

BLACK-TAILED PRAIRIE DOG
AND LARGE UNGULATE RESPONSE TO
FIRE ON MIXED-GRASS PRAIRIE

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CHAPTER I

BLACK-TAILED PRAIRIE DOG RESPONSE TO FIRE AND GRAZING

Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) are a keystone species and an ecosystem engineer (Kotliar et al. 1999). Throughout its range the black-tailed prairie dog creates and maintains critical habitat for a wide variety of wildlife including over 163 vertebrate species (Wuerthner 1997). Additionally, many invertebrates and plants occur on colonies at higher densities than on uncolonized grasslands (Koford 1958, Winter et al. 2002). Although not necessary for the entire life history of many of these organisms, several species of conservation concern rely on prairie dog colonies for food and cover resources. As concern for threatened and endangered species conservation grows, restoration of prairie dogs for the benefit of wildlife such as the black-footed ferret (*Mustela nigripes*) and swift fox (*Vulpes velox*) does as well (Johnsgard 2005, Hoogland 2006).

Like many grassland species experiencing habitat loss, degradation, and isolation, the prairie dog has experienced significant rangewide population declines. These declines have been estimated to be 98% (Johnsgard 2005). Unlike many other wildlife species, the

prairie dog has been subjected to range-wide poisoning, trapping, and recreational shooting as it is often considered a nuisance animal. An introduced disease, sylvatic plague (*Yersinia pestis*), causes 90 to 100% mortality in infected colonies (Barko 1997, Hoogland 2006). While prairie dogs persist across a broad range of North America's grasslands, the species has become functionally extinct in many areas as colonies have become smaller and more isolated (Wuerthner 1997, Lomolino and Smith 2003).

To restore the black-tailed prairie dog to ecologically significant levels, habitat management must shift to accommodate prairie dogs at the landscape level rather than simply preserve existing colonies. This will entail increasing colonization of potentially suitable habitat and connecting existing colonies to allow for increased genetic movement. However, few studies have examined how land management practices might facilitate prairie dog colonization and expansion to restore functioning metapopulations.

Prairie dogs are highly social with multiple levels within their social structure. From simplest to most complex, these include coterie, colonies, and metapopulations. The most basic unit is the coterie, a family group typically containing a breeding male, 2 or 3 adult females, and their offspring (Hoogland 1995). Occasionally a coterie will have two males, a father-son pair, but it is more common for yearling males to disperse (Hoogland 2006). Due to the highly territorial nature of the species, dispersed individuals are not commonly accepted by other coterie within a colony. Therefore, dispersing prairie dogs often must either establish their own coterie or immigrate to a neighboring colony (Hoogland 1995). Survival rates are very low for these dispersing prairie dogs (Garrett and Franklin 1988), yet they are critical to prairie dog persistence.

Colonies are not necessarily isolated units and typically interact as a complex when close to one another (<6.4 km) and not separated by an impenetrable barrier. Movement of individuals primarily occurs during dispersal. Although highly variable, dispersal distance averages 2.4 kilometers with maximum distances of 9.6 kilometers (Hoogland 2006). Dispersal plays an important role in maintaining genetic integrity and stable populations within metapopulations (Garrett and Franklin 1988, Hoogland 2006). Occasionally, prairie dog colonies will be depopulated by human activities (trapping or poisoning), disease, or other stochastic events. Dispersal from nearby colonies is necessary to repopulate these areas. Arguably, this has become increasingly important since the introduction of plague to black-tailed prairie dogs in 1947 (Hoogland 2006). Thus, having colonies within reasonable dispersal distance should be a management priority for prairie dog recovery.

Prairie dog colony expansion is concentrated in May, June, and July (Garrett and Franklin 1988). During this time juveniles have recently emerged from natal burrows and prairie dog densities are at their highest, likely creating an increased competition for resources (Koford 1958, Hoogland 1996, Hoogland 2006). Others suggest that prairie dogs disperse once they are sexually mature in order to prevent in-breeding within coterries, or family units (Hoogland 1996). Regardless of the reason, dispersal of prairie dogs is vital to gene flow between populations.

Conditions favorable for colonization include slopes of <6 percent; deep, well drained, medium textured soils; and low vegetation structure (<15 cm; Hoogland 1995, Truett et al. 2001, Avila-Flores et al. 2010). While the first two characteristics cannot be manipulated, the third can be. Northcott et al. (2008) suggest that reducing standing

vegetation mimics conditions found on established prairie dog colonies, enhancing predator detection and communication between prairie dogs, which includes both visual and auditory signals. 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.

Most vegetation within a colony is kept clipped close to the ground by prairie dogs to maintain a defined perimeter and increase visibility for predator detection. Thus plants are clipped regardless of palatability to prairie dogs (Hoogland 1995, Roe and Roe 2003). This inherently increases levels of heterogeneity within grasslands and shrublands. Even abandoned colonies are often visible on the landscape for many years following localized prairie dog extirpation. Burrows and plant community characteristics persist within these remnant colonies and provide sites that can readily be recolonized by dispersing prairie dogs (Knowles et al. 2002).

While prairie dog colonies obviously create heterogeneity within grasslands there also exists heterogeneity within the colonies themselves. The central, oldest portion of an active colony is typically dominated by a forb and/or dwarf shrub plant community, and the younger perimeter of a colony consists of grasses more suitable for large ungulate grazing (Koford 1958, Hoogland 2006). Although burrow mounds have less vegetative cover than surrounding colonized areas, these highly disturbed sites often support species not encountered elsewhere within grasslands (Hoogland 2006).

Black-tailed prairie dogs are selective herbivores with diets that vary seasonally and spatially. In the summer months, prairie dogs consume graminoids such as buffalo

grass (*Buchloe dactyloides*), purple three awn (*Aristida purpurea*), tumblegrass (*Schedonnardus paniculatus*), and brome (*Bromus spp.*; Fagerstone et al. 1981). During the winter prairie dogs feed on prickly pear cactus (*Opuntia macrorhiza*) and thistle (*Cirsium spp.*; Koford 1958, Fagerstone et al. 1981, Hoogland 1995). Diet varies within a colony to reflect the structural and compositional patterns of vegetation noted previously. Prairie dogs in the center of a colony have a mixed diet of forbs, shrubs, and grasses. Along the edge of a colony diets are primarily graminoid and very similar to that of bison (Krueger 1986). Aside from typical forage habits, Hoogland (1995) also observed cannibalism during the weaning of offspring and occasional consumption of bison scat and insects.

Previously, prairie dogs were thought to compete with livestock, 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, density of prairie dogs, and other factors (O'Meilia et al. 1982, Guenther and Detling 2003). In South Dakota, estimated competition between cattle and prairie dogs is 4-7% (Miller et al. 2007). Derner et al. (2006) found that the effects on cattle weight gains were dependent on many variables, including colony age and size, plant community, site productivity, and seasonal and annual variations in precipitation. Although prairie dogs do reduce the amount of forage available to livestock, the forage on colonies is often of higher quality (O'Meilia et al. 1982, Coppock et al. 1983a). Additionally, intense prairie dog herbivory can help limit woody species and select for shortgrass species which are better adapted to heavy grazing (Coppock et al. 1983a, Winter et al. 2002, Miller et al. 2007). Livestock may encourage colony expansion 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. 1983*b*). Thus, interactions between cattle and prairie dogs are quite complex and not completely understood. This is particularly evident when fire and grazing interactions are considered.

Recently, studies have examined the effects of mowing and prescribed fire on colonization rates and found that there is 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 (either alone or in combination with fire), a common disturbance throughout the black-tailed prairie dog's range. While mowing can be used on finer scales, in many cases it may be too expensive, time consuming, or the terrain or remoteness of a site may not be conducive to mowing (Ford et al. 2008). Furthermore, results of mowing studies cannot be extrapolated for herbivory as the two are not comparable. 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.

Historically, fire and large herbivore grazing were common natural disturbances on North American grasslands. Over time, fire has been suppressed and grazing practices have been dramatically altered throughout the black-tailed prairie dog's historic range.

Native large herbivores have been largely replaced with domestic livestock operations. There exists a great disparity between historic grazing patterns of free-ranging, native herbivores (American bison [*Bison bison*], elk [*Cervus elaphus*], pronghorn antelope [*Antilocapra americana*]) and fenced, domestic cattle (Coppock et al. 1983b, Hartnett et al. 1997, Steuter and Hidinger 1999, Towne et al. 2005). Additionally, livestock management varies widely throughout the Great Plains, ranging from very low to high stocking rates with various breeds of cattle (Towne et al. 2005).

These two elements of grassland ecology, fire and grazing, have been recoupled with the patch-burn grazing concept (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). This land management approach has been evaluated for many plant species (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-burn grazing interactions have not yet been studied in grasslands colonized by prairie dogs.

Current management of prairie dog populations is focused on relocation of animals to create new colonies on public and private lands. Growing interest in restoring functioning metapopulations and managing existing colonies 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. While the effects of fire and grazing have been documented for several species much remains unknown. Thus, my study sought to build on existing literature. My objective was to examine the combined effects of prescribed fire and grazing by large herbivores (Texas longhorn cattle and American Bison) on colony expansion rates of

black-tailed prairie dogs. Hypotheses were tested within sites containing colonized prairie, burned prairie, and mixed-grass prairie that was neither burned nor colonized (controls). All sites were exposed to cattle and bison grazing throughout the study. This is described in detail in the Methods section. Hypotheses to be tested included:

1. H0: Prairie dogs colonize controls and burned treatments at the same rate.
HA: Prairie dogs colonize burned treatments at a significantly higher rate than controls.
2. H0: Prairie dog foraging effort on colonies does not significantly differ from prairie dog foraging effort on burn treatments.
HA: Prairie dog foraging effort on burn treatments is significantly higher than prairie dog foraging effort on colonies.
3. H0: Prairie dog weights do not significantly differ between animals on burned treatments and colonies.
HA: Prairie dog weights are significantly greater on burn treatments than on colonies.

Study Area

Wichita Mountains Wildlife Refuge

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 (Figure 1.1). The refuge is 23,885 hectares of mixed-grass prairie, short-grass prairie, and crosstimbers forest (USFWS 2002). WMWR was established for the

preservation of the American bison and Texas longhorn, of which there are currently approximately 650 bison and 280 longhorn. Elk, which were once native to the Wichita Mountains, have been reintroduced and currently have an approximate population of 1,000 animals (W. Munsterman, U.S. Fish and Wildlife Service, personal communication). All of these herbivores were present throughout the study area. In addition, white-tailed deer (*Odocoileus virginianus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*) and a variety of grassland birds, small mammals, and herpetofauna occupied the grasslands (USFWS 2002).

An active prescribed fire program was being developed on the refuge, with an ultimate goal of burning 4,047 to 4,856 hectares per year. Large patches of the refuge are burned on a rotational basis to create a landscape of diverse habitat conditions for wildlife. The total burned area was 191 hectares in 2009 and 4,785 hectares in 2010. In 2010, prescribed burns accounted for 3,557 hectares and wildfire accounted for 1,227 hectares (W. Munsterman, U.S. Fish and Wildlife Service, personal communication).

Grasslands on WMWR were characterized primarily by little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), hairy grama (*Bouteloua hirsuta*), and blue grama (*Bouteloua gracilis*). Common forbs included western ragweed (*Ambrosia psilostachya*), Indian blanket (*Gaillardia pulchella*), plains coreopsis (*Coreopsis tinctoria*), fineleaf greenthread (*Thelesperma filifolium*), and bitter sneezeweed (*Helenium amarum*; USFWS 2002). No significant shrub cover existed within the study sites.

Average annual precipitation is 79 centimeters, occurring on an average of 61 days per year. The annual average temperature is 17° C with average highs and lows of 36° C and -3° C, respectively. Growing seasons are typically 218 days (OCS 2010). It should be noted that precipitation was variable in both years of study, however July 2010 was marked by multiple excessive rain events (Table 1.1). This resulted in some burrow flooding at all sites.

Mountainous terrain dominates the refuge with elevations ranging from 412 meters to 756 meters on some peaks. Peaks are primarily granite and gabbro, but also consist of limestone hills and sandstone, and are surrounded by level plains (Blair and Hubbel 1938). The refuge has a total of 11 soil types, with a broad range of characteristics including barren granite peaks, moderately deep colluvial soils, shallow alluvial soils, fine sandy and silt loams, and silty clay. 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 0 and 5% (Crockett 1964).

Black-tailed prairie dogs historically occurred scattered in suitable soils throughout most of the WMWR and covered an estimated 770 hectares in 1922. Colonies on WMWR were depopulated in 1922 and 1923 with treatments of carbon bisulphide and strychnine (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 on some of these sites beginning in 1991 (W. Munsterman, U.S. Fish and Wildlife Service, personal communication). Currently prairie dog colonies occupy approximately 26 hectares. The three prairie dog colonies monitored

in my study were Turkey Creek colony, Holy City colony, and Quanah Parker colony (Figure 1.2).

Turkey Creek colony. Turkey Creek colony was poisoned in 1922-1923 and reestablished in 1991 through the efforts of the staff at WMWR. Black-tailed prairie dogs were collected from private lands and released at the previously occupied site (W. Munsterman, U.S. Fish and Wildlife Service, personal communication). At the initiation of this study in March 2009, Turkey Creek colony was approximately 15 hectares. Soils on the colony, burn, and control treatments were Granite Cobbly Land (Gc) with slopes of 5 to 40%. Soils on all treatments were well-drained deep loam to clay loam with considerable levels of gravel and 25 to 70% granite cobblestones and scattered boulders.

Holy City colony. The Holy City colony was reestablished in 1999 using prairie dogs from the Turkey Creek colony (W. Munsterman, U.S. Fish and Wildlife Service, personal communication). The colony was approximately 8.6 hectares at the beginning of this study. Soils on this colony include Granite Cobbly Land (Gc), Foard-slickspots Complex (FsB), and Rock Land (Ro). These soils were associated with low slopes and grassland vegetation suitable for prairie dog colonization. In 2009 burn and control treatments were located on Granite Cobbly Land (Gc), Foard-slickspots Complex (FsB), and Lawton Loam (LaC). Treatments in 2010 were located on Granite Cobbly Land (Gc).

Quanah Parker colony. Historically known as the Crater Lake, Crater Creek or Telephone colony, the Quanah Parker colony was once one of the largest colonies on the WMWR (P.J. Depuy, Bureau of Biological Survey, unpublished report; A.A. Putnam, Bureau of Biological Survey, unpublished report). In 1998 staff at WMWR reintroduced

prairie dogs to an area slightly west of the original colony location, as that area was not adequately drained for prairie dog colonization and was partially converted into the visitor's center (W. Munsterman, U.S. Fish and Wildlife Service, personal communication). In 2009 the colony only covered approximately 0.7 hectares. Quannah Parker colony is located on Cobbly Granite Land (Gc), Foard-slickspots Complex (FsB), and Rock Land (Ro). Burns and controls in both 2009 and 2010 were located on Foard-slickspots Complex (FsB) and Cobbly Granite Land (Gc).

Methods

Prescribed fire and control treatments

On 23 and 24 March 2009 and 29 March 2010, prior to juvenile emergence and yearling dispersal, 2-hectare treatment plots were burned adjacent to colonies. Additionally, 2-hectare control plots of untreated native grassland were established directly adjacent to each colony (Figure 1.3). Where possible, control and burn treatments were adjacent to one another in order to have the most uniform site conditions. Treatment boundaries were marked with fiberglass stakes where necessary to distinguish burn and control treatments from the colony or area beyond the study site. Burns and controls were located on sites with comparable vegetation structure, slope, and soil types that were sufficient to allow prairie dog excavation of new burrows. Refuge staff from WMWR completed all prescribed burns within a one week window. All colonies, controls, and fire treatments were accessible to bison, cattle and elk for the duration of the study.

Grazing treatments

American bison and Texas longhorn cattle both had equal and continuous access to all treatments and study sites in both years of study. The only exception to this was the small 1.2-m² exclosures described below (see Chapter III) that were ungrazed. The refuge maintains herds of 650 bison and 280 cattle, however, these numbers will vary throughout the year due to reproduction. The timing of my study coincided with the calving season (April and May; Meagher 1986) and therefore densities may have been slightly greater. Thus estimated stocking densities of <37 hectares per bison, <85 hectares per head of cattle, and <27 hectares per either of these large herbivores are likely conservative. Also, not all of the refuge is accessible to large herbivores; especially steep rock outcroppings, lakes, and areas developed for administrative and visitor services. Still, these densities are relatively low within this productive mixed-grass prairie landscape.

Population assessment and observations

Black-tailed prairie dog populations were estimated for each colony three times during each year of study (2009 and 2010). Black-tailed prairie dog activity peaks following juvenile emergence and during yearling dispersal, making this the best time to make population estimates (Severson and Plumb 1998). Estimates were conducted before and after juvenile emergence in April and May and following the dispersal season in late July.

Colonies were divided into portions and then maximum counts were recorded using alternating fifteen minute count and rest intervals totaling 3 counts and 2 rests each

day. These counts were repeated for three consecutive days during weather conditions favorable to black-tailed prairie dog activity characterized by no rain, wind speeds not exceeding 32 km/h, and ambient temperatures greater than 10° C (Menkens and Anderson 1993, Milne-Laux and Sweitzer 2006). I reached the area for observation at least 10 minutes prior to initiating counts, which began no earlier than 30 minutes after sunrise or 2 hours before sunset (Powell et al. 1994; Severson and Plumb 1998). All observations were made from an elevated location with a spotting scope (15x – 45x, Denali by Eagle Optics, Middleton, WI) and binoculars (10 x 42, Crossfire by Vortex Optics, Middleton, WI). By surveying colonies in the morning and evening, all three colonies could be surveyed within the same day. This reduced variation in conditions during observations. To further reduce bias, the order in which colonies were surveyed was randomized for each day of observations.

Following the application of all prescribed fire treatments, weekly counts were conducted to supplement the intense counts described above. Weekly counts were conducted from 3 April to 30 July 2009 and 6 April to 20 July 2010. Protocol was the same and counts were similarly structured with count and rest intervals, but counts were only completed for one day per week. The number of prairie dogs observed during counts was categorized as foraging or not foraging to allow for analysis of foraging effort within treatments. Weekly counts were used for all analysis of treatment use.

While active burrow density has been used to estimate populations of black-tailed prairie dogs, the reliability of this technique has been questioned (Powell et al. 1994; Biggins et al. 2006). Although burrow locations were mapped (discussed below), weekly visual counts were used for population estimation. Accuracy of visual counts is second

only to entire colony census through mark-recapture techniques. When using the visual count method maximum counts provide the strongest population estimate (Severson and Plumb 1998). Severson and Plumb (1998) warn that models based on maximum visual counts may not be strong enough for some predictive applications, but suggest that the method is reliable for the temporal comparison of prairie dog populations. They also found no significant observer bias in varying vegetation heights.

Trapping was conducted in April and May in 2009 and April, May, and July of 2010. Prairie dogs were trapped using 15 x 15 x 60 cm double door livetraps (Tomahawk Livetrapp Company, Tomahawk, WI) baited with oats in both years of study. All trapping was completed in compliance with Oklahoma State University's Institutional Animal Care and Use Committee (AG-08-14). Traps were placed on colonies and burns approximately 1-2 meters from active burrow entrances at least 30 minutes prior to daily emergence of prairie dogs (Hoogland 1995). I marked each trap with a unique number to ensure each prairie dog was released within the coterie of capture. Due to the common presence of predators (i.e. coyotes and bobcats) on prairie dog colonies, traps were not left unattended at Turkey Creek colony. However, predators were never sighted around Quanah Parker colony and traps had to be left out of sight due to the location of the colony. This time was kept to a minimum and no prairie dogs were injured during my study. Additionally, trapping was not conducted during inclement weather or extreme temperatures (Dullum et al. 2005). Individuals were uniquely marked with numbered fingerling ear tags and Nyanzol-D fur dye (Hoogland 1995). Upon capture, prairie dogs were weighed, sexed and aged (as adult or <1 year). Capture locations were recorded to allow for comparisons of recaptures.

Spatial data

A Garmin eTrex Vista HCx (Olathe, KS) was used to record colony, treatment and control boundaries, vegetation zones within the colony, and burrows (Augustine et al. 2007). Within each colony, vegetation zones were mapped to reflect the change in plant community from old to new colony areas. The centers of colonies have been occupied the longest and are characterized by forbs and increased bare ground. The perimeters of colonies are more recently colonized areas and are still characterized by graminoids (Hoogland 1995, Roe and Roe 2003). The perceived edge between these two areas were mapped and then buffered in ArcMAP 9.3 to ensure sampling of these two vegetation zones were well within the designated colony area types. Colony boundaries were determined using vegetation height and burrow distribution (Magle et al. 2007). The status of a burrow (active or inactive) was determined using the presence of fresh scat, fresh digging, or visual observation of use (Augustine et al. 2007).

