation of post-burn vegetation heights (Fuhlendorf and Engle 2001). Large herbivores which were grazing the 2009 treatment plots were redistributed, consistent with the literature, to more recent burn treatments completed in 2010, releasing these older treatment plots from grazing pressure. Had there been a single burn treatment during this study, large ungulate grazing may have been sustained in both years and coterries may have persisted. Higher stocking densities might also increase the colonization response; however, this is yet untested.

While reduction of vertical structure provides a logical explanation, it is also a very simplistic view. Some additional factors which likely attract prairie dogs to grazed and burned sites include increased forage palatability and reduced litter. All of these are qualities common, consistent, and well established in the literature to both burned patches and prairie dog colonies (Coppock et al. 1983a, Wilson and Shay 1990, Fahnestock and Detling 2002). Comparable foraging effort in recently burned areas and colonies suggests similar quantity and quality of forage. Similar foraging effort also showed that the prairie dogs within the burned treat-

ments were able to maintain a clipped colony area with similar effort as that required in established colonies.

The colonization response to habitat manipulation can be attributed to many factors, including weather, population density, and predation (Milne-Laux and Sweitzer 2006). Augustine et al. (2007) linked stronger responses to burn treatments to yearly precipitation patterns, suggesting that stronger responses may be observed in wet years when biomass production is higher. We also observed a relationship between colonization of burns and precipitation; however, we found that above average precipitation reduced the colonization response to burn treatments on the Turkey Creek and Holy City colonies. Augustine et al.'s (2007) study took place in shortgrass prairie where vegetation density and structure is likely not as limiting as in the more productive grasslands of Oklahoma's mixed-grass prairie and precipitation patterns are markedly different. We suspect that the limited colonization response in 2010 was due to either increases in plant biomass production which limited expansion, burrow flooding which increased mortality, or a combination of these factors. As the prairie dog counts dropped rapidly following flooding, prairie dog mortality likely occurred which influenced trends.

It should be noted that our study sites were located on the extreme eastern boundary of the black-tailed prairie dog's current range, where dense vegetation is likely more limiting than elsewhere. This may explain why there was no colonization of controls at our study sites, unlike the shortgrass studies in which colonies expanded into controls and burns (Augustine et al. 2007, Milne-Laux and Sweitzer 2006). Thus, it is probable that fire and large ungulate grazing were critical forces behind the colonization and perhaps maintenance of colonies along the extreme eastern edge of the black-tailed prairie dog's historic range. Without these disturbances, prairie dogs might have had a range restricted to less productive grasslands or been absent.

### Management Recommendations

Given the responses of prairie dogs to prescribed fire and grazing in multiple studies and our current understanding of how fire can benefit grassland diversity, restoration of the fire/grazing interaction should be considered in habitat management for the black-tailed prairie dog (Milne-Laux and Sweitzer 2006, Augustine et al. 2007, Northcott et al. 2008). Our data certainly support this. This could be especially true on more productive sites where vegetation structure is limiting expansion of colonies. Where vegetation height is limiting to prairie dogs, fire may have the ability to influence the direction of expansion to direct colonization away from conflict areas such as agricultural crop fields. Further work is needed to evaluate this.

Wuerthner (1997) equates the historic ecological impacts of prairie dog disturbance to that of wildfire and bison, suggesting that the effects of prairie dogs may have even surpassed these other disturbance forces. Throughout the range of the black-tailed prairie dog, restoration of prairie dog fire-grazing interactions should be a primary management goal, if grassland ecosystems are to function similarly to historic patterns.

Effective management of individual colonies as well as landscapes will be necessary to promote colony stability, growth, and connectivity. Colony complexes promote successful inter-colony dispersal, which can aid in the resilience of colonies exposed to disease, heavy predation, or other mortality (Lomolino and Smith 2001). Although we examined the expansion of existing colonies, fire and grazing may have the potential to initiate new colonies within a complex. This could be especially true when coupling vegetation management with relocation (Truett et al. 2001, Avila-Flores et al. 2010). To restore the black-tailed prairie dog to ecologically significant levels, active habitat management must be incorporated into prairie dog conservation.