Burrow counts were conducted during periods of stable weather, as heavy rains can complicate burrow activity assessment with disintegration or washing away of feces and stimulation of mound reconstruction (Severson and Plumb 1998). Burrow surveys were conducted at the beginning, middle, and end of each field season in coordination with population estimates to determine activity of existing burrows and addition of new burrows. Some burrows were probably missed during the mapping process, especially peripheral burrows in taller vegetation. Even so, a sufficient proportion of burrows were documented to give an accurate description of colonization patterns in response to treatments (Matchett 1994).

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) (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 between controls, colonies, and burned treatments (Zar 1999; SAS 2003). All inferential tests with $P < 0.05$ were considered significant.

Results

Populations

Pretreatment populations were zero on all burned and control treatments. I rejected the null hypothesis that prairie dogs colonize control and burn treatments at similar rates. There was no colonization of controls in 2009 or 2010. There was a significant increase in the number of prairie dogs within all burn treatments in 2009. This was true when colonies were analyzed separately or collectively (i.e. all colonies combined; Holy City [HC]: $t_1 = 6.95$, $\beta = 1.05$, $P < 0.001$; Turkey Creek [TC]: $t_1 = 5.69$, $\beta = 3.31$, $P < 0.001$; Quanah Parker [QP]: $t_1 = 3.95$, $\beta = 1.56$, $P = 0.002$; Total: $t_1 = 11.84$, $\beta = 5.93$, $P < 0.001$ Figure 1.4). Maximum populations within burned treatments were 17 (HC), 58 (TC), and 36 (QP) animals. Populations on colonies increased throughout the growing season; however this was only significant on Holy City colony (HC: $t_1 = 4.22$, $\beta = 7.70$, $P < 0.001$; TC: $t_1 = 1.19$, $\beta = 5.73$, $P = 0.26$, QP: $t_1 = 3.95$, $\beta = 0.18$, $P = 0.88$; Total: $t_1 = 1.92$, $\beta = 13.61$, $P = 0.075$; Figure 1.5).

In 2010, prairie dog populations increased within burns, but this was only significant at Quannah Parker (HC: $t_1 = 0.38$, $\beta = 0.12$, $P = 0.71$; TC: $t_1 = 0.36$, $\beta = 0.76$, $P = 0.73$; QP: $t_1 = 2.20$, $\beta = 0.66$, $P = 0.045$; Total: $t_1 = 1.06$, $\beta = 0.83$, $P = 0.31$; Figure 1.6). Maximum populations within burned treatments were 14 (HC), 32 (TC), and 19 (QP) animals. There were no significant changes in colony populations and population growth was variable between colonies (HC: $t_1 = 1.17$, $\beta = 1.86$, $P = 0.26$; TC: $t_1 = 1.02$, $\beta = 2.69$, $P = 0.33$; QP: $t_1 = -0.59$, $\beta = -0.43$, $P = 0.056$; Total: $t_1 = -0.7$, $\beta = -4.51$, $P = 0.49$; Figure 1.7).

Populations within all burn treatments significantly declined as time since fire increased beyond 12 months except for Holy City (HC: $t_1 = -0.36$, $\beta = -0.06$, $P = 0.73$; TC: $t_1 = -7.66$, $\beta = -2.04$, $P < 0.001$; QP: $t_1 = -2.53$, $\beta = -0.78$, $P = 0.024$; Total: $t_1 = -5.15$, $\beta = -2.97$, $P < 0.001$; Figure 1.8). Although prairie dog numbers did decrease, all three 2009 burn treatments remained colonized throughout the 2010 field season with minimum and maximum counts of 4 and 14 (HC), 5 and 39 (TC), and 5 and 30 (QP) animals, respectively.

Burrows

As with populations, pretreatment burrow densities were zero within control and burn treatments. No prairie dog burrows were detected within controls in 2009 or 2010. Burrows increased within all burn treatments with maximum burrow counts of 19 (HC), 34 (TC), and 55 (QP; Figure 1.9). Burrows within colonies declined or remained stable throughout the 2009 growing season (Figure 1.10). Similarly, in 2010 burrows increased within burns <12 months old to maximums of 35 (HC), 62 (TC), 24 (QP) burrows

(Figure 1.11). However, burrows decreased following the heavy precipitation of June and July 2010. Burrows decreased within burns >12 months old during 2010 (Figure 1.11). Colony burrow counts remained stable or declined throughout the 2010 growing season (Figure 1.12).

Foraging

I failed to reject the null hypothesis that prairie dog foraging effort was not significantly different between colonies and burn treatments ($\chi^2 = 5.99$, $P = 0.995$). The total proportion of animals foraging was 72% on colonies, 68% on burns in the first year, and 66% one year following fire. These summary results were consistent with those of individual colonies (Table 1.2).

Weights

I neither accepted nor rejected the null hypothesis that prairie dog weights do not significantly differ between animals on burned treatments and colonies. While trapping did result in collection of weight data, sample sizes were not sufficient for any age or gender group to make valid conclusions. Sampling days were restricted in the summer due to large herbivore activity on study sites throughout my field seasons. This coincided with the bison and longhorn breeding season (June through September), a time of year when the animals are aggressive and territorial (Meagher 1986). Therefore, there were many times when it was not safe to trap on colonies and burns, where these animals often concentrate in large herds. Due to physiological differences, juvenile males, juvenile females, adult males, and adult females would need to be analyzed separately. Thus, the sample size would have to be much larger than my sample to adequately evaluate each of

these groups. Raw data for Turkey Creek and Quannah Parker colonies can be found in Appendix A.

Discussion

Black-tailed prairie dogs responded to the change in site conditions following the application of fire at all study sites in both years. Although only significant in 2009, activity within burn treatments sharply contrasted controls in both years, which were consistently avoided by prairie dogs throughout the study. Thus, burrow establishment and population growth differed within mixed-grass prairie managed with fire and grazing versus just grazing.

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 in my study exceeded 80 cm (see Chapter III) in some areas. This far surpasses 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). While reduction of vertical structure provides a logical explanation, it is also a very simplistic view. Prairie dogs are a dynamic, social species, and therefore likely respond to multiple habitat parameters. Some additional factors which likely attract prairie dogs to grazed and burned sites include increased forage palatability, increased forage quality, and reduced litter. All of these are qualities common to both burned patches and prairie dog colonies (Coppock et al. 1983a, Wilson and Shay 1990, Fahnestock and Detling 2002).

My study sites were located on the extreme eastern boundary of the 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 my 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 along the extreme eastern edge of the prairie dog's historic range. Without these disturbances, prairie dogs might have had a range restricted to less productive grasslands or been absent.

As with relocations, the success of habitat manipulation can be attributed to many factors, including weather patterns, population density, and predation (Milne-Laux and Sweitzer 2006). Augustine et al. (2007) linked the success of burn treatments to yearly precipitation patterns, suggesting that stronger responses may be observed in wet years when biomass production is higher. I also linked the success of burn treatments to precipitation; however I found that above average precipitation reduced the colonization response to burn treatments on the Turkey Creek and Holy City colonies. However, 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.

Another effect of precipitation on colonization is flood events. In my study, burrow flooding was observed within all treatment types during the storms of July 2010. Flooding of burrows within newly established colonies may reduce populations as there are likely fewer dry burrows to use as refugia compared to colonies with extensive burrow systems (W. Musterman, U.S. Fish and Wildlife Service, personal

communication). While this affected the persistence of coteries in 2010 within burns completed and colonized in 2009, other factors likely reduced the colonization of burns one year following fire treatments. Large herbivores which were grazing the 2009 burns were redistributed to more recent burns completed in 2010. Once released from cattle and bison grazing, vertical structure increased in uncolonized areas of the burns. This combined with the effects of increased precipitation in July likely resulted in vegetation heights too great for young coteries to keep clipped. Had there been a single burn treatment during my study, large ungulate grazing may have been sustained in both years and coteries may have persisted. With only two years of data with highly variable precipitation patterns, the importance of precipitation or grazing to young coteries is yet unclear.

Additionally, as standing vegetation increased, predators including coyotes and a bobcat were frequently observed within those more densely vegetated areas at the Turkey Creek colony. I witnessed the predation of two prairie dogs, one by a bobcat and one by a coyote. While this is not likely the cause of all prairie dog declines in treatments and predators were only observed at one of the colonies, it can be a contributing factor to localized coterie declines (Hoogland 1995).

Populations on colonies increased in 2009 and were stable or decreasing in 2010. In 2010 Quannah Parker was the only colony with a decreasing population. Quannah Parker colony is younger and much smaller than the other study colonies, and therefore the dispersal of animals into neighboring burn treatments likely translated to a detectable decrease in population on the colony. This response may have been stronger in 2010 than in 2009 because of the previously discussed effects of above average precipitation. As for

the other colonies, populations within colony and burn treatments generally had similar trends. This might indicate that when prairie dogs decreased within burns they were not abandoning burns and returning to their original coterie. However, the populations of the Turkey Creek and Holy City colonies were much larger than that of burns. Therefore movement from burns to colonies may have not been large enough to be detected with simple population estimates.

By examining prairie dog foraging behavior on colonies and burn treatments I found that there were no significant differences at any of the three study sites (Holy City, Turkey Creek, and Quanah Parker). Similar foraging effort might suggest that animals are able to maintain a low vegetation structure on burned treatments with similar effort as animals on colonies. This is also likely related to increased palatability, although one might expect to see even higher foraging effort on burns if forage quality was higher than that of colonies. However, it is important to note the mediation of post-burn vegetation heights by focal grazing by large herbivores on burn patches (Fuhlendorf and Engle 2001). This type of grazing can be facultative to colony expansion within burns as dispersal and coterie establishment extends throughout the growing season (Hoogland 2006). Thus, in the absence of large grazers, prairie dogs might not be expected to colonize burns as readily as found in my study in productive grasslands. At higher stocking densities responses may have been stronger. This is untested. Similar observations comparing other important behaviors, like alarm calls and predator scanning, may provide further insight into the use of newly colonized areas.

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 cycle should be considered in habitat management for the black-tailed prairie dog where colony expansion is desired (Milne-Laux and Sweitzer 2006, Augustine et al. 2007, Northcott et al. 2008). With further study, application of fire and grazing may also be appropriate in prairie dog relocations and in stimulating new colony formation within a complex. This could be especially true on more productive sites where vegetation structure is likely limiting to colony expansion. Where vegetation height is limiting to prairie dogs fire may have the ability to control the direction of expansion where future colonization is a concern as well. Thus the application of fire may be useful in directing colonization away from conflict areas. Further work is needed to evaluate this. Even in cases where prairie dog responses to prescribed fire and grazing do not reach the desired levels, land managers can get the added benefits of increased habitat diversity and forage quality for a variety of native flora and fauna by restoring historic disturbance patterns with fire and grazing (Fuhlendorf et al. 2009).

Wuerthner (1997) equates the historic ecological impacts of prairie dog disturbance to that of wildfire and bison, suggesting that impacts of prairie dogs may have even surpassed these other disturbance forces. However, some consider this keystone species to be functionally extinct due to its severely altered distribution (Miller and Cully 2001). Today, black-tailed prairie dog populations are only an estimated 2% of historic levels and remaining colonies are becoming increasingly isolated from one another (Hoogland 1995). Throughout the range of the black-tailed prairie dog, restoration of functioning metapopulations should be a primary management goal. Maintaining colony stability and connectivity are critical to accomplish this in the face of ever increasing isolation (Lomolino and Smith 2001).

Colony complexes aid in successful inter-colony dispersal, which can help maintain colonies that might otherwise face extinction from disease, heavy predation, flooding, or other events (Lomolino and Smith 2001). Although my study examined expansion of existing colonies, the potential exists for applying fire and grazing to initiate new colonies within a complex. By further investigating the relationship between fire, grazing, and colonization, this management tool could be valuable in restoring complexes of prairie dog colonies. Also, coupling habitat management with relocations could increase success rates in man-made colonies (Truett et al. 2001, Avila-Flores et al. 2010).

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Tables

Table 1.1 Summary precipitation data for Comanche County, Oklahoma, USA (^a Averages from 1971 to 2000; OCS 2010).

Month	2009 (cm)	2010 (cm)	Average (cm) ^a
April	16.27	6.9342	6.78
May	10.92	5.26	12.62
June	2.57	7.85	10.57
July	10.46	15.1892	5.54

Table 1.2. Chi-square test comparing proportion of black-tailed prairie dogs foraging on colonies^a and burn treatments <12 months^b and >12 months^c time since fire from April through July of 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

Year	Colony	Proportion Foraging	χ^2	df	<i>P</i>
2009	Holy City	0.80 ^a , 0.80 ^b	3.841	1	0.317
	Quanah Parker	0.72 ^a , 0.46 ^b	3.841	1	0.301
	Turkey Creek	0.76 ^a , 0.76 ^b	3.841	1	0.317
2010	Holy City	0.68 ^a , 0.57 ^b , 0.67 ^c	5.991	2	0.414
	Quanah Parker	0.66 ^a , 0.55 ^b , 0.50 ^c	5.991	2	0.465
	Turkey Creek	0.68 ^a , 0.72 ^b , 0.62 ^c	5.991	2	0.456
Total	Holy City	0.68 ^a , 0.63 ^b	5.991	2	0.287
	Quanah Parker	0.66 ^a , 0.52 ^b	5.991	2	0.312
	Turkey Creek	0.68 ^a , 0.67 ^b	5.991	2	0.309

Figures

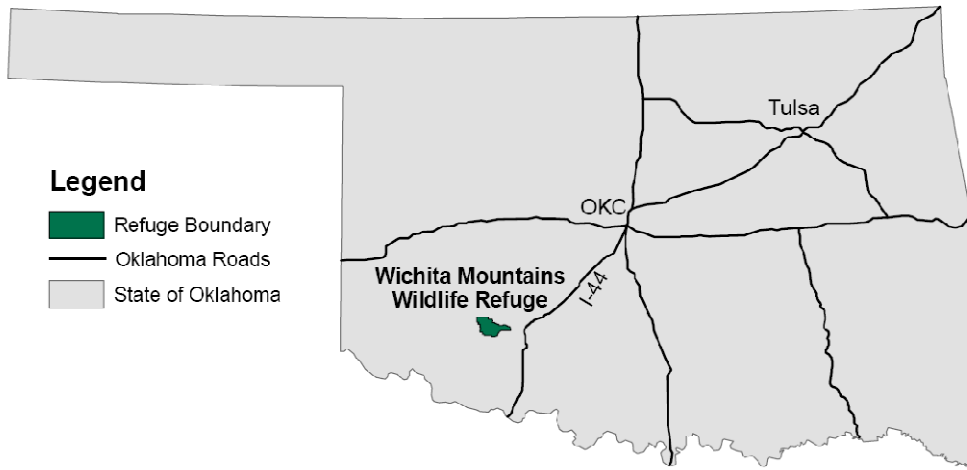


Figure 1.1 Location of Wichita Mountains Wildlife Refuge in Oklahoma, USA (USFWS 2010).

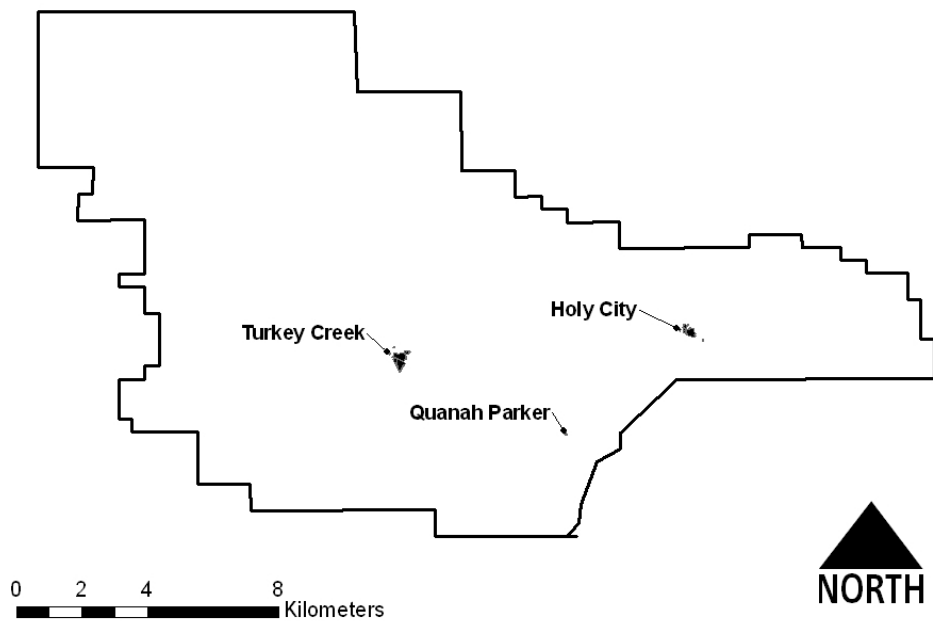


Figure 1.2 Black-tailed prairie dog colonies at the Wichita Mountains Wildlife Refuge, Oklahoma in 2009 and 2010.

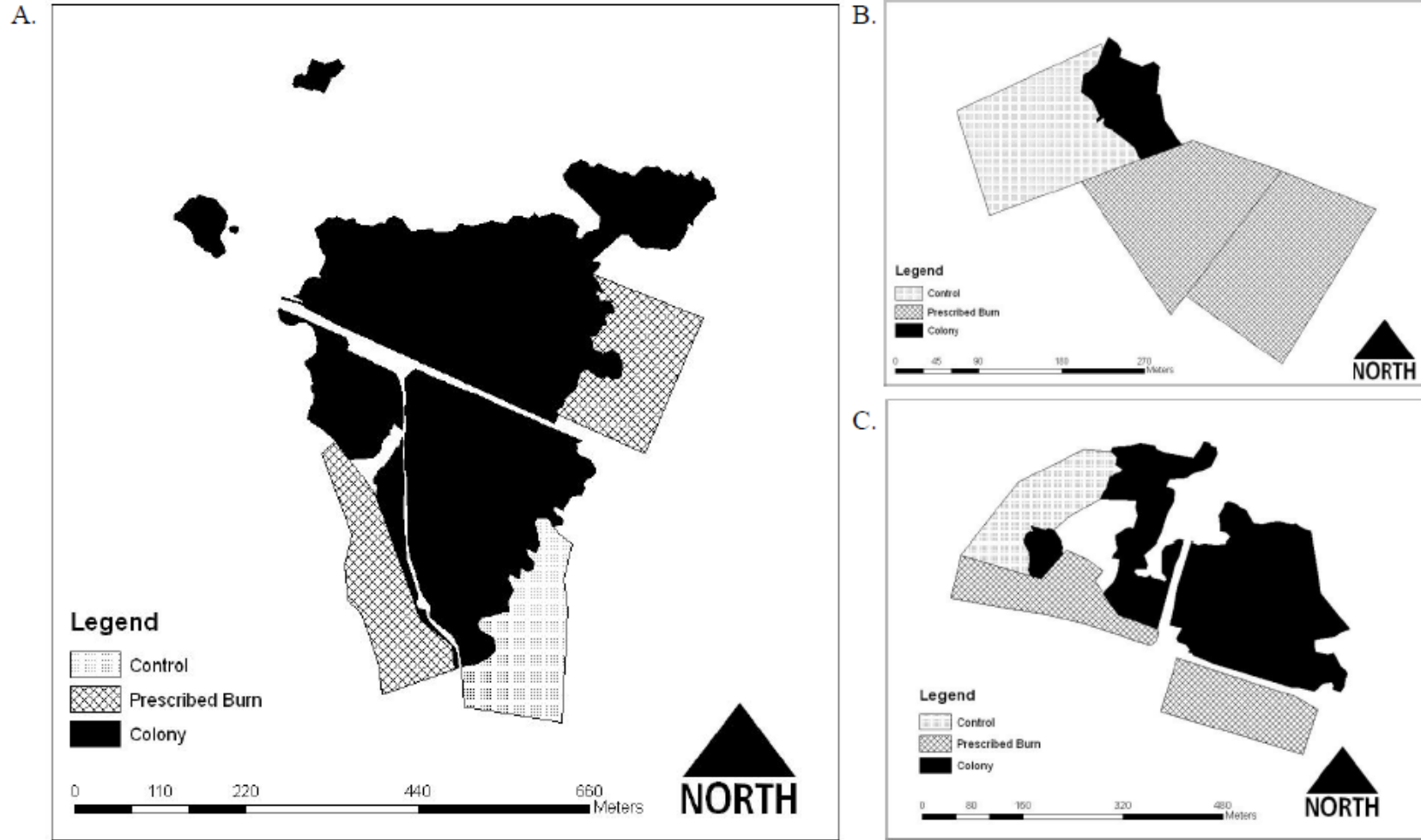


Figure 1.3. (A) Turkey Creek, (B) Quanah Parker, and (C) Holy City colony treatment locations at Wichita Mountains Wildlife Refuge, Oklahoma in 2009 and 2010.

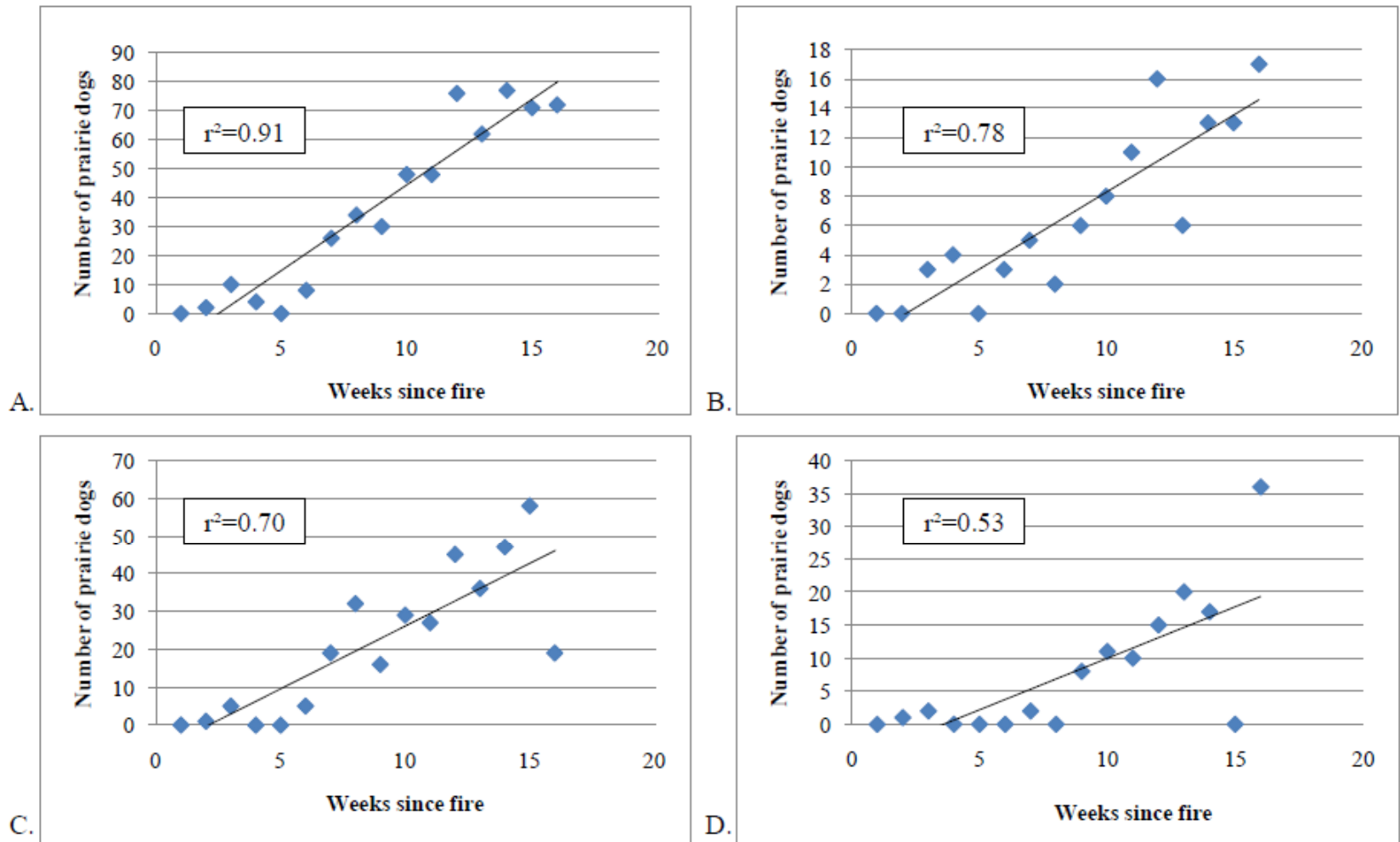


Figure 1.4. Number of black-tailed prairie dogs detected between April and July 2009 within 2-ha treatments burned on 23 or 24 March 2009 at (A) all colonies combined, (B) Holy City colony, (C) Turkey Creek colony, and (D) Quanah Parker colony at Wichita Mountains Wildlife Refuge, Oklahoma.

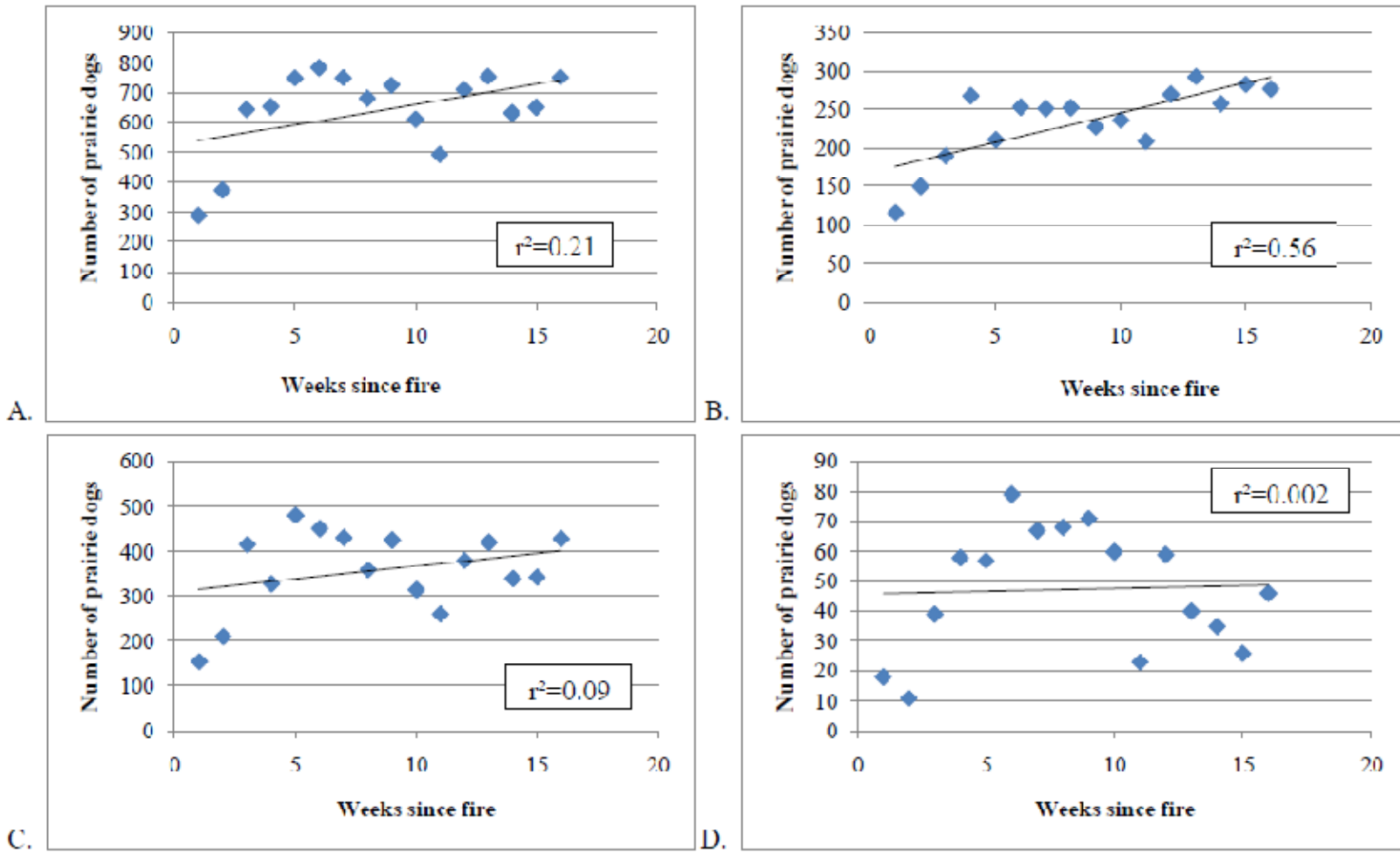


Figure 1.5. Number of black-tailed prairie dogs detected between April and July 2009 within (A) all prairie dog colonies combined, (B) Holy City colony, (C) Turkey Creek colony, and (D) Quanah Parker colony at Wichita Mountains Wildlife Refuge, Oklahoma.

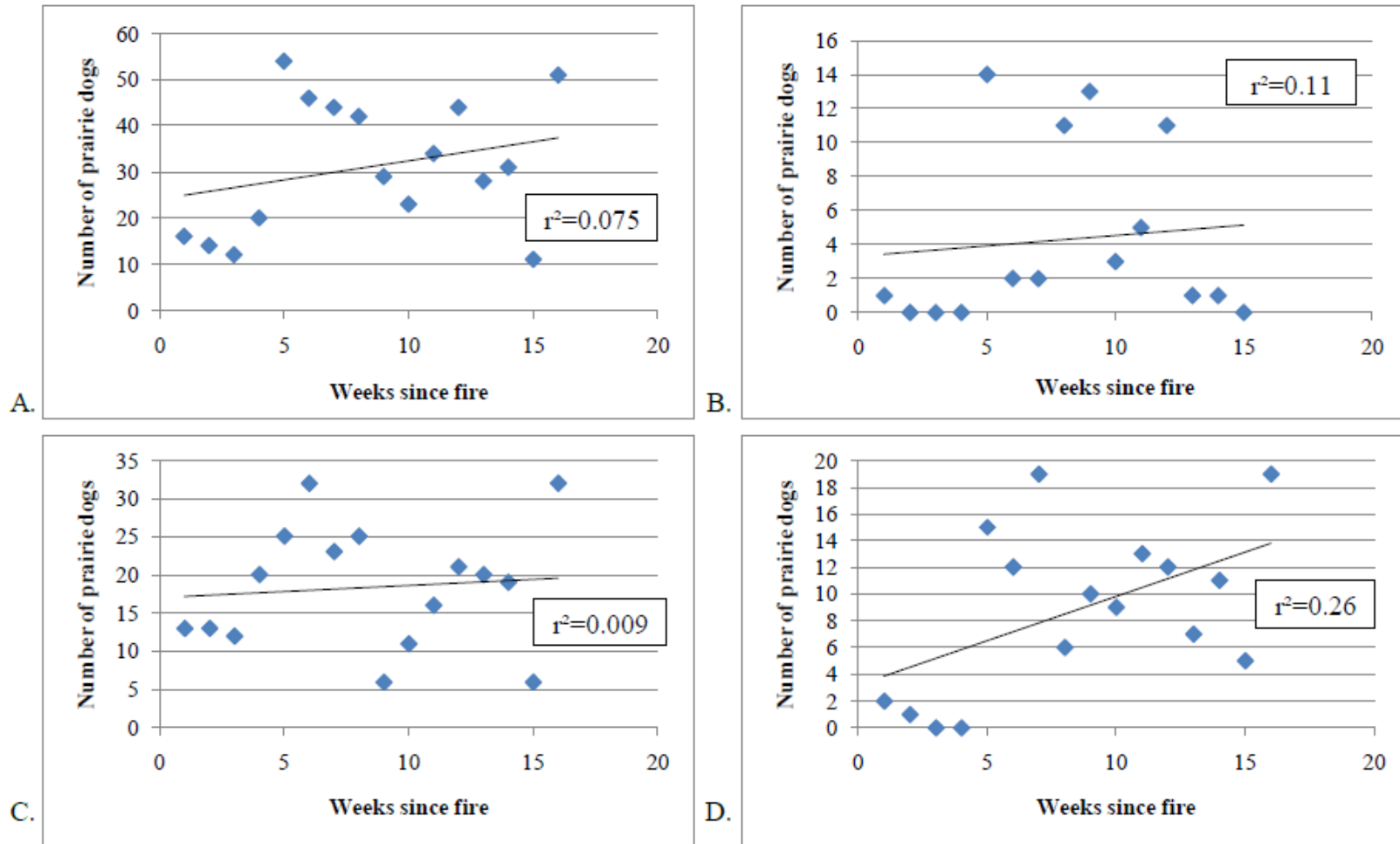


Figure 1.6. Number of black-tailed prairie dogs detected between April and July 2010 within 2-ha treatments burned on 29 March 2010 at (A) all colonies combined, (B) Holy City colony, (C) Turkey Creek colony, and (D) Quannah Parker colony at Wichita Mountains Wildlife Refuge, Oklahoma.

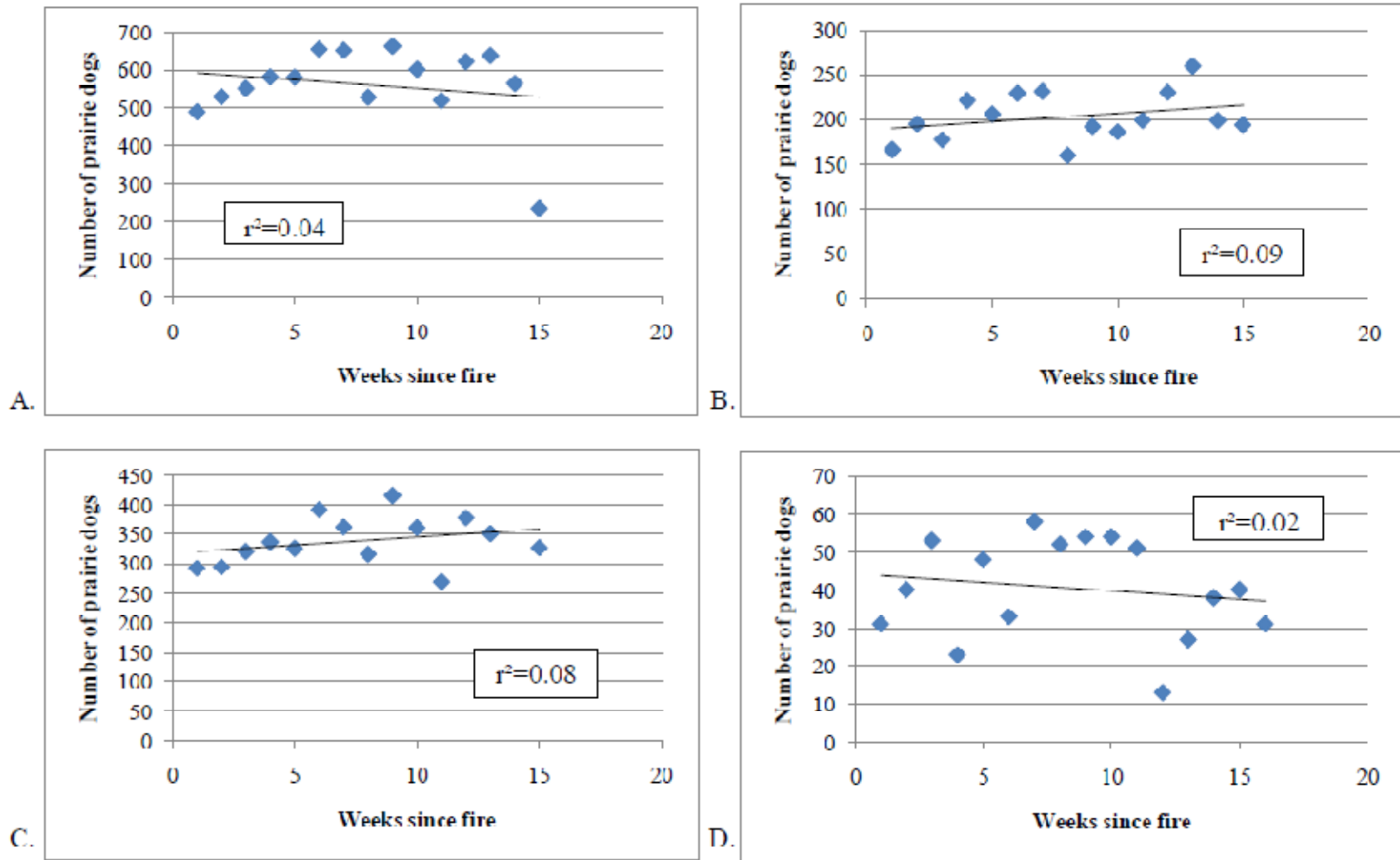


Figure 1.7. Number of black-tailed prairie dogs detected between April and July 2010 within (A) all colonies combined, (B) Holy City colony, (C) Turkey Creek colony, and (D) Quanah Parker colony at Wichita Mountains Wildlife Refuge, Oklahoma.

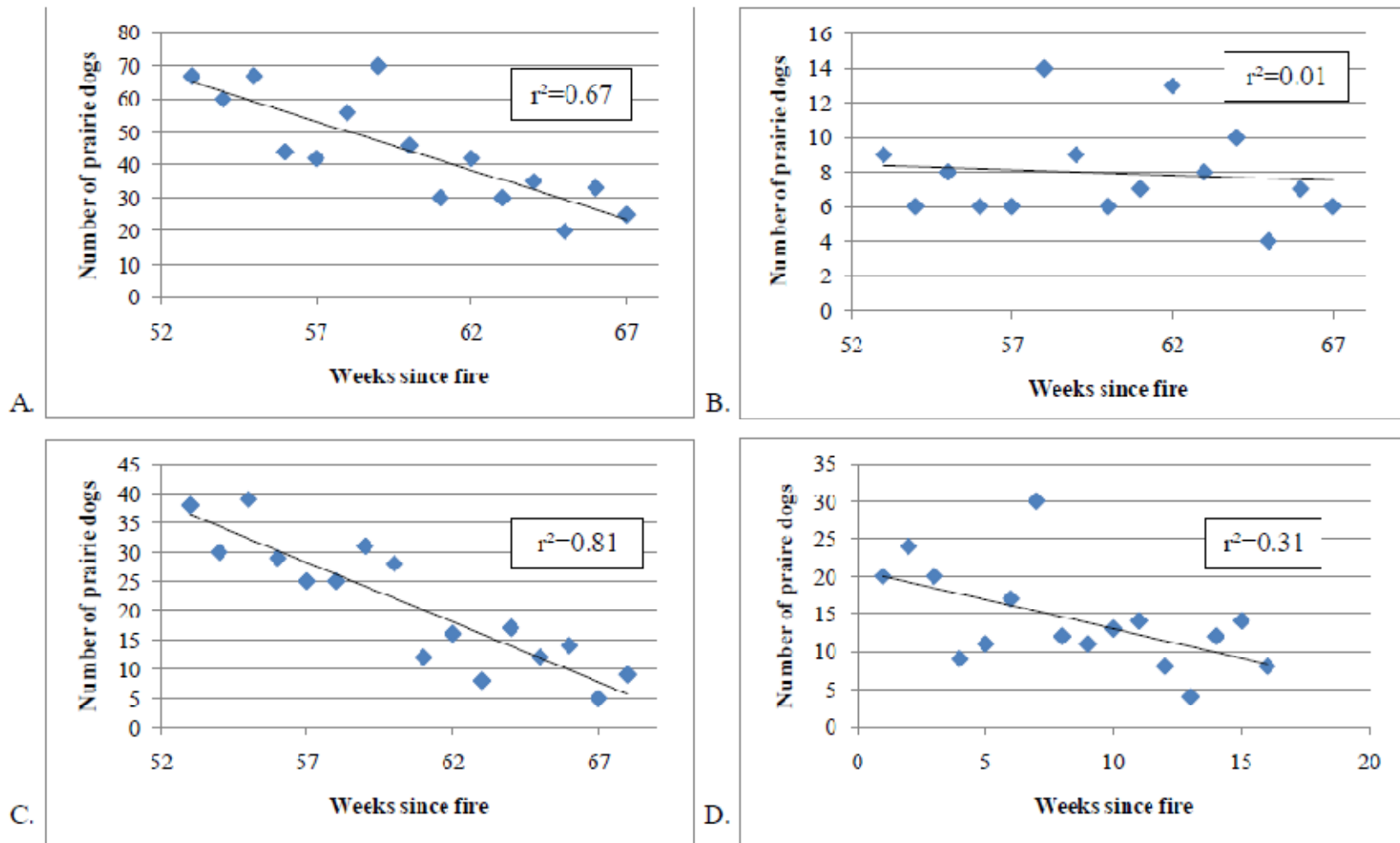


Figure 1.8. Number of black-tailed prairie dogs detected between April and July 2010 within 2-ha treatments burned on 23 and 24 March 2009 at (A) all colonies combined, (B) Holy City colony, (C) Turkey Creek colony, and (D) Quannah Parker colony at Wichita Mountains Wildlife Refuge, Oklahoma.