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### Literature Cited

- Augustine, D.J., J.F. Cully, Jr., and T.L. Johnson. 2007. Influence of fire on black-tailed prairie dog colony expansion in shortgrass steppe. *Range-land Ecology and Management* 60:538–542.
- Avila-Flores, R., M.S. Boyce, and S. Boutin. 2010. Habitat selection by prairie dogs in a disturbed landscape at the edge of their geographic range. *Journal of Wildlife Management* 74:945–953.
- Barko, V.A. 1997. History of the policies concerning the black-tailed prairie dog: a review. *Proceedings of the Oklahoma Academy of Sciences* 77:27–33.
- Biondini, M.E., A.A. Steuter, and R.G. Hamilton. 1999. Bison use of fire-managed remnant prairies. *Journal of Range Management* 52:454–461.
- Churchwell, R.T., C.A. Davis, S.D. Fuhlendorf, and D.M. Engle. 2007. Effects of patch burn management on dickcissel nest success in a tallgrass prairie. *Journal of Wildlife Management* 72:1596–1604.
- Coppedge, B.R., S.D. Fuhlendorf, W.C. Harrell, and D.M. Engle. 2008. Avian community response to vegetation and structural features in grasslands managed with fire and grazing. *Biological Conservation* 141:1196–1203.
- \_\_\_\_\_, and J.H. Shaw. 1998. Bison grazing patterns on seasonally burned tall-grass prairie. *Journal of Range Management* 51:258–264.
- Coppock, D.L., J.K. Detling, J.E. Ellis, and M.I. Dyer. 1983a. Plant-herbivore interactions in a North American mixed-grass prairie I. Effects of black-

- tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* 56:1–9
- \_\_\_\_\_, \_\_\_\_\_, \_\_\_\_\_, and \_\_\_\_\_. 1983b. Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. *Oecologia* 56:10–15.
- Crockett, J.J. 1964. Influence of soils and parent materials on grasslands of the Wichita Mountains Wildlife Refuge, Oklahoma. *Ecology* 45:326–335.
- Fahnestock, J.T. and J.K. Detling. 2002. Bison-prairie dog-plant interactions in a North American mixed-grass prairie. *Oecologia* 132:86–95.
- Fay, P.A. 2003. Insect diversity in two burned and grazed grasslands. *Environmental Entomology* 32:1099–1104.
- Ford, P.L., M.C. Andersen, E.L. Fredrickson, J. Truett, and G.W. Roemer. 2008. Effects of fire and mowing on expansion of re-established black-tailed prairie dog colonies in Chihuahuan Desert grassland. USDA Forest Service General Technical Report PSW-FTR-189.
- Fuhlendorf, S.D. and D.M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* 51:625–632.
- \_\_\_\_\_, \_\_\_\_\_, J. Kerby, and R. Hamilton. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology* 23:588–598.
- \_\_\_\_\_, W.C. Harrell, D.M. Engle, R.G. Hamilton, C.A. Davis, and D.M. Leslie, Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecological Applications* 16:1706–1716.
- Garrett, M.G. and W.L. Franklin. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. *Journal of Mammalogy* 69:236–250.
- Guenther, D.A. and J.K. Detling. 2003. Observations of cattle use of prairie dog towns. *Journal of Range Management* 56:410–417.
- Hartnett, D.C., A.A. Steuter, and K.R. Hickman. 1997. Comparative ecology of native and introduced ungulates. Pages 73–101 in F.L. Knopf and F.B. Samson, editors. *Ecology and conservation of Great Plains vertebrates*. Springer-Verlag, New York, New York.
- Hoogland, J.L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois.
- \_\_\_\_\_. 2006. Conservation of the black-tailed prairie dog: saving North America's western grasslands. Island Press, Washington D.C.
- Johnsgard, P.A. 2005. Prairie dog empire: a saga of the shortgrass prairie. University of Nebraska Press, Lincoln, Nebraska.
- Knowles, C., J. Proctor, and S. Forest. 2002. Black-tailed prairie dog abundance and distribution in the Great Plains based on historic and contemporary information. *Great Plains Research* 12:219–254.
- Koford, C.B. 1958. Prairie dogs, whitefaces, and blue grama. *Wildlife Monographs* 3:1–78.
- Kotliar, N.B., B.W. Baker, and A.D. Whicker. 1999. A critical review of assumptions about the prairie dog as a keystone species. *Environmental Management* 24:177–192.
- Lomolino, M.V. and G.A. Smith. 2001. Dynamic biogeography of prairie dog (*Cynomys ludovicianus*) towns near the edge of their range. *Journal of Mammalogy* 82:937–945.
- \_\_\_\_\_ and \_\_\_\_\_. 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.
- Magle, S.B., B.T. McClintock, D.W. Tripp, G.C. White, M.F. Antolin, and K.R. Crooks. 2007. Techniques and technology note: mark-resight methodology for estimating population densities for prairie dogs. *Journal of Wildlife Management* 71:2067–2073.
- Meagher, M. 1986. Mammalian species: *Bison bison*. American Society of Mammalogists 266:1–8.
- Menkens, G.E., Jr. and S.H. Anderson. 1993. Mark-recapture and visual counts for estimating population size of white-tailed prairie dogs. Pages 62–72 in J.L. Oldemeyer, D.E. Biggins, and B.J. Miller, editors. *Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret*. Biological Report 13. U.S. Fish and Wildlife Service, Washington, D.C.
- Milne-Laux, S. and R.A. Sweitzer. 2006. Experimentally induced colony expansion by black-tailed prairie dogs (*Cynomys ludovicianus*) and implications for conservation. *Journal of Mammalogy* 87:296–303.
- Northcott, J., et al. 2008. Spatial analysis of effects of mowing and burning on colony expansion in reintroduced black-tailed prairie dog (*Cynomys ludovicianus*). *Restoration Ecology* 16:495–502.
- Oklahoma Climatological Survey (OCS). 2010. Oklahoma climate data pages. <[http://climate.mesonet.org/monthly\\_summary.html](http://climate.mesonet.org/monthly_summary.html)>. Accessed 10 Sep 2010.
- O'Meilia, M.E., F.L. Knopf, and J.C. Lewis. 1982. Some consequences of competition between prairie dogs and beef cattle. *Journal of Range Management* 35:580–585.
- SAS Institute 2003. Version 9.1.3. SAS Institute, Inc. Cary, North Carolina.
- Severson, K.E. and G.E. Plumb. 1998. Comparison of methods to estimate population densities of black-tailed prairie dogs. *Wildlife Society Bulletin* 26:859–866.
- Shaw, J.H. and T.S. Carter. 1990. Bison movements in relation to fire and seasonality. *Wildlife Society Bulletin* 18:426–430.
- Steuter, A. and L. Hiding. 1999. Comparative ecology of bison and cattle on mixed-grass prairie. *Great Plains Research* 9:329–342.
- Towne, E.G., D. Hartnett, and R.C. Cochran. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. *Ecological Applications* 15:1550–1559.
- Truett, J.C., J.L. Dullum, M.R. Matchett, E. Owens, and D. Seery. 2001. Translocating prairie dogs: a review. *Wildlife Society Bulletin* 29:863–872.
- U.S. Fish and Wildlife Service (USFWS). 2002. Briefing information. USFWS Wichita Mountains Wildlife Refuge, Indianola, Oklahoma.
- Vermeire, L.T., R.B. Mitchell, S.D. Fuhlendorf, and R.L. Gillen. 2004. Patch burning effects on grazing distribution. *Journal of Range Management* 57:248–252.
- Whicker, A.D. and J.K. Detling. 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38:778–785.
- Wilson, S.D. and J.M. Shay. 1990. Competition, fire, and nutrients in a mixed-grass prairie. *Ecology* 71:1959–1967.
- Winter, S.L., J.F. Cully, Jr., and J.S. Pontius. 2002. Vegetation of prairie dog colonies and non-colonized shortgrass prairie. *Journal of Range Management* 55:502–508.
- Wuerthner, G. 1997. Viewpoint: the black-tailed prairie dog—headed for extinction? *Journal of Range Management* 50:459–466.
- Zar, J.H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Upper Saddle River, New Jersey.