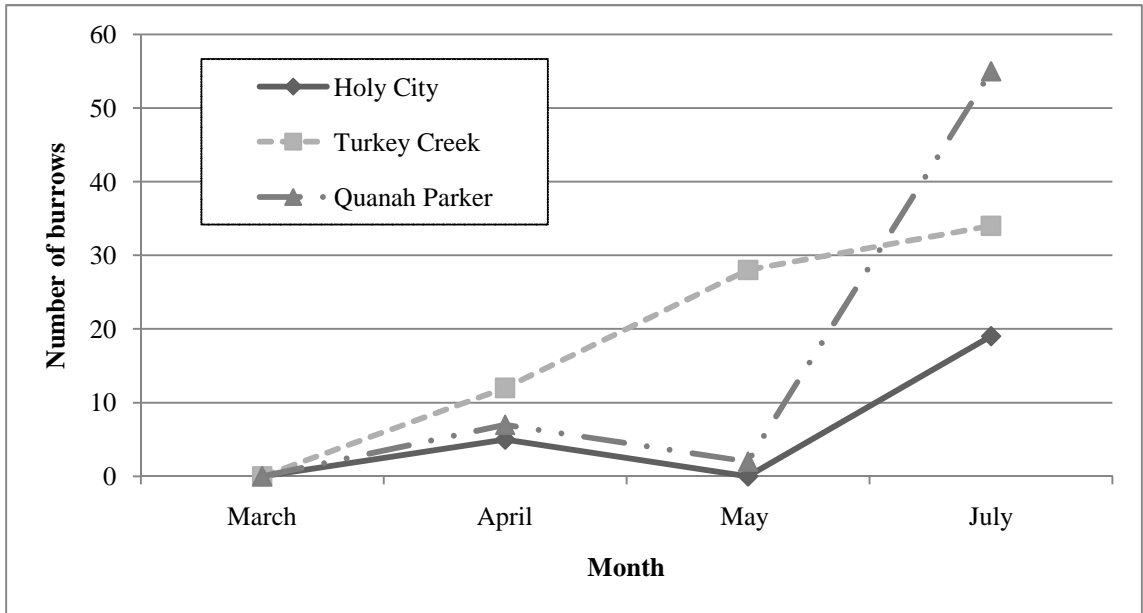


Figure **Error! No text of specified style in document.**1.9. Number of active black-tailed prairie dog burrows detected between March and July 2009 within 2-ha treatments burned on 23 and 24 March 2009 at Wichita Mountains Wildlife Refuge, Oklahoma.

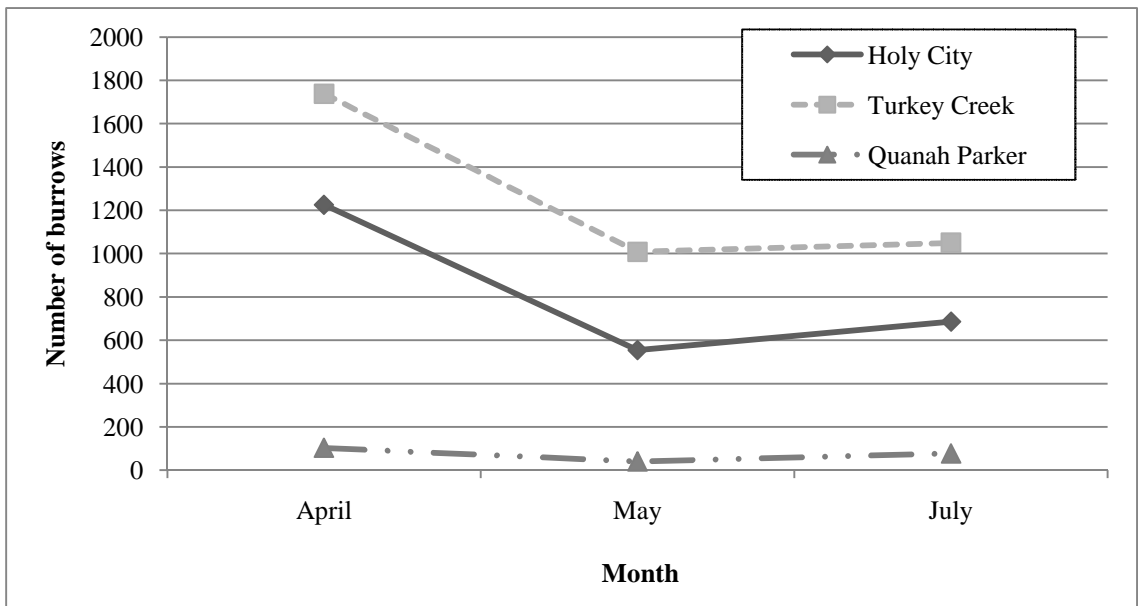


Figure 1.10 Number of active black-tailed prairie dog burrows detected between April and July 2009 within prairie dog colonies at Wichita Mountains Wildlife Refuge, Oklahoma.

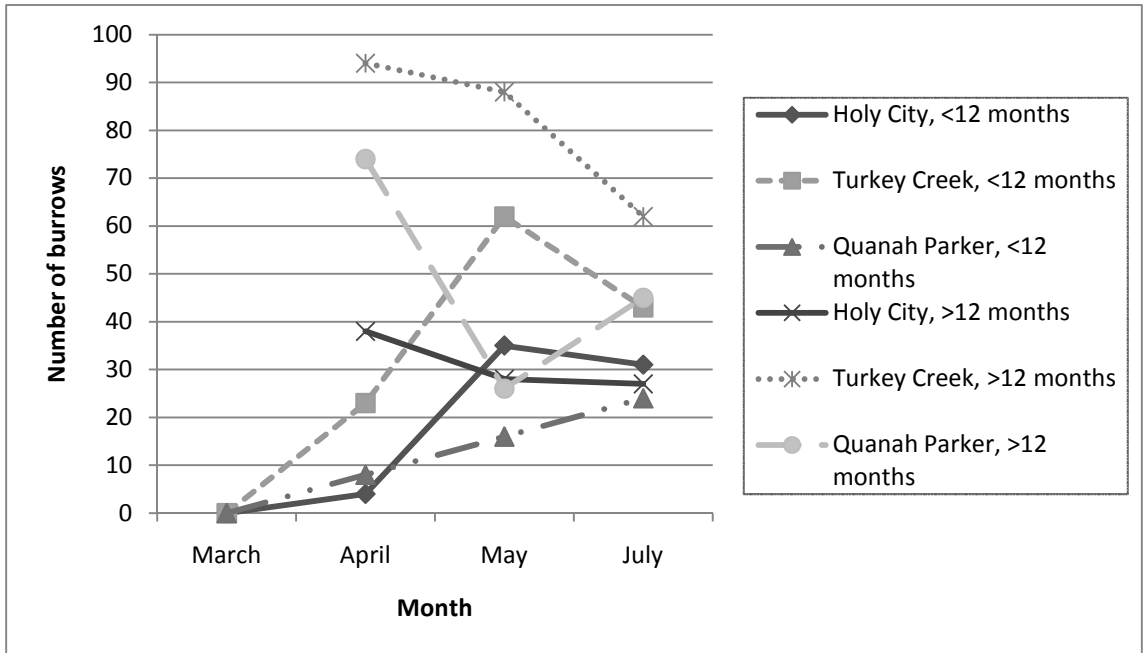


Figure 1.11. Number of active black-tailed prairie dog burrows detected between March and July 2010 within 2-ha treatments burned on 23 and 24 March 2009 or 29 March 2010 at Wichita Mountains Wildlife Refuge, Oklahoma

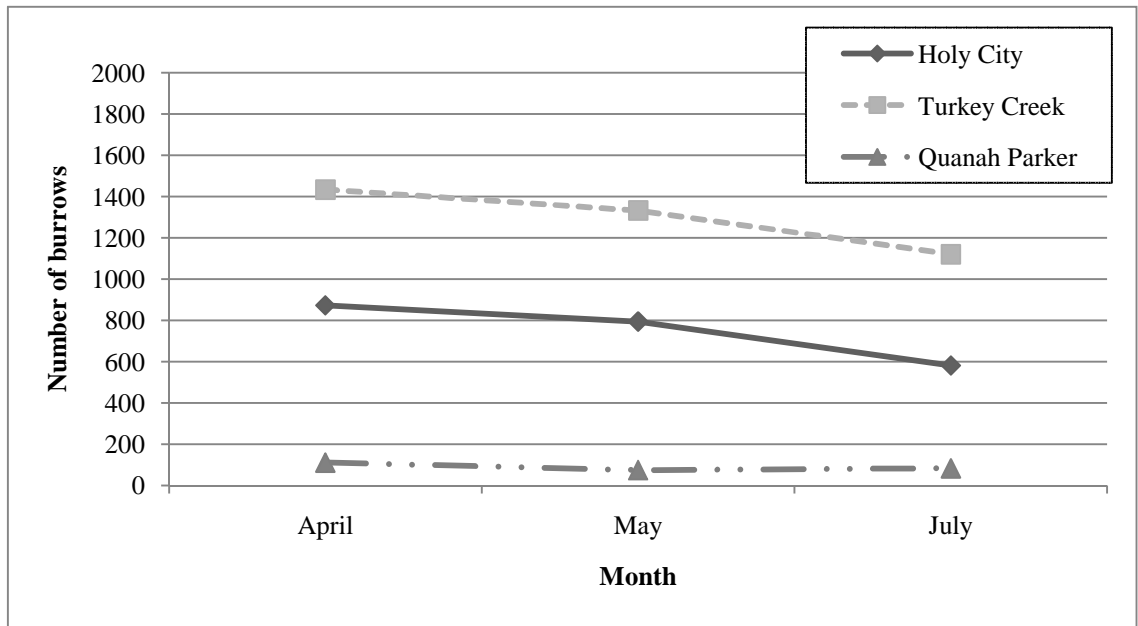


Figure 1.12. Number of active black-tailed prairie dog colonies detected between April and July 2010 within prairie dog colonies at Wichita Mountains Wildlife Refuge, Oklahoma.

CHAPTER II

BISON AND CATTLE RESPONSES TO FIRE AND PRAIRIE DOGS

Introduction

Once common throughout the Great Plains, the American bison (*Bison bison*) has largely been replaced by domestic livestock (*Bos taurus*). There are many known differences between the two species, including physical characteristics (i.e. growth rate, body size, mouth morphology, and gut morphology), social organization, thermoregulation strategies, and stress response to human handling (Schwartz and Ellis 1981, Plumb and Dodd 1993, Hartnett et al. 1997, Steuter and Hidingier 1999). While these differences are generally accepted, studies comparing bison and cattle ecology are less common and therefore these relationships are less understood. Comparisons of native and non-native ungulate habitat use are further complicated by the need to separate actual species differences from management techniques. Management goals often differ between bison and domestic cattle, raising the question of what is really impacting the grasslands: replacement of a native ungulate with a non-native one, or replacing natural, free-ranging grazing systems with homogenous, fenced pasture grazing. This issue has only recently been addressed in study designs (Hartnett et al. 1997, Towne et al. 2005).

In general, habitat selection varies by species. Bison, a native herbivore which evolved in the Great Plains, typically favor uplands and avoid wooded or hilly sites. Most breeds of cattle currently managed in North America originated in Europe within dissected, highly modified landscapes. This may explain why cattle are less selective of habitat types, opportunistically using drainages, riparian areas, and other habitats typically not used by bison (Schwartz and Ellis 1981, Hartnett et al. 1997). While cattle appear to use a wider range of habitat types, they are more dependent on water sources than bison. Water availability can therefore influence cattle distribution, while bison appear to move through landscapes independent of water locations (Steuter and Hidingner 1999).

Differences in selectivity are reflected in diet. Cattle have higher forage class diversity than native ungulates and will spend time locating high-quality forage like forbs and woody species. This forage can account for 10 to 20% of their diet (Hartnett et al. 1997). Bison have a narrower diet, with forbs contributing less than 10% to total forage, and spend significantly less time grazing. These factors result in cattle having higher quality diets than bison (Schwartz and Ellis 1981, Hartnett et al. 1997). Yet, bison have higher digestibility of lower quality forage (low protein, high fiber) than cattle (Meagher 1986). Still, there is high dietary overlap in the graminoid dominated diets of bison and cattle. Only 3 or 4 species account for 65-75% of bison and cattle diets, respectively (Schwartz and Ellis 1981). Thus, from a dietary perspective, bison may be more similar to cattle than other native herbivores (Schwartz and Ellis 1981, Meagher 1986, Hartnett et al. 1997).

A more prominent difference between the two species is in non-foraging behaviors. Bison devote significantly more time to these behaviors, which include aggression, rutting and wallowing (Hartnett et al. 1997, Steuter and Hiding 1999). Wallowing, in particular, is unique to bison and creates microhabitats which can increase plant species richness and provide ephemeral pools for herpetofauna and other wildlife (Hartnett et al. 1997).

Prairie dog colony use

Historically, American bison and black-tailed prairie dogs (*Cynomys ludovicianus*) occurred together on North America's grasslands. Since settlement of the American West both species have undergone significant population reductions (Johnsgard 2005). Today these species are of interest to restore the historic functions of grasslands (Coppock et al. 1983, Coppock and Detling 1986, Fahnestock and Detling 2002).

While bison no longer migrate freely throughout the Great Plains, they often select prairie dog colonies and avoid adjacent uncolonized grasslands when both habitats are accessible (Coppock et al. 1983, Krueger 1986, Whicker and Detling 1988). Domestic cattle differ from bison in their affinity for prairie dog colonies, utilizing these areas for grazing but at a lower frequency (Guenther and Detling 2003). Although cattle do not appear to prefer colonies, Guenther and Detling (2003) found that they do not avoid them and most of the time (91%) spent on a colony is devoted to grazing. Like bison, cattle forage on many of the same species as black-tailed prairie dogs (60-64% in shortgrass and mix-grass prairies; Miller et al 2007). The primary differences between bison and

cattle grazing are that bison are more selective herbivores with a narrow diet while cattle are more dependent on water sources and appear to be less willing to leave areas with troughs and ponds to forage on colonies (Hartnett et al. 1997, Steuter and Hidinger 1999, Johnsgard 2005). Cattle preference likely also varies with annual precipitation and age of colony, which is reflected in plant communities both on and off of a colony (Guenther and Detling 2003). As discussed in Chapter I, large ungulates can have a positive or negative relationship with prairie dogs if foraging either assists colony expansion or removes significant amounts of forage. Miller et al. (2007) suggests that bison may be more likely to compete with domestic herbivores than prairie dogs. The relationship between domestic cattle and prairie dogs and other native herbivores has rarely been addressed in research.

Burned native grassland use

Many studies have helped develop and support the concept of a patch burn mosaic to enhance heterogeneity across grassland landscapes (Biondini et al. 1999, Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004, Schuler et al. 2006). Patch burning can increase heterogeneity by performing spatially and temporally randomized prescribed burns (Fuhlendorf and Engle 2001). Adding to the dynamic of the patch burn concept is grazing, which influences fuel loads (Coppedge and Shaw 1998, Fuhlendorf et al. 2009). Many large herbivores are attracted to recently burned sites, including bison, cattle, and elk (*Cervus elaphus*; Jourdonnais and Bedunah 1990, Coppedge and Shaw 1998, Biondini et al. 1999, Fuhlendorf and Engle 2004, and Vermeire et al. 2004). By selectively grazing burned sites, large herbivores manipulate fuel loads, altering the intensity and probability of future fires occurring on a given site (Coppedge and Shaw

1998, Fuhlendorf et al. 2009). Patch size can influence the intensity and uniformity of grazing pressure, which increases as the total burned area decreases (Fuhlendorf et al. 2009).

Bison and cattle strongly select for burned areas and the increased forage quality provided by these sites (Shaw and Carter 1990, Coppedge and Shaw 1998, Biondini et al. 1999, Fuhlendorf and Engle 2004). In bison, this response is strongest within the first five months following fire (Whicker and Detling 1988, Shaw and Carter 1990). The movement of patch burning across the landscape focuses bison and other herbivore grazing intensively on these smaller areas, leaving unburned patches lightly grazed. This heterogeneous dispersal of grazing fosters a diversity of flora and fauna within grasslands (Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004, Schuler et al. 2006).

While many studies have addressed large ungulate patch selection, much remains unknown about bison and cattle patch selection within the context of heterogeneous landscapes (Fuhlendorf and Engle 2001, Guenther and Detling 2003, Wallace and Croswaite 2005). As noted, studies have shown that bison and cattle both use colonies and burned patches, sometimes at greater frequencies than unburned or uncolonized grasslands. Yet studies often can't be compared to one another due to study designs which neglect differences in management of native herbivores and livestock. Furthermore, patch selection has not been tested where all three patch types are accessible to both cattle and bison. My study sought to refine previously formulated concepts of large ungulate selection of grassland, colony, and burned patches in mixed-grass prairie. The hypothesis tested was:

H0: Bison select and use habitat in proportion to its availability.

HA: Bison select prairie dog colonies more than burns, and disturbed sites (colonies and burns) more than unburned or uncolonized mixed-grass prairie.

H0: Cattle select and use habitat in proportion to its availability.

HA: Cattle select burns more than prairie dog colonies, and disturbed sites (burns and colonies) more than unburned or uncolonized mixed-grass prairie.

H0: Bison and cattle select similar habitat and use that habitat in proportion to availability.

HA: Bison select for colonies more than cattle. Cattle select for burns more than bison. Both species select against controls.

Study Area

This study was conducted on the U.S. Fish and Wildlife Service's Wichita Mountains Wildlife Refuge (Figure 1.1 and Figure 1.2). Study sites (Figure 1.3) were native mixed-grass prairie with treatments being areas colonized by black-tailed prairie dogs, 2 ha prescribed burns, and 2-hectare control plots of undisturbed grasslands. Chapter I contains a detailed description of all study sites.

Methods

Prescribed fire treatments

Prescribed fires were completed on 23 and 24 March 2009 and 29 March 2010. Both fire and control treatments are described in detail in Chapter I.

Grazing treatments

Grazing treatments were similar in both years of study and are described in detail in Chapter I.

Large ungulate observations

Ungulate use was documented for all three treatment types at each study site. Visual observations of American bison and Texas longhorn cattle were conducted weekly from April through July in 2009 and 2010. Although elk use was documented, sufficient data did not exist for meaningful analysis. Observations were completed within 3 hours of sunrise or sunset, as these are times of peak activity for large ungulates (Biondini et al. 1999). The structure of these observations mirrored those described in Chapter I, where bison and cattle treatment use was recorded during three 15-minute intervals each separated by 15 minutes of rest. Data recorded during observations included the number of each species present in each plot and behavior of each animal (loafing, grazing, or traveling).

Data analysis

Ivlev's Electivity Indices E_i (Jacobs 1974) were calculated for large ungulate foraging, loafing, and total treatment use with the following formula:

$$E_i = \frac{(r_i - p_i)}{(r_i + p_i)}$$

where r_i = proportion of animals occurring in treatment type i

and p_i = proportion of study site composed of treatment type i

Calculated indices range from 1 (highly preferred) to -1 (completely avoided), with 0 indicating neither preference nor avoidance of the treatment type. The Wilcoxon two-sample test (Zar 1999) was used to test for differences in behavior and treatment use by bison and cattle (SAS 2003) as the data were not normally distributed. Comparisons were made both within and between species. All inferential tests with $P < 0.05$ were considered significant.

Results

Bison

I rejected the null hypothesis that bison use habitat types in proportion to their availability. Controls were avoided for grazing, loafing, and overall treatment use (Figure 2.1, Figure 2.2, and Figure 2.3). Colonies and burns were both selected by bison (Figure 2.1); yet use of the two treatment types differed significantly, with bison selecting burns for grazing and colonies predominately for loafing (Figures 2.2 and 2.3). Time since fire did not significantly affect loafing ($W_{15} = 218.5$, $P = 0.504$), but grazing preference declined in the year following fire ($W_{25} = 413$, $P = <0.001$; Figure 2.2).

Cattle

I also rejected the null hypothesis that cattle use habitat types in proportion to their availability. As with bison, controls were avoided by cattle for grazing, loafing, and overall treatment use (Figure 2.1, Figure 2.2, and Figure 2.3). Cattle preferred to graze and loaf on colonies (Figure 2.2 and Figure 2.3). However, overall there was no significant difference between use of colonies and burns ($W_{41} = 1470$, $P = 0.27$).

Behavior on and use of burns were not significantly affected by time since fire (grazing:

$W_{18} = 401.5$, $P = 0.10$; loafing: $W_{18} = 386.5$, $P = 0.06$) although there was a trend toward declining use as time since fire increased.

Bison and cattle

I also rejected the null hypothesis that bison and cattle select similar habitats. Where the two species differed was their selection of sites for grazing (Figure 2.2). Bison preferred to graze on burns and cattle preferred to graze on colonies, although this was only significant in 2010 (Table 2.1). While the null hypothesis was rejected, significant differences in treatment use between cattle and bison were few (Table 2.2). Both species showed similar overall preferences for colonies and burns and strong avoidance of controls (Table 2.2). Additionally, site selection for loafing did not vary between species (Table 2.3); although in 2010 bison used both colonies and burns for loafing, while cattle only selected colonies (Figure 2.3).

Discussion

While results from my study support previous research that large ungulates, both native and introduced, prefer disturbed patches, their preference for disturbed patch types differed from previous studies and hypotheses. It has been well established that bison and cattle graze differently. Where bison diets are dominated by graminoids, cattle diets are more complex as they contain both forbs and graminoids (Schwartz and Ellis 1981, Hartnett et al. 1997, Steuter and Hidinger 1999). It has also been shown that both species utilize burned grasslands and prairie dog colonies disproportionately to unburned or uncolonized grassland (Whicker and Detling 1988, Guether and Detling 2003, Fuhlendorf

and Engle 2004). Until my study, there have been no comparisons of either bison or cattle preferences for these patch types when all three are present on the landscape.

While my study confirms that large ungulates are attracted to disturbed patches, it also expands current understandings of how bison and cattle are ecologically different. Bison use of prairie dog colonies has been shown to vary from month to month, with greatest use occurring during the summer months (Coppock et al. 1983). Even so, when all three patch types were present, bison preferred burns over colonies for grazing. Colonies were primarily used for wallowing and dusting (loafing activities). Conversely, cattle preferred colonies for all activities and began to show a trend toward avoiding burns as time since fire increased beyond one year. Although the significance of these relationships varied between years there appears to be differences in cattle and bison site utilization.

It is important to note that the close proximity of all three treatment types may have influenced these results. Although cattle used the same patch types for both foraging and loafing, bison selected patches differently according to behavior. If burned patches and colonies were separated by greater distances animals might have selected one patch more than another as distance between patches increased. This issue could be addressed in future research, as fire is often applied in a shifting mosaic. This adds complexity to patch selection, as in some years fire will occur close to colonies and in others there may not be any fire on the landscape. Additionally, time since fire affects patch selection, as patch use often declines as time since fire increases. This response may have been stronger if the study had continued to monitor responses over several years. Furthermore, availability of new burns will also affect the use of less recently burned patches

(Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). My study provides insight that cattle and bison do have behavioral differences when multiple disturbance types are present on the landscape.

As suggested in previous studies, the trends I observed in patch selection may be related to differences in diet. Both colonies and burns provide forage with increased palatability and quality compared to mixed-grass prairie that has not been recently disturbed by fire or grazing. Bison selected burns, which are characterized by graminoids and increased live:dead plant ratios (Coppock and Detling 1986). Cattle selected colonies, which provide a diversity of forbs and some graminoids with the same benefit of reduced standing dead biomass (Coppock et al. 1983).

Cattle selection of colonies could explain why there is a perceived competition between cattle and prairie dogs. This relationship has typically been associated with negative impacts to cattle weight gains with no known effects on prairie dogs, suggesting that it is not a true competitive relationship. However, it is unlikely that grazing never affects prairie dogs. For example, Cheng and Ritchie (2006) found that moderate and high levels of grazing can negatively affect Utah prairie dogs (a related species) on sagebrush steppe sites with low productivity. Utah prairie dogs had lower weight gains when grazing was simulated with clipping. Although clipping is not equivalent to grazing, clipping reduced biomass and increased forage quality in this study. Prairie dogs gained more weight within ungrazed controls, however, individuals showed a preference for grazed treatments. While Cheng and Ritchie (2006) demonstrated the potential negative effects of moderate to high density large herbivore grazing on prairie dogs, this may represent an extreme case where prairie dogs and high levels of livestock herbivory

occurred within a less productive site. They also suggest that grazing is likely facultative in more productive mixed-grass sites where vertical obstruction limits prairie dog activity. Miller et al. (2007) support this theory as prairie dogs are attracted to disturbed areas.

Large ungulates have the ability to move between patches as quality and quantity of forage varies throughout the year. Forage utilization studies suggest that cattle significantly reduce forage on prairie dog colonies and that this is additive to prairie dog herbivory (Knowles 1986). While prairie dogs and large herbivores share dietary habits, prairie dogs will cache food within their burrows and consume many resources not commonly used by cattle or bison. These include physically defended plants like prickly pear cactus (*Opuntia macrorhiza*) and other food items including deceased prairie dogs (cannibalism), invertebrates, and scat (Hoogland 1995). Additionally, cattle have largely replaced bison throughout the prairie dog's range. With our current understanding of bison and cattle grazing ecology, we could expect this to have impacts on prairie dog colonies if cattle have a greater affinity for grazing on colonies, as my study suggests. This could translate into a shift from a facultative bison-prairie dog relationship to a competitive cattle-prairie dog relationship, especially on sites with low productivity and/or high stocking densities. It may be possible to avoid or minimize potential negative impacts to cattle and prairie dogs by maintaining appropriate stocking rates in colonized pastures (O'Meilia et al. 1982, Miller et al. 2007). Further research is needed to clarify interspecies competition issues and quantify impacts to prairie dogs and cattle. Specifically, prairie dog body condition and survival data would help elucidate this.

Although patch selection differs between bison and cattle, they can both benefit prairie dog colonies and grassland diversity. Both species affect plant communities by trampling, selective grazing, modification of plant growth stages, and digestion of plant material (Coppock et al. 1983, Hartnett et al. 1997, Towne et al. 2005). In doing so, cattle can help maintain low vegetation structure on existing colonies and bison can promote colony expansion into burned patches to restore colonies, and possibly metapopulations. Thus, both can play important roles in management of grasslands with prairie dogs. As with the patch-burn grazing model, focal grazing by cattle on colonies can also alter fuel loads in surrounding grasslands (Fuhlendorf and Engle 2001). This not only influences fire dynamics, but also provides habitat diversity for nesting birds, small mammals, and other wildlife. While many species use prairie dog colonies for food resources, many still require the dense cover provided by surrounding grasslands. Thus, the juxtaposition of patches with distinct disturbance intervals and intensities can provide a suite of resources required throughout the life history of many native species (Fuhlendorf et al. 2006, Fuhlendorf et al. 2009).

It should be noted that my study location has an active prescribed fire program and therefore there were multiple burns of varying sizes available to all animals throughout the study. By providing newly burned patches to animals, the avoidance of less recent burns likely increased and resulted in the decline in use of burned patches in the second year by both bison and cattle (Fuhlendorf and Engle 2004).

The stronger grazing selection of colonies by cattle and burns by bison may have been magnified by above average precipitation in 2010. Higher precipitation translates to higher productivity (Patton et al. 2007). It is likely that in a year with above average

productivity, forage isn't as limited and therefore animals can be more selective in their grazing.

One source of potential bias in my study design is the interaction of bison and cattle and the possibility of avoidance between the two species. Bison may reduce the use of burns by cattle and cause an increase in their use of colonies. Due to the management of large herbivores on the Wichita Mountains Wildlife Refuge this was unavoidable. Also, studying species separately and then comparing results can have bias due to site differences, including topography and site productivity (Towne et al. 2005).

Additionally, my study compared American bison and Texas longhorn cattle. Longhorn cattle are better adapted to the short and mixed-grass prairies of the southern Great Plains than many introduced European breeds. This is important to the interpretation of any study comparing cattle ecology. It is also an aspect which is oversimplified or ignored in most studies. Texas longhorn cattle were bred to be a hardy breed, requiring less shelter and supplementation from humans. As the breed may be considered highly adapted to my study location they likely responded differently than more common European breeds might. As longhorn are better adapted to this environment, responses were likely stronger than would be expected from other breeds.

Finally, although cattle preferred colonies in this study; burned patches have been identified as quality grazing patches for cattle as well (Fuhlendorf and Engle 2004, Vermeire et al. 2004). Current comparative studies of bison and cattle suggest that the effects of bison and cattle grazing do not significantly differ. Additionally, the species of large herbivore, even where there may be more than one, is not as important as the

system under which the animals are managed. Domestic large herbivores can be used to achieve biodiversity and range health management goals as effectively at native ungulate grazing (Towne et al. 2005, Fuhlendorf et al. 2009). So whether a property has bison, cattle, or both, prairie dog colonies and burned patches can provide forage as well as promote diversity for native wildlife including many declining, threatened, and endangered species when interspersed with less disturbed patches throughout a grassland matrix.

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Tables

Table 2.1. Wilcoxon two sample test comparing treatment use by grazing American bison and Texas longhorn cattle from April through July of 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

Treatment	Year	<i>n</i>	<i>W</i>	<i>Z</i>	<i>P</i>
Burn, <1 year since fire	2009	16	298	0.3721	0.71
	2010	25	347.5	-1.9200	0.05
	Total	51	1328.5	-1.9797	0.5
2009 Burn, >1 year since fire	2010	25	452	0.8068	0.42
Colony	2009	16	249.5	-1.2922	0.20
	2010	25	443	0.3735	0.71
	Both	41	1643.5	1.2399	0.22
Control	2009	16	310	1.2884	0.20
	2010	25	439	0.4369	0.66
	Both	41	1489	-0.518	0.60

Table 2.2. Wilcoxon two sample test comparing total treatment use by American bison and Texas longhorn cattle from April through July of 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

Treatment	Year	<i>n</i>	<i>W</i>	<i>Z</i>	<i>P</i>
Burn, <1 year since fire	2009	22	411.5	-0.5202	0.60
	2010	27	514.5	0	1
	Total	49	1823.5	-0.3717	0.71
2009 Burn, >1 year since fire	2010	27	469.5	-1.0821	0.28
Colony	2009	22	497	1.7163	0.09
	2010	27	532.5	0.369	0.71
	Both	49	2040.5	1.4333	0.15
Control	2009	22	422	-0.291	0.77
	2010	27	555	1.9811	0.05
	Both	49	1929.5	0.9429	0.35

Table 2.3. Wilcoxon two sample test comparing treatment use by loafing American bison and Texas longhorn cattle from April through July of 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

Treatment	Year	<i>n</i>	<i>W</i>	<i>Z</i>	<i>P</i>
Burn, <1 year since fire	2009	19	393.5	0.7615	0.45
	2010	18	222	-1.3074	0.19
	Total	37	1202	-0.2807	0.78
2009 Burn, >1 year since fire	2010	18	273.5	0.7757	0.44
Colony	2009	19	339	-0.9322	0.35
	2010	18	280	0.9235	0.36
	Total	37	1224	0	1
Control	2009	19	381	0.6242	0.53
	2010	18	232.5	-1.5946	0.11
	Total	37	1193	-0.7277	0.47

Figures

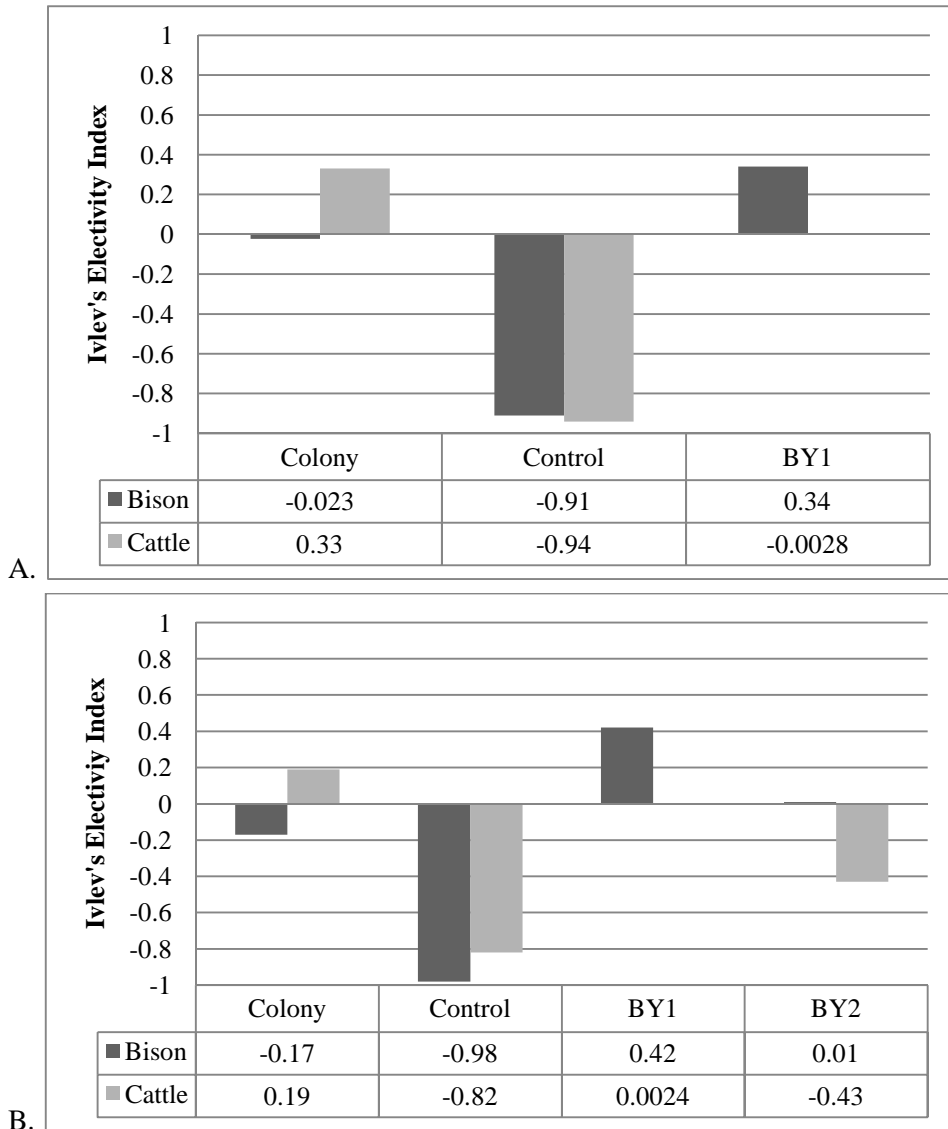


Figure 2.1 Ivlev's electivity indices for cumulative grazing by large ungulates from April through July in (A) 2009 and (B) 2010 at Wichita Mountains Wildlife Refuge, Oklahoma (BY1 = units burned <12 months prior to sampling; BY2 = units burned >12 months prior to sampling).

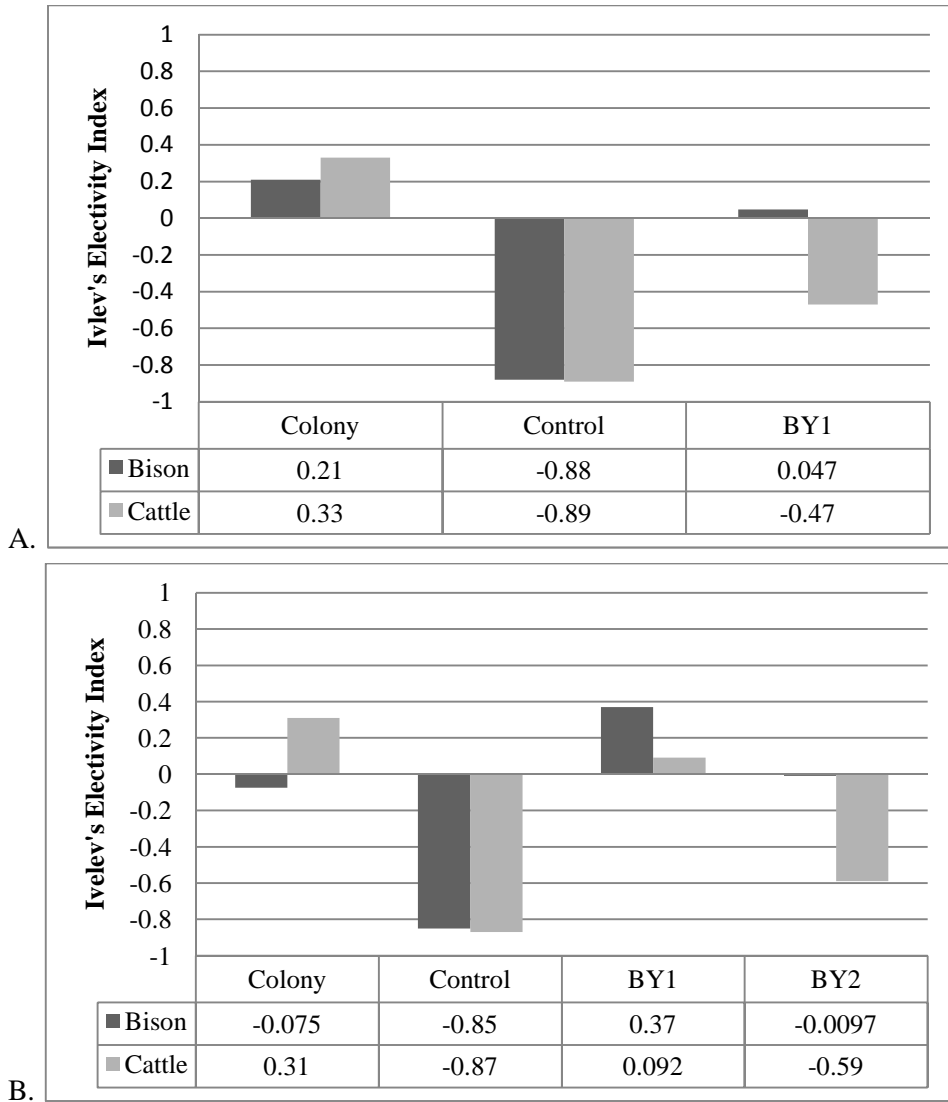


Figure 2.2. Ivlev's electivity indices for cumulative treatment use by large ungulates from April through July in (A) 2009 and (B) 2010 at Wichita Mountains Wildlife Refuge, Oklahoma (BY1 = units burned <12 months prior to sampling; BY2 = units burned >12 months prior to sampling).

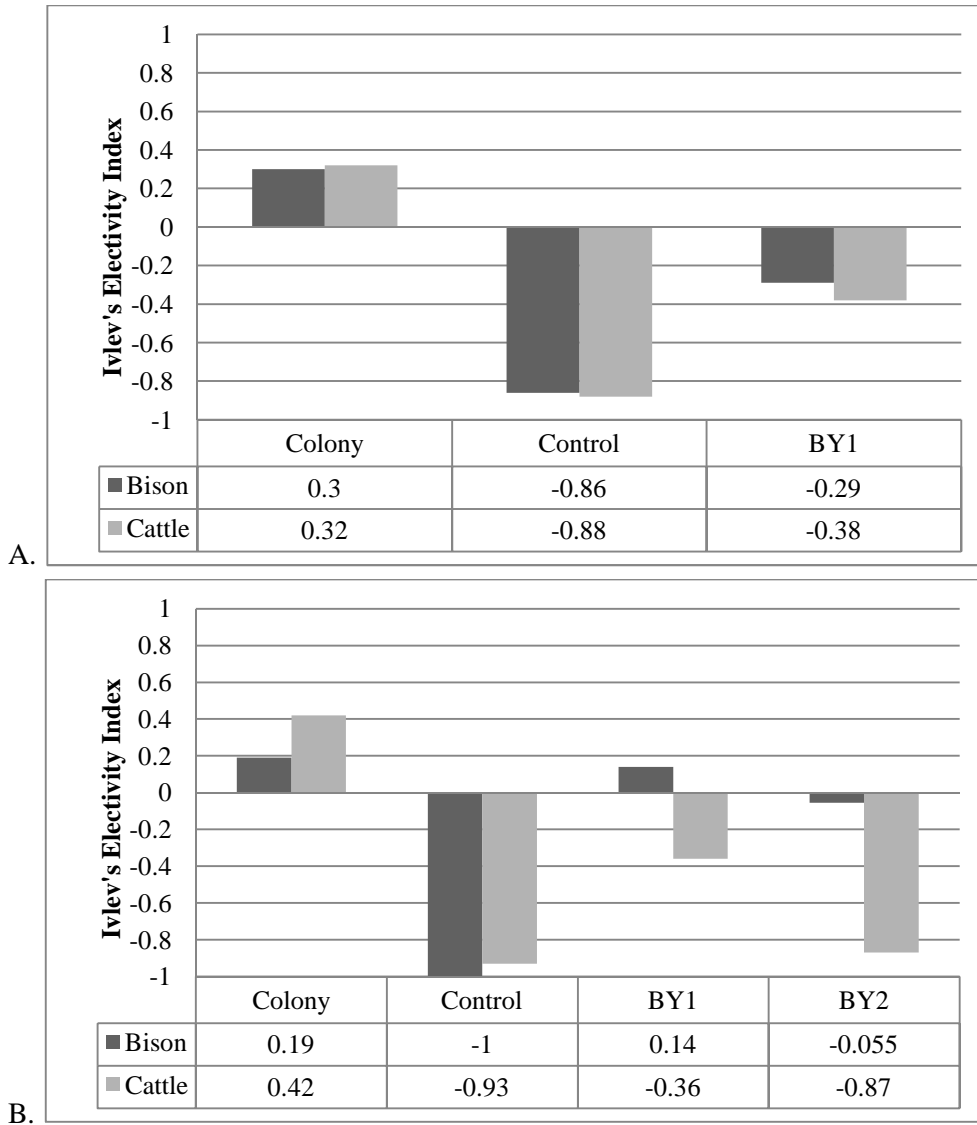


Figure 2.3. Ivlev's electivity indices for cumulative loafing by large ungulates from April through July in (A) 2009 and (B) 2010 at Wichita Mountains Wildlife Refuge, Oklahoma (BY1 = units burned <12 months prior to sampling; BY2 = units burned > 12 months prior to sampling).

CHAPTER III

EFFECTS OF FIRE, HERBIVORY AND PRAIRIE DOG COLONIZATION ON MIXED-GRASS PRAIRIE PLANT COMMUNITIES

Introduction

Grasslands are dynamic and the level of diversity within grasslands can be significantly affected by disturbances, including fire and herbivory (Fuhlendorf and Engle 2001, Wallace and Crosthwaite 2005). As herbivores, prairie dogs create unique patches within grasslands, increasing heterogeneity (Whicker and Detling 1988). Fire can also increase landscape heterogeneity by creating distinct patches within grasslands that differ in both plant composition and structure (Fuhlendorf and Engle 2004). These modifications of the landscape in turn influence behavior of large herbivores, including bison and cattle, which themselves impact grassland heterogeneity (Coppock et al. 1983*b*, Whicker and Detling 1988, Fuhlendorf et al. 2008). Additionally, the interaction of grazers with fire influences the probability of future disturbance events (Biondini et al. 1999, Fuhlendorf and Engle 2001). Historically all of these disturbance processes would have interacted across landscapes, maintaining a shifting mosaic of habitat patches (Wuerthner 1997).

Prairie dogs

Prairie dogs alter the structure, composition, and nutritional quality of forage (Coppock et al. 1983*a, b*, Krueger 1986, Whicker and Detling 1988). Areas exposed to prairie dog foraging contain plants with higher crude protein and nitrogen content and increased digestibility (Coppock et al. 1983*a, b*, Krueger 1986). Additionally, plant communities on prairie dog colonies typically have higher species richness and diversity compared to surrounding grasslands, although this tends to decrease as time since colonization increases beyond 3 to 8 years (Coppock et al. 1983*a*, Fahnestock and Detling 2002). This can be seen by examining an expanding prairie dog colony. The central, oldest portion of the colony is typically dominated by forbs, has high proportions of bare ground, and minimal graminoid coverage. Conversely, the perimeter of an expanding colony is often characterized by a high proportion of graminoid species, decreased bare ground, and fewer forbs. Both have reduced litter and vertical structure compared to uncolonized grasslands (Coppock et al. 1983*b*, Fahnestock and Detling 2002).

Grazing

In most cases, cattle have replaced bison throughout the Great Plains (Steuter and Hidinger 1999). While there are many differences between these two species, they both have been shown to prefer disturbed patches for grazing (i.e. recent burns and prairie dog colonies) and have similar impacts on plant communities (Coppock et al. 1983*b*, Krueger 1986, Fuhlendorf and Engle 2004, Wallace and Croswaite 2005). Changes in plant

communities may be more dependent on management systems than species of large herbivore (Hartnett et al. 1997, Truett et al. 2005).

As large herbivores focus grazing within disturbed patches, they further modify the site through trampling of vegetation, wallowing, selective grazing, and cycling nutrients (Coppock and Detling 1986, Hartnett et al. 1997, Fuhlendorf et al. 2004). At moderate stocking levels, these behaviors can increase available soil moisture, forage production, perennial forbs, low-growing perennials, cool-season grasses, plant species richness, and plant species diversity (Hartnett et al. 1997, Towne et al. 2005, Patton et al. 2007). Forb abundance can be important in evaluating environmental conditions and disturbance patterns, as they are often the strongest indicator of small and mid-scale plant diversity (Hartnett et al. 1997).

It is important to note that such effects of grazing are variable and highly dependent on multiple factors including site quality, annual precipitation, and stocking density. For example, extreme low and high stocking densities can decrease patch heterogeneity while moderate grazing can increase heterogeneity, as with the intermediate disturbance hypothesis (Hartnett et al. 1997, Patton et al. 2007, Fuhlendorf et al. 2009).

Fire

Fire has strong influences on grassland plant communities. Within grassland ecosystems, many effects of fire are well known and can include increased bare ground, increased quality of forage, reduced woody vegetation, reduced litter, increased live:dead plant material, and reduced vertical structure (Wilson and Shay 1990, Fuhlendorf et al.

2006). Depending on the intensity of the fire and continuity of fuels, fire can remove significant amounts of both live and dead plant material (Wilson and Shay 1990). Young vegetation which dominates recently burned sites is more palatable than mature or dead plant material. Additionally, the increased nutrient availability translates to increased forage quality. Thus, post-fire regrowth is attractive to many herbivores and is an accepted management practice for livestock operations (Fuhlendorf and Engle 2001).

The intense grazing of burned patches not only extends the direct effects of fire, it also allows unburned areas to accumulate litter (i.e. fuels). This is a situation where the species of grazer can alter grasslands. Towne et al. (2005) found that while bison and cattle do not alter plant communities directly through foraging patterns, they indirectly do so by influencing fire intensity and distribution. Bison tend to create heterogenous fuel loads, resulting in patchy burns. Cattle graze more evenly and remove less fuel, favoring more intense homogenous fires (Towne et al. 2005). Therefore, different species may favor fire adapted species or fire sensitive species. In either case, large herbivores shift focal grazing to recently burned patches and over time fire may be applied to unburned patches to perpetuate fire within a landscape. When applied in this type of patchy distribution, fire can increase landscape heterogeneity of vegetation structure and food resources to benefit domestic cattle, wildlife, and fire-dependent plant communities (Fuhlendorf et al. 2006, Churchwell et al. 2007).

Justification and objectives

Large herbivores selectively use prairie dog colonies and burned prairie more than grasslands lacking recent disturbance (Knowles 1986, Vermeire et al. 2004). Fire and

prairie dog colonization can result in similar plant communities, characterized by increases in forb cover, increased bare ground, reduced vertical structure, and increased species diversity and richness. However the spatial and temporal dynamics of these two patch types vary significantly, with colonies generally characterized as static and persistent and fires as shifting, short-lived disturbances. Data collected in my study was used to compare and contrast plant communities of native mixed-grass prairie, prairie dog colonies, and prescribed burns.

Fire-grazing interactions and prairie dog restoration are two separate concepts which are becoming increasingly common in both research and management of grasslands. While studied intensively as separate disturbances within native prairies, few studies have incorporated these elements within the same years of study and the same site conditions. In this study I sought to compare and contrast plant communities found within each of these treatment types. By doing so, managers will be better able to understand the type of habitat being provided by each treatment. Hypotheses tested included:

1. H₀: Forb cover does not significantly differ between mixed grass prairie, burned grasslands, and grasslands colonized by black-tailed prairie dogs.
H_A: Forb cover on grasslands colonized by prairie dogs is greater than that on burned prairie. Forb cover on burned grasslands is greater than that on unburned mixed-grass prairie.
2. H₀: Graminoid cover does not significantly differ between mixed-grass prairie, burned prairie, and prairie colonized by black-tailed prairie dogs.

HA: Graminoid cover on mixed-grass prairie is higher than that on burned grasslands. Graminoid cover on burned grasslands is higher than that on grasslands colonized by black-tailed prairie dogs.

3. H0: Standing biomass does not significantly differ between mixed-grass prairie, burned prairie, and prairie colonized by black-tailed prairie dogs.

HA: Standing biomass is greater on mixed-grass prairie than burned prairie. Standing biomass is lowest on prairie dog colonies.

4. H0: Plant species richness and diversity does not significantly differ between mixed-grass prairie, burned prairie, and prairie colonized by black-tailed prairie dogs.

HA: Plant species richness and diversity is higher on prairie dog colonies than burned grasslands. Both richness and diversity are lowest on mixed-grass prairie.

Study Area

This study occurred on the US Fish and Wildlife Service's Wichita Mountains Wildlife Refuge (Figure 1.1 and Figure 1.2). Study sites (Figure 1.3) were native mixed-grass prairie with treatments including: areas colonized by black-tailed prairie dogs, 2-hectare prescribed burns, and 2-hectare control plots of undisturbed grassland. Chapter I provides a detailed description of all study sites.

Methods

Percent cover

Percent cover of forbs and graminoids was determined by stratifying each treatment into old and new colony areas, as plant communities are known to differ significantly between long colonized and recently colonized areas (Koford 1958, Hoogland 2006). This was accomplished by using a Global Positioning System (GPS) to map the transition from the older, forb-dominated center of the colonies to the newer, graminoid-dominated perimeter of the colonies. This transition was visually evident on all colonies. A buffer of 10 meters was then applied on both sides of this apparent line of transition using ArcMap 9.3 to ensure that sampling occurred within the two distinct plant communities. Using ArcMap 9.3 and Hawth's Tools (Beyer 2004), each treatment was divided into quarters and a transect measuring 20 meters was randomly located in each quarter section. This resulted in four transects each within the burn and control treatments and 8 within the colony (four in the interior and four in the perimeter) at each site. Once established, transects remained fixed throughout the study.

Along each transect I placed six 20 x 50 cm frames spaced evenly at 5-meter intervals (Daubenmire 1959). The number of frames was determined using a species accumulation curve. To do this I completed transects within each treatment. Along each transect I recorded each species occurring within a 20 X 50 cm frame. Once I had sampled 40 frames I graphed the increase in total species richness for the treatment as each frame was added to the sample. The addition of new species (i.e. increase in species richness) dramatically slowed as sampling extended beyond 20 frames. Therefore I

arrived at a conservative sampling effort of 24 frames for each treatment. Within each frame, the exact value of percent cover was visually estimated for each plant species (Tyrl et al. 2008, Tyrl 2009), bare ground, litter, and rock (Symnstad et al. 2008). This provided species composition data while allowing for analysis of general cover type (graminoid, forb, dwarf shrub). Plant species richness and diversity were calculated using this data as well.

Biomass

Following application of prescribed burns as described in Chapter I, exclosures measuring 1.2-m² were randomly placed on each colony within each treatment type (control, burn, colony) to exclude both small and large herbivores (prairie dogs, bison, elk, and Texas longhorn; Wallace and Crosthwaite 2005). Within each colony, an exclosure was placed both in the interior and within the perimeter to capture the plant community of both recently and long colonized prairie (Krueger 1986). Thus I was able to compare biomass production between grazed and ungrazed plots for each treatment (control, burn, colony). Exclosures were moved between field seasons to prevent bias from sampling areas that had been excluded from grazing for multiple growing seasons. At the end of 2009 and 2010, growing season aboveground biomass was sampled by clipping all vegetation within one 0.25 m² circular frame randomly placed both inside and outside of each exclosure. Collected plant materials were sorted by growth form (grass, forb, and litter), dried in an oven for 48 hours and weighed in order to estimate site productivity (Cid et al. 1991).

Vertical structure

At either end of each 20-meter transect, vertical structure was measured using the digital photography method described in Limb et al. (2007). I also used Robel et al.'s (1970) method. However I used the digital obstruction data in all analysis as this has been shown to have increased accuracy (Limb et al. 2007).

Data analysis

The experimental unit for the vegetation data was the plot (12 in 2009 and 15 in 2010), which were control, burn (2009 and 2010), old colony, or young colony. The sample unit was the colony site (three), which was nested within treatment. Variables analyzed included percent cover of forbs, percent cover of graminoids, species richness, Shannon-Weaver diversity indices, forb biomass (g), graminoid biomass (g), and visual obstruction. Due to the repeated measurements design, PROC Mixed was used to analyze all vegetation data. Random statements included colony and year (SAS 2003). All inferential tests with $P < 0.05$ were considered significant.

Results

Percent cover

All plant community characteristics were significantly affected by treatment type. No dwarf shrubs or other woody cover were encountered during sampling. I rejected the hypothesis that graminoid cover did not differ by treatment type. Old colonies had significantly less graminoid cover than the other treatments (Table 3.1, Figure 3.2). Controls, burns (both $<$ and $>$ 12 months since fire), and young colonies had similar

coverage of graminoids (Table 3.1, Figure 3.2). Thus, percent cover of graminoids was influenced by treatment ($F_{4, 14} = 13.80$, $P < 0.001$).

I also rejected the hypothesis that forb cover did not differ by treatment type. Forb coverage was highest within old colonies, which had significantly greater coverage than controls (Table 3.1, Figure 3.3). Canopy coverage by forbs was lowest within patches burned <12 months ago and was significantly lower than that of young and old colonies (Table 3.1, Figure 3.3). Percent cover of forbs was therefore significantly affected by treatment ($F_{4, 14} = 3.08$, $P = 0.037$),

Biomass

The null hypothesis which predicted similar standing biomass within grazed and ungrazed treatments was rejected. Biomass of graminoids was significantly reduced by grazing within all treatments except old and young colonies, although the trend was similar for the colonies as well (Table 3.2). The highest levels of both grazed and ungrazed graminoid biomass were associated with controls while the lowest levels were observed within old colonies (Figure 3.4). This corresponded to percent cover of graminoids, which were highest within controls and lowest within old colonies (Figure 3.2).

Although not always significant, grazing did reduce forb biomass to some extent in all treatments except for old colonies, where there was a minor increase (Figure 3.5). These decreases in forb biomass were only significant within burns <12 month old and young colonies (Table 3.2). Grazed forb biomass was highest within old colonies and

ungrazed forb biomass was highest within burns, regardless of time since fire. Whether exposed to grazing or not, forb biomass was always lowest within controls (Figure 3.5).

Time since fire (up to 16 months post burn) did not appear to affect forb and graminoid biomass within burned treatments, regardless of grazing (Figure 3.4, Figure 3.5, and Table 3.3). Young colonies and burns both <12 months and >12 months old had similar forb and graminoid biomass production.

Richness and diversity

I rejected the null hypothesis which stated that plant species richness and diversity do not differ among prairie dog colonies, burns, and controls. Both richness and diversity were highest within burns >12 months old and young colonies. Richness was lowest within burns <12 months old and diversity was lowest within controls (Figure 3.6 and Figure 3.7). No differences in richness or diversity were found between burns <12 months old and controls; burns <12 months old and old colonies; and burns >12 months and young colonies (Table 3.4).

Where trends in richness and diversity differed were: richness was greater in (1) young colonies and (2) burns >12 months old than old colonies and diversity was greater in (3) old colonies than controls (Table 3.4, Figure 3.6, Figure 3.7). These relationships were not significant for diversity (1 and 2) and richness (3), respectively. Thus, treatments significantly affected plant species diversity ($F_{4, 14} = 4.66, P = 0.017$) and richness ($F_{4, 14} = 5.45, P = 0.01$).

Vertical structure

Vertical structure was significantly different between all treatments except for control and burns >12 months old, and young and old colonies (Table 3.1). These two cases of no significant differences represented the highest and lowest vertical obstruction values (Figure 3.8). I therefore rejected the null hypothesis, as treatments strongly influenced vertical structure ($F_{4, 222} = 42.35, P < 0.001$).

Note: Appendix B contains a complete list of species identified in my study.

Discussion

Fire, large ungulate grazing, and prairie dog colonization all produce marked changes in plant communities. These effects include both structural and compositional elements, such as vertical structure, plant species richness, diversity, forage quality, and site productivity (Wilson and Shay 1990, Coppock et al. 1983*b*, Winter et al. 2002).

While these disturbance effects are well established in the literature, few studies have compared all three simultaneously. As many prairie dog studies have been limited to the northern or western extent of the species' range, it is valuable to assess colony characteristics in other locations, particularly in regions where the species has undergone serious decline and restoration is a key management goal. By doing so, management practices may be implemented and applied based on comparable site conditions.

Prairie dog colonies have been characterized as having high species richness and diversity (Coppock et al. 1983*b*, Hoogland 1995). Richness was highest on young colony areas and less recent burns, yet it was not significantly different between old colony areas and controls. It has been suggested that richness is not a strong indicator of habitat

quality, as often species occur within different treatments but at different proportions (Knowles et al. 2002). So although richness may not significantly differ among treatments, the plant community composition can vary greatly.

Increased plant species diversity can enhance interannual stability of net primary production and species composition within grasslands (Hartnett et al. 1997). While plant diversity was higher on the older portion of the colonies than controls, it was not significantly different between young and old colony areas or from patches burned more than 12 months prior. Plant diversity on less recent burns was not significantly different from colonies. Reduced diversity is commonly observed within older colonies as a few species of forbs or dwarf shrubs come to dominate sites (Coppock et al. 1983b, Fahnestock and Detling 2002). Thus, the similarity of plant species diversity on old colonies, controls, and burns may be explained by the extended length of colonization. Winter et al. (2002) also found no significant differences between colonies and shortgrass prairie. Although colony age affects diversity, results in Winter et al. (2002) and my study could be due to the time of sampling, as species peak at different times throughout the growing season. Some forbs are more dominant in the early spring, but are rarely encountered throughout the rest of the year. This is especially true of annual forbs which are dominant on prairie dog colonies (Winter et al. 2002). Had I sampled throughout the growing season, I might have observed variable differences in diversity and richness between treatments as colonies have a larger forb component compared to graminoid dominated controls.

Control and recently burned patches had high cover and biomass of grasses; young colony and less recently burned patches had a more equal cover of forbs and

grasses; and old colony areas had a high level of forbs. This is also reflected in vertical obstruction on sites, which followed a similar trend, shifting from high obstruction to low as time since initial disturbance increased. This supports findings by studies in other parts of the black-tailed prairie dog's range which have found that colonies have more short-statured perennial grasses and annual forbs than surrounding grasslands (Coppock et al. 1983b, Winter et al. 2002).

The significant increases in vertical obstruction following fire could be explained by multiple factors. Time since disturbance (i.e. fire) appears to be one of the most important. My study sites were in the eastern extent of the prairie dog's range and therefore productivity was inherently greater than in studies of prairie dog colony expansion in shortgrass prairie. Stocking density is also a factor, as a low stocking density could have allowed for greater regrowth in burn treatments. Fuhlendorf et al. (2009) found that plant community composition returned to pre-burn states within 2 or 3 years and standing biomass returned to pre-burn levels within 3 years of the initial disturbance. Comparing biomass of grazed treatments and exclosures suggested that grazing removed a significant amount of vegetation. This is also supported by Fuhlendorf et al. (2009), who attributed reduced biomass primarily to grazing since fire increases herbaceous productivity.

Although I did not consider the age of each colony in my study, I did separate newly established areas from long colonized areas within each colony for sampling and analysis. This was done by identifying key differences in plant community composition and structure. The results of this analysis complement that of other studies which analyzed distinctly young and old colonies. Young colonies had higher levels of

graminoids and slightly higher vertical structure than that of older colonies, which were characterized by forbs and very low levels of grasses (Coppock et al. 1983*b*). Coppock et al. (1983*b*) suggest significant changes in plant communities occur sometime after 3 to 8 years of colonization. The colonies in my study were originally depopulated in the 1920s and 1930s and reestablished in the late 1990s and early 2000s, thus they could be classified as old colonies in regards to plant community. However, as they expand, both plant community types will be present together on the landscape, increasing patch diversity. This is the case in my study, where long established colonies provided the typical ‘old colony’ community and newly established colonies on colony edges provided the typical ‘new colony’ community. When metapopulations are present and functional, this may also be true on a landscape scale, as complexes can contain both old and new colonies.

Similarities between fire and prairie dog colonization include increased shoot nitrogen, increased palatability and digestibility of forage, increased plant diversity (depending on frequency and intensity of disturbance), reduced standing biomass, increased bare ground, decreased litter, and suppressed woody plant establishment (Wilson and Shay 1990, Coppock et al. 1983*b*, Fuhlendorf and Engle 2001, Fahnestock and Detling 2002). Where they differ is the temporal effects of each treatment. Prairie dogs, unless removed from the site, continuously disturb the soil and vegetation through foraging, clipping vegetation, and burrowing. Effects of colonization gradually decline following colony extinction (Cid et al. 1991, Hoogland 1995). Fire is a more discrete disturbance and once complete the plant community moves towards its pre-fire state until

sufficient fuels have accumulated to support another fire event (Fuhlendorf and Engle 2001). A third disturbance type, large ungulate herbivory, is distinctly different from fire and prairie dogs, as it moves across the landscape, targets functional groups of plants, and has varying levels of intensity based on site quality and stocking rates (Hartnett et al. 1997, Steuter and Hidinger 1999). By focusing grazing within recently burned patches, herbivory can extend the initial effects of fire, such as production of young, succulent forage and reduction of structure (Fahnestock and Detling 2002). The most notable factor in regards to prairie dogs is vertical structure. Forb and graminoid biomass were significantly reduced with grazing within recent burns, as was graminoid biomass within less recent burns (>12 months old) in my study.

While commonly studied, the effects of large ungulate grazing are highly dependent on many factors including stocking density and site quality (Hartnett et al. 1997, Towne et al. 2005). For example, I found significant reductions in biomass of forbs and graminoids when recently burned treatments were exposed to large ungulate grazing. I also saw significant reductions in graminoid biomass within mixed-grass prairie controls, yet Fahnestock and Detling (2002) found that bison grazing had little impact on biomass within mixed-grass prairies. Their study sites, however, had very low bison densities (<52 ha per animal) and therefore those findings may not be accurately extrapolated to other sites. During my study there were approximately 650 bison and 280 cattle on WMWR. As in Fahnestock and Detling's (2002) study, not all of the 23,885 ha refuge comprising my study location was usable by cattle due to terrain and rock formations. The stocking density at WMWR in 2009 and 2010 was <37 hectares per animal for bison, <85 hectares per animal for cattle, and <27 hectares per animal when

both species were combined. Thus, my study area also had low stocking rates, but not as low as Fahnestock and Detling (2002).

Cid et al. (1991) found that bison can remove significant amounts of forage on prairie dog colonies, even though they do not frequently use these areas for grazing. Thus, he found large ungulate grazing to be additive to prairie dog herbivory. My exclosures did not separate grazing effects by species or size class of herbivore. Therefore, while prairie dogs, cattle, and bison were all observed using prairie dog colonies for grazing I cannot attribute any foraging effects to a single species.

While prairie dog colonization and fire have different effects on grasslands, particularly from a temporal aspect, they are both natural disturbances which reduce standing biomass and alter plant community composition. Maintaining colony complexes with varying colony ages can have benefits to landscape heterogeneity and biodiversity. These benefits can be compared to having a combination of old and recent fires on the landscape for similar benefits. For example, forb cover, plant species richness, and vertical obstruction all increased between the first and second year in my mixed-grass burn treatments. Conversely, graminoid cover, graminoid biomass, and plant species richness was lower in old colony areas than in young colony areas. Plant community characteristics differ with time in both cases, be it time since fire or length of colonization. It is important to remember that just as fires should be applied with varying times and sizes, colonies within functional complexes should have varying ages and sizes if grassland heterogeneity is the goal. As some colonies will remain stable, others might decline or disappear. Dynamic colony complexes and fire regimes within grasslands will therefore increase both landscape and patch diversity.

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Tables

Table 3.1 Comparisons of vertical obstruction, percent forb cover, and percent graminoid cover between treatments sampled in June and July 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma and analyzed with PROC Mixed (SAS 2003).

Comparison		Vertical Obstruction			Forb Cover			Graminoid Cover		
Treatment 1	Treatment 2	<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>
Burn, <12 months	Control	-7.26	222	<0.001	-0.82	14	0.426	-1.35	14	0.19
Burn, <12 months	Young Colony	2.46	222	0.015	-2.18	14	0.05	-0.87	14	0.396
Burn, <12 months	Old Colony	2.97	222	0.003	3.02	14	0.011	5.26	14	<0.001
Burn, <12 months	Burn, >12 months	-5.16	222	<0.001	-1.99	14	0.07	-0.81	14	0.424
Control	Young Colony	9.71	222	<0.001	-1.49	14	0.162	0.4	14	0.696
Control	Old Colony	10.26	222	<0.001	-2.37	14	0.036	6.6	14	<0.001
Control	Burn, >12 months	0.92	222	0.361	-1.36	14	0.2	0.31	14	0.757
Young Colony	Old Colony	0.51	222	0.613	-0.82	14	0.428	5.94	14	<0.001
Young Colony	Burn, >12 months	-7.26	222	<0.001	-0.04	14	0.968	-0.04	14	0.968
Old Colony	Burn, >12 months	-7.71	222	<0.001	0.69	14	0.502	-5.27	14	<0.001

Table 3.2. Comparisons of forb and graminoid biomass within treatments exposed to or excluded from large ungulate and prairie dog grazing for a single growing season in 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma and analyzed with PROC Mixed (SAS 2003).

Treatment	Forb Biomass			Graminoid Biomass		
	<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>
Burn, <12 months	2.63	48	0.01	3.4	48	0.004
Control	0.96	48	0.34	2.32	48	0.02
Young Colony	2.03	48	0.05	1.53	48	0.13
Old Colony	-0.26	48	0.8	1.2	48	0.23
Burn, >12 months	1.67	48	0.1	2.88	48	0.006

Table 3.3. Comparisons of forb and graminoids biomass within treatments exposed to or excluded from large ungulate and prairie dog grazing for a single growing season at Wichita Mountains Wildlife Refuge, Oklahoma and analyzed with PROC Mixed (SAS 2003).

Treatment 1	Treatment 2	Forb Biomass						Graminoid Biomass					
		Grazed			Ungrazed			Grazed			Ungrazed		
		<i>t</i>	<i>df</i>	<i>P</i>	<i>t</i>	<i>df</i>	<i>P</i>	<i>t</i>	<i>df</i>	<i>P</i>	<i>t</i>	<i>df</i>	<i>P</i>
Burn, <12 months	Control	0.95	48	0.3459	2.74	48	0.0115	-4.47	48	<.0001	-3.2	48	0.0025
Burn, <12 months	Young colony	0.66	48	0.5139	1.07	48	0.2886	-0.86	48	0.3916	0.81	48	0.4191
Burn, <12 months	Old Colony	-1.32	48	0.1915	1.47	48	0.0026	1.23	48	0.2237	3.25	48	0.0021
Burn, <12 months	Burn, >12 months	-0.45	48	0.6516	-0.1	48	0.9246	0.25	48	0.8065	-0.1	48	0.9169
Control	Young colony	-0.23	48	0.8154	-1.52	48	0.1357	3.39	48	0.0014	3.9	48	0.0003
Control	Old Colony	-2.28	48	0.0273	-1.11	48	0.2727	5.55	48	<.0001	6.41	48	<.0001
Control	Burn, >12 months	-1.27	48	0.2104	-2.41	48	0.0198	4.03	48	0.0002	2.59	48	0.0126

Table 3.3 continued

Treatment 1	Treatment 2	Forb Biomass						Graminoid Biomass					
		Grazed			Ungrazed			Grazed			Ungrazed		
		<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>
Young colony	Old Colony	-1.27	48	0.2104	0.38	48	0.7047	2.02	48	0.0489	2.35	48	0.0229
Young colony	Bum, >12 months	-1.91	48	0.0621	-1.02	48	0.3141	0.98	48	0.3299	-0.8	48	0.4252
Old Colony	Bum, >12 months	0.7	48	0.4868	-1.36	48	0.1807	-0.82	48	0.4144	-2.91	48	0.0055

Table 3.4 Comparisons of plant species richness and Shannon-Weaver diversity between treatments sampled in June and July 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma and analyzed with PROC Mixed (SAS 2003).

Comparison		Richness			Diversity		
Treatment 1	Treatment 2	<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>
Burn, <12 months	Control	1.13	14	0.279	1.32	14	0.20
Burn, <12 months	Young Colony	-3.98	14	0.002	-3.13	14	0.005
Burn, <12 months	Old Colony	-0.91	14	0.383	-1.38	14	0.182
Burn, <12 months	Burn, >12 months	-2.96	14	0.012	-2.22	14	0.037
Control	Young Colony	3.09	14	0.009	-4.4	14	<0.001
Control	Old Colony	0.16	14	0.874	-2.63	14	0.015
Control	Burn, >12 months	-2.19	14	0.049	-3.39	14	0.003
Young Colony	Old Colony	3.01	14	0.01	1.71	14	0.102
Young Colony	Burn, >12 months	0.4	14	0.698	0.43	14	0.672
Old Colony	Burn, >12 months	-2.22	14	0.047	-1.01	14	0.324

Figures

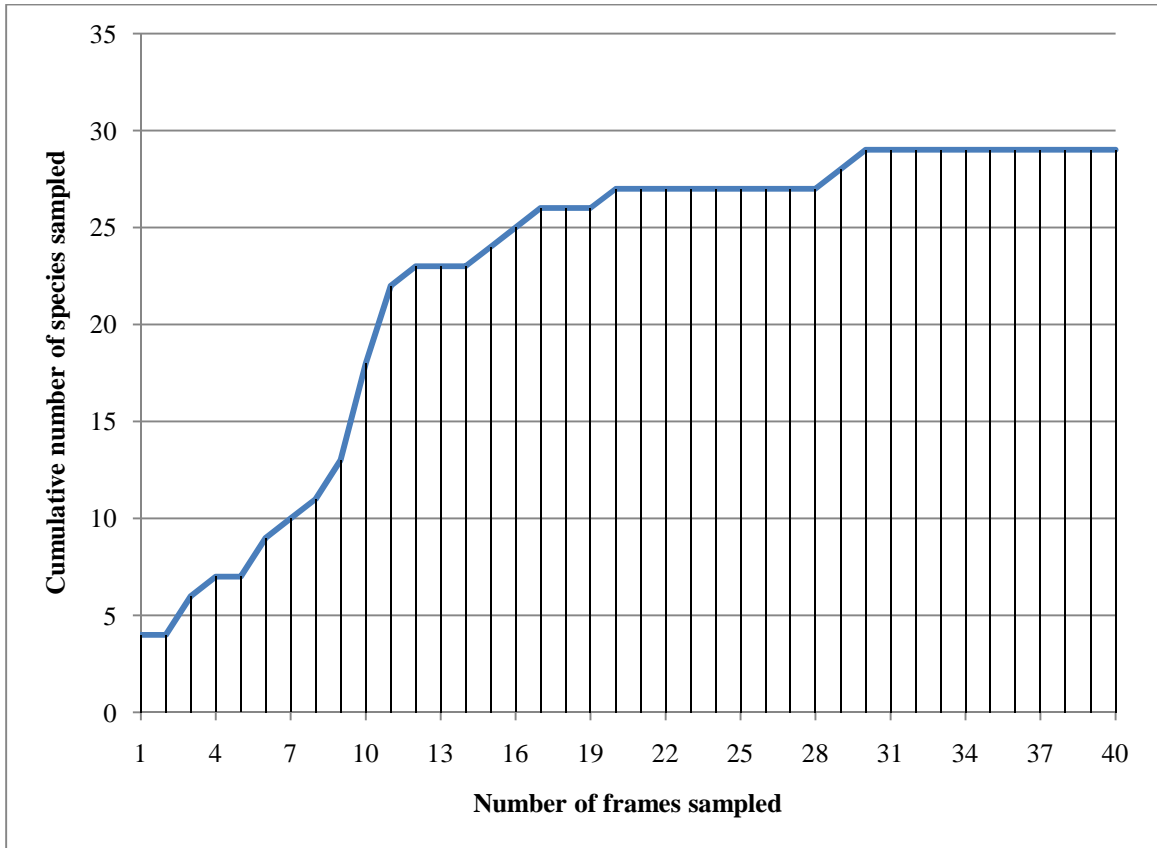


Figure 3.1. Species accumulation curve calculated using samples from prairie dog colonies to determine optimum sampling effort for canopy coverage estimation on burn, control, old colony, and young colony treatments in June and July of 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma. Approximately 94% of the plant community may be sampled with 20 frames.

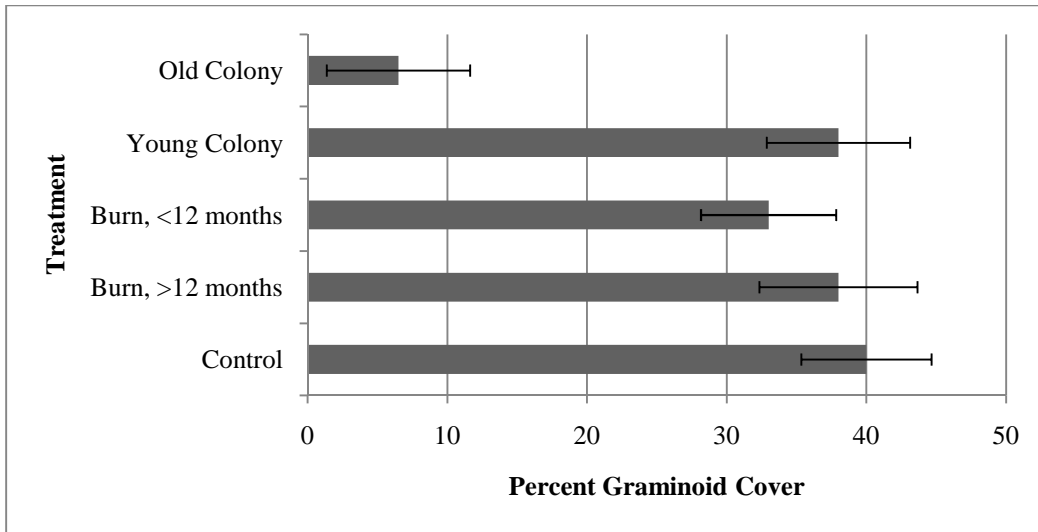


Figure 3.2. Percent graminoid cover with 95% confidence intervals within treatments sampled in June and July 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

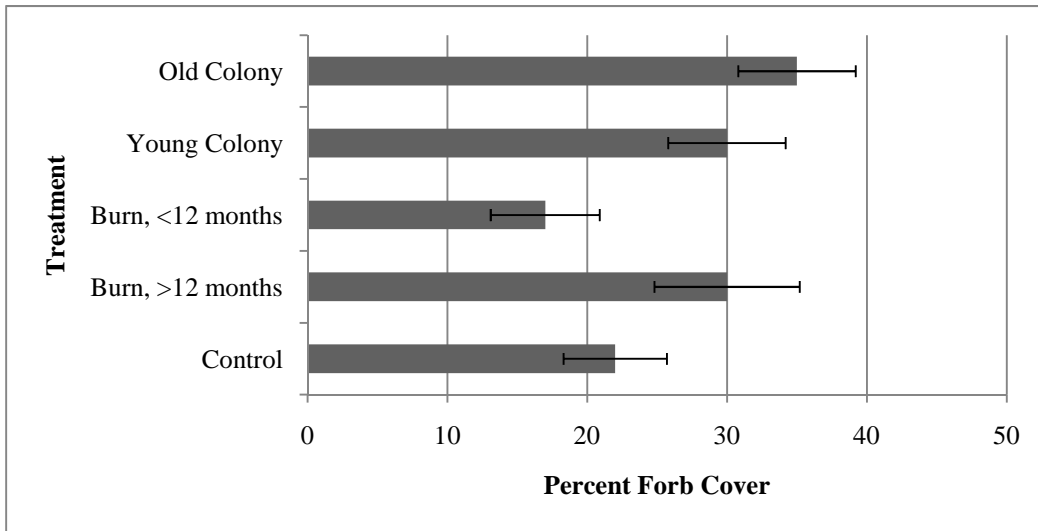


Figure 3.3. Percent forb cover with 95% confidence intervals within treatments sampled in June and July 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

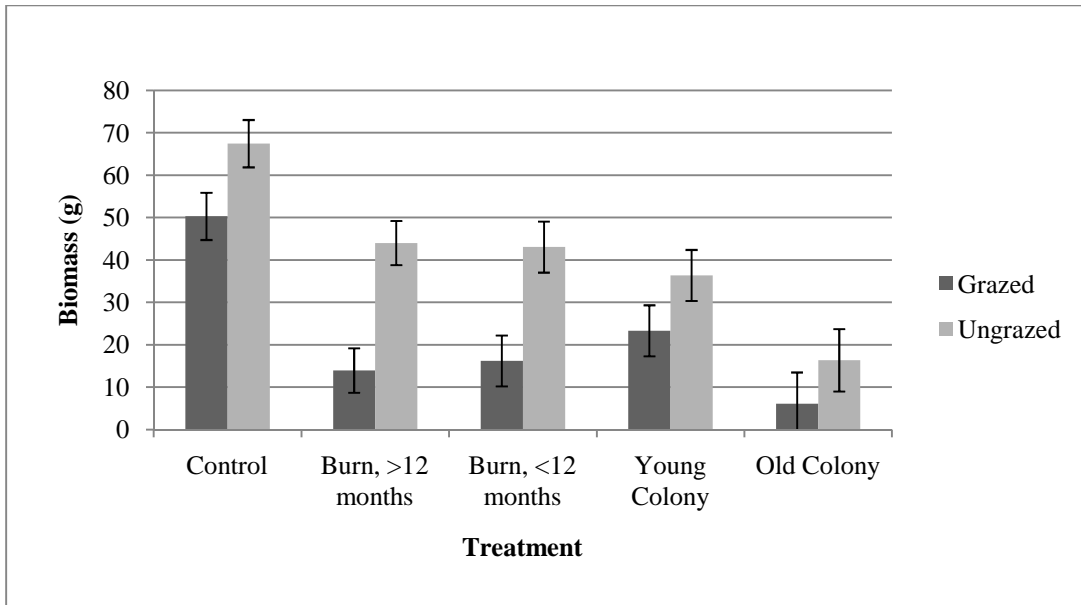


Figure 2.4. Graminoid biomass with 95% confidence intervals for treatments exposed to or excluded from large ungulate and prairie dog grazing for a single growing season in 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

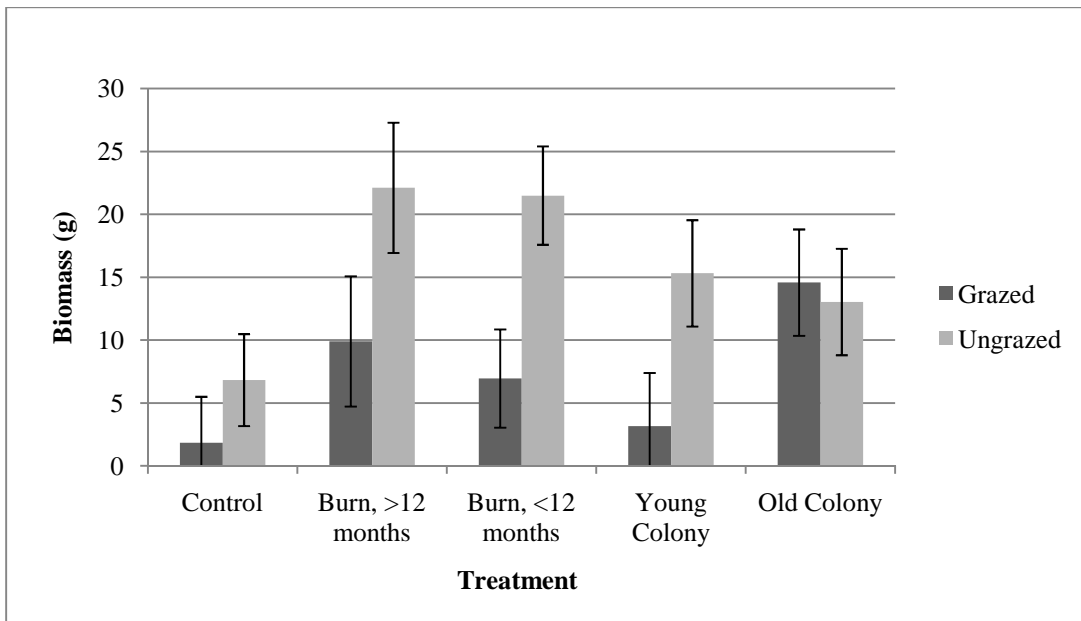


Figure 3.5. Forb biomass with 95% confidence intervals for treatments exposed to or excluded from large ungulate and prairie dog grazing for a single growing season in 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

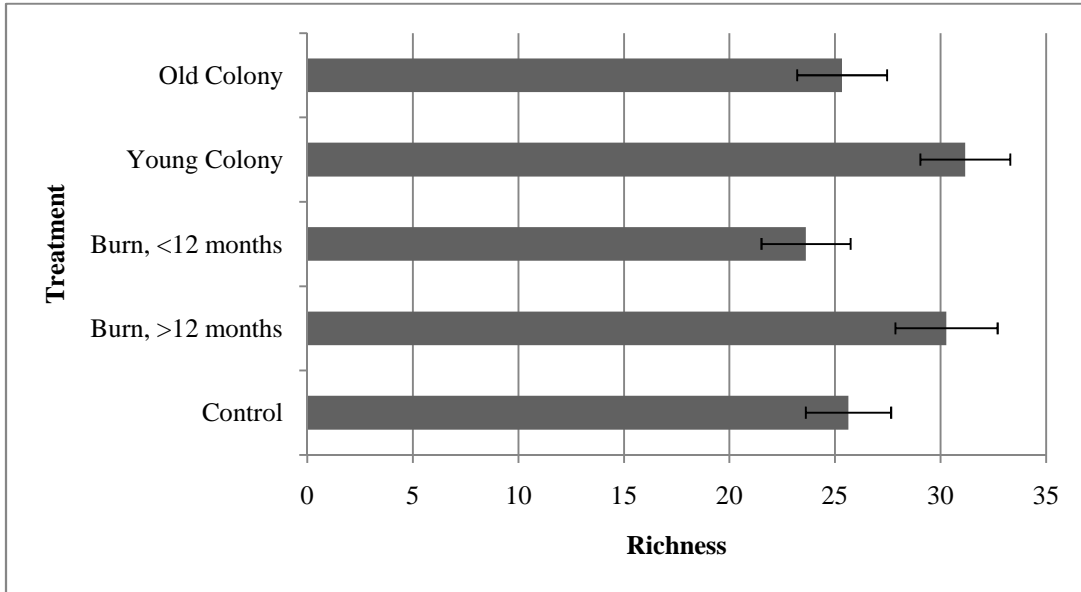


Figure 3.6. Plant species richness with 95% confidence intervals for treatments sampled in June and July 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

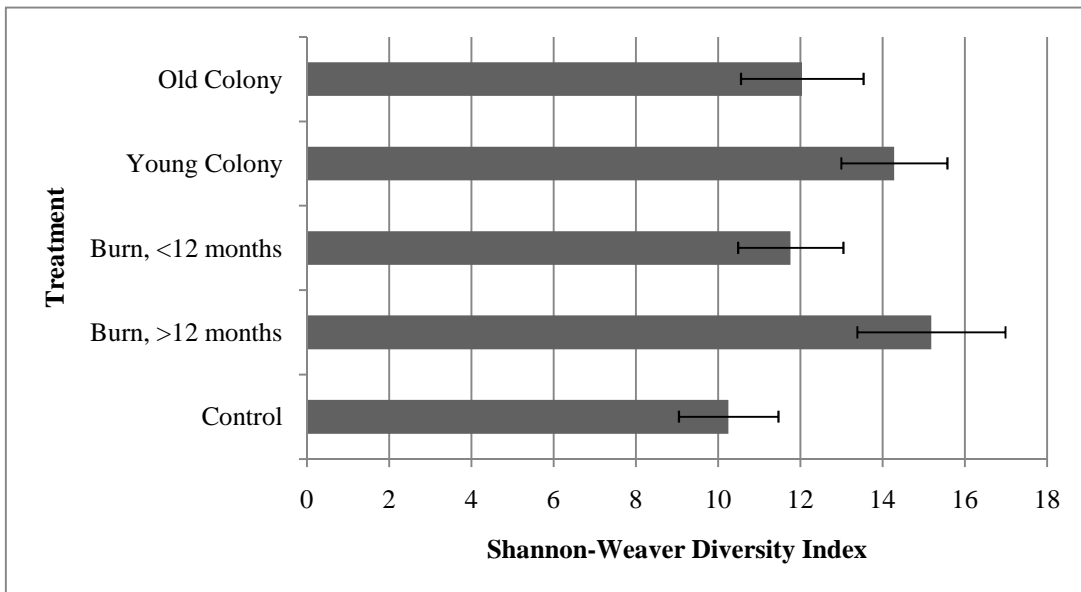


Figure 3.7. Shannon-Weaver diversity indices with 95% confidence intervals for treatments sampled in June and July 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

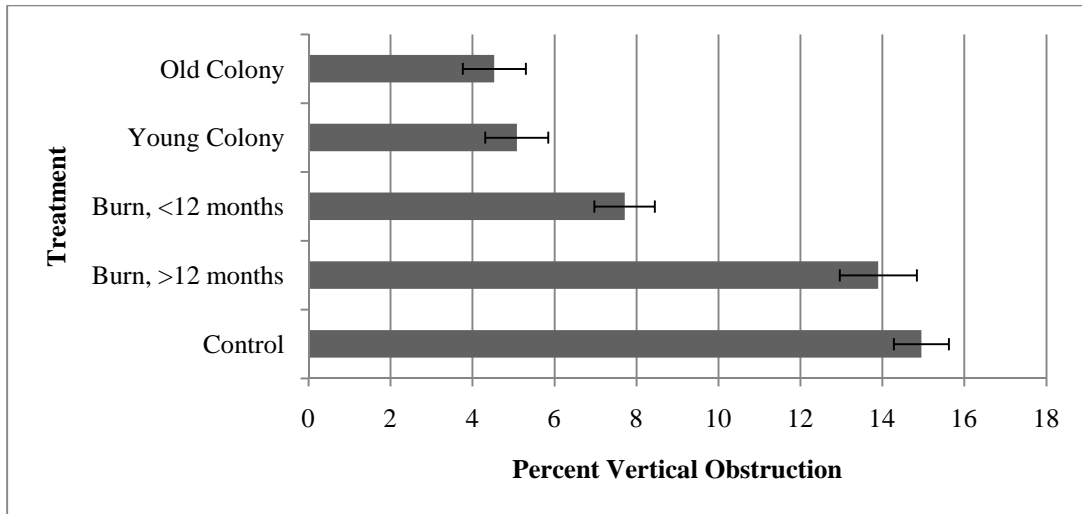


Figure 3.8. Vertical obstruction by vegetation with 95% confidence intervals for treatments sampled in June and July 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

CHAPTER IV

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Discussion

Fire and herbivory are common disturbances which can interact and shape plant community structure and composition in grasslands (Fuhlendorf et al. 2009). In modern landscapes grazing can occur by both native (i.e. bison and prairie dogs) and introduced herbivores (i.e. livestock). I found that patch selection differed between bison and cattle, however both species preferred disturbed grasslands. Similarly, prairie dogs readily used recently disturbed (burned) grasslands for foraging and colony expansion. Thus, it appears that both small and large herbivores can be incorporated into patch-burn grazing management. Prairie dogs and large herbivores not only preferred disturbed sites, their behaviors and activities can result in disturbed patches at multiple scales as well. For example, focal grazing by large ungulates can maintain the low vegetation structure initially created with fire, altering fuel loads and increasing habitat availability for prairie dogs. Prairie dog herbivory and burrowing of prairie dogs is known to decrease dominance of graminoids and increase the abundance of forbs, creating altered plant communities which attract cattle and other herbivores.

Patch-burn grazing interactions are dynamic and their implications for prairie dog conservation and management undoubtedly extend beyond the scope of this study. While further study is needed to better understand the effects of grassland fires on wildlife and plant communities, current research supports the use of fire as a tool to provide heterogeneous habitat for a variety of wildlife species. These include grassland passerines (Fuhlendorf et al. 2006, Churchwell et al. 2007, Coppedge et al. 2008), prairie chickens (Cannon and Knopf 1979), swift foxes (*Vulpes velox*; Thompson et al. 2008), American bison (*Bison bison*; Coppedge et al. 1998, Biondini et al. 1999), elk (*Cervus elaphus*; Jourdonnais and Bedunah 1990), mule deer (*Odocoileus hemionus*; Hobbs and Spowart 1984), and black-tailed prairie dogs (*Cynomys ludovicianus*; Milne-Laux and Sweitzer 2006, Augustine et al. 2007, Northcott et al. 2008).

Additionally, fire influences grazing patterns of domestic livestock which has implications to both livestock production and grassland heterogeneity. Plant diversity also increases within burned patches as is shown in my study as well as Collins and Barber (1985). While the presence of recently burned patches provide valuable forage resources, unburned patches are equally important as they provide various forms of cover. The presence of burned, colonized, and recently undisturbed grasslands within a landscape increases the diversity of plant communities and their associated resources (Fuhlendorf et al. 2009).

Forb and graminoid abundance and diversity vary by disturbance type, intensity, and frequency. For example, grazing by ungulates typically reduces standing biomass on a particular site. Closer study has revealed that different species of herbivores remove forbs and grasses at different proportions and can cause shifts in plant communities when

sustained over time (Schwartz and Ellis 1981, Steuter and Hidingier 1999, Towne et al. 2005). Although not significant, such grazing differences are seen in cattle and bison, as cattle consume more forbs than bison. Multiple studies have suggested that bison and cattle differ in many aspects, including behaviors which can influence the spatial heterogeneity of grasslands (Schwartz and Ellis 1981, Plumb and Dodd 1993, Stuetter and Hidingier 1999, Towne et al. 2005). However, Towne et al. (2005) is the only one of these which actually involved a side by side comparison of bison and cattle under uniform management conditions and they found that effects on plant communities were more dependent on management than species, and species effects appeared to be indirectly linked through feedback of the fire-grazing cycle.

Prairie dogs have long been associated with negative effects to livestock. However I found that cattle spent more time on colonies than bison and cattle preferred to graze on colonies. Colonies are known to have increased forage quality and O'Meilie et al. (1982) found no significant differences in cattle weight gain between colonized and uncolonized pastures. However, Cheng and Ritchie (2006) observed reduced weight gain in Utah prairie dogs when colonies were grazed at moderate and high stocking densities by cattle. While we do not know what the thresholds are for these competitive relationships, it is important to acknowledge that both livestock and prairie dogs have the potential to negatively affect the other, as is expected in true competition. However, as with grassland conservation, negative effects to prairie dogs may be reduced through proper rangeland management practices, including following moderate stocking densities.

My study sites were located on the extreme eastern boundary of the prairie dog's current range where dense vegetation is likely more limiting than elsewhere to prairie dog

expansion and dispersal. This may explain why there was no colonization of controls at my study sites, unlike the shortgrass studies in which colonies expanded into both controls and burns (Augustine et al. 2007, Milne-Laux and Sweitzer 2006). Thus, fire and large ungulate grazing may have historically been the driving force behind the colonization of the eastern edge of the prairie dog's range (Wuerthner 1997). Without these disturbances, prairie dogs could theoretically have had a range restricted to less productive grasslands or simply been absent.

Today the black-tailed prairie dog is continuing to decline in population, increase in colony isolation, and shrink in rangewide distribution (Wuerthner 1997). The negative trends in prairie dog populations are largely tied to habitat loss, the introduction and spread of sylvatic plague (*Yersinia pestis*), and a long history of eradication campaigns (Wuerthner 1997, Lomolino and Smith 2001). The eastern extent of the species' range is not currently impacted by plague events, which presents the greatest threat to colony stability throughout the rest of the species' range (Lomolino and Smith 2001, Augustine et al. 2008). The receding eastern boundary of the black-tailed prairie dog's range could be partially attributed to reduced disturbance from fire suppression. Mixed and tallgrass prairie that is not disturbed by fire can form dense, homogenous grasslands (Wuerthner 1997). Without a significant disturbance like fire, litter accumulates and vegetation becomes taller and denser, eventually culminating in encroachment of woody species. Further complicating this issue is the widespread invasion and seeding of non-native grasses which often reduce native plant diversity and form dense homogenous patches (D'Antonio and Vitousek 1992). These factors would be expected to have serious

ramifications for prairie dog complexes, which are composed of both persistent and ephemeral colonies that contribute to increased local population and genetic stability.

When using fire for prairie dog colony expansion, regional variations in site productivity should be considered. In the west habitat is shortgrass, where structure is typically not limiting. Additionally, conditions are arid, so expansion responds positively to increased precipitation, as forage appears to be limiting for those populations (Knowles 1987). In the east, where productivity is higher and habitat includes both mixed and shortgrass plant communities, structure appears to be a limiting factor whereas forage is not. In years of below average precipitation colonization responses may be stronger (Knowles et al. 2002). However, forage availability can be highly variable by site and age of colony throughout the prairie dog's range (Koford 1958, Hoogland 1995).

Concerning the application of patch-burn grazing management, Fuhlendorf et al. (2009) explains “if fires are many and dispersed, they can contribute to the dispersal of herbivores, whereas if they are few and large they can lead to congregations of grazers”. While the authors may have been referring to large ungulates, this is also an appropriate perspective for prairie dog management. I evaluated the use of fire for colony expansion, but fire may also be a valuable tool in reestablishing complexes. In the case of both natural and artificial colony establishment fire can create preferred prairie dog habitat with reduced vertical structure and increased forage quality. While the use of fire to increase the success of colony establishment by dispersing prairie dogs is untested, I did observe the establishment and persistence of a coterie of 3 prairie dogs within burned mixed-grass prairie approximately 3.5 kilometers away from the Turkey Creek colony at Wichita Mountains Wildlife Refuge. These prairie dogs were first sighted in fall 2009

and were still at the new coterie when my study ended in September 2010. While this is only anecdotal evidence, it could be tested in future research to see how fire might influence dispersal patterns. Fire treatments have been proven effective in expanding colonies in shortgrass and mixed-grass prairies. The next step in this line of study is to address metapopulation restoration within fragmented populations (Milne-Laux and Sweitzer 2006, Augustine et al. 2008, Northcott et al. 2008).

Thus, future research directed at prairie dog management should address the following issues:

(1) Suitability of fire and grazing treatments for restoration of other prairie dog species. Black-tailed prairie dogs are the most common and widespread of five species found in North America. The Utah and Mexican species are listed as federally endangered (Wuerthner 1997). While the black-tailed prairie dog is commonly studied, colony characteristics and habitat vary greatly between black-tailed prairie dogs and the other four species. Black-tailed prairie dog colonies have denser populations and appear to be less tolerant of vertical obstruction (Hoogland 2006).

(2) Potential of burned patches to be colonized through intercolony dispersal. All studies to date have tested intracolony dispersal to burns which abut existing colonies. Future studies might apply fire at varying distances from colonies and monitor colonization. Prairie dogs have been observed dispersing to maximum distances of 9.6 km and Hoogland (2006) suggests that efforts to establish colonies be 2 to 4 kilometers from existing colonies to allow for continued dispersal.

(3) Response to fire and grazing treatments over time when only one fire is applied in direct contact to a colony. It is possible that applying burns every year may reduce the facultative effects of large ungulate grazing to prairie dog colonization. The presence of more recent burns shift grazing pressure away from less recently burned patches, possibly reducing the persistence of prairie dogs within burns colonized the previous year. Therefore, long-term viability of fire-induced colonies should be monitored. I saw reductions in prairie dog populations within burns one year after the burn occurred, but this was likely due to above average precipitation. The population response in a year with average precipitation patterns is unknown.

(4) Effects of large ungulate grazing on prairie dog populations. Colonies have not been shown to have significant negative effects on cattle, and cattle have been shown to use and in some cases be attracted to colonies (O'Meilia 1982). A question which has not received adequate attention is the effect of grazing on prairie dogs. As previously discussed, bison and cattle do not use landscapes in the same way. My study suggests that cattle graze on colonies at higher rates than bison. Therefore cattle may have a higher potential for competition with prairie dogs than bison. Cattle can move around a landscape, grazing preferred patches (colonies) when adequate forage is available and moving on to less preferred areas (uncolonized grassland) when resources are low. Prairie dogs are limited in their ability to move to areas with greater forage and have been shown to dramatically shift diet during the winter, when food availability is restricted (Fagerstone et al. 1981). Focal grazing by cattle on colonies, especially when densities are high, may affect prairie dog survival in severe winters. However, these effects may be less significant than expected due to caching of food for the winter in burrows. These

effects likely vary by species as well, since black-tailed prairie dogs are the only species which does not hibernate (Hoogland 1995). Negative effects may also be reduced within recently burned and colonized areas by the increased production of quality forage.

Livestock, bison, and prairie dogs can all benefit from fire treatments. However, the relationship between these species and burned treatments is not a simple, unidirectional one. Fire as a habitat and rangeland management tool is a growing interest in both research and management, and yet we are just beginning to understand the complex relationships which are interwoven between floral and faunal responses to fire. Similarly, many studies have characterized prairie dog colony attributes and their utilization by wildlife and livestock, but the actual feedbacks between prairie dog colonies and other animals is not well understood. Current studies would suggest that prairie dog colonies have ecological value for not only native plants and animals, but for domestic livestock as well (O'Meilia 1982, Guenther and Detling 2003). Similarly, fire has been identified as a critical part of fire-dependent ecosystems which should be restored at some spatial and temporal scale to improve heterogeneity and ecosystem health. Further study is needed to identify appropriate scales of disturbance, in the context of both time and space.

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Appendix A

Black-tailed prairie dog weight data

Table A.1. Black-tailed prairie dog weights of juvenile males (JM), juvenile females (JF), adult males (AM), and adult females (AF) on burned plots (B) and colonies (C) during 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

Spring 2009								
Turkey Creek	JM, B	JM, C	JF, B	JF, C	AM, B	AM, C	AF, B	AF, C
<i>n</i>	0	9	0	3	5	4	1	2
Min		375		400	1015	980	950	1050
Max		700		750	1400	1060	950	1050
<i>x</i>		523		517	1149	1022	950	1050
SE		105		202	170	38		
Spring 2010								
Turkey Creek	JM, B	JM, C	JF, B	JF, C	AM, B	AM, C	AF, B	AF, C
<i>n</i>	0	1	0	1	6	5	6	9
Min		475		500	1050	1150	825	950
Max		475		500	1225	1500	1250	1175
<i>x</i>		475		500	1146	1275	1065	1063
SE					62	132	154	82

Table A.1 continued.

Spring 2010								
Quanah Parker	JM, B	JM, C	JF, B	JF, C	AM, B	AM, C	AF, B	AF, C
<i>n</i>	2	5	1	3	1	4	0	5
Min	450	250	500	325	1100	570		990
Max	475	375	500	500	1100	1200		1200
<i>x</i>	463	286	500	408	1100	955		1038
SE	18	54		88		276		91
Summer 2010								
Turkey Creek	JM, B	JM, C	JF, B	JF, C	AM, B	AM, C	AF, B	AF, C
<i>n</i>	0	2	0	2	3	5	4	5
Min		720		600	775	900	1075	900
Max		775		650	1300	1375	1300	1150
<i>x</i>		747.5		625	1108	1095	1194	1030
SE		39		35	290	203	92	93

Appendix B

Plant species encountered on Wichita Mountains Wildlife Refuge, Oklahoma

Table B.1. Plant species recorded during vegetation sampling in 2009 and 2010 at Wichita Mountains Wildlife Refuge, Oklahoma.

Family	Genus	Species	Old Colony	New Colony	Burn	1 Year Post-Burn	Control
Acanthaceae	Ruellia	humilis	x	x	x	x	x
Amaranthaceae	Amaranthus	blitoides	x	x	x		x
Amaranthaceae	Amaranthus	retroflexus	x				
Asclepidaceae	Asclepias	viridis	x	x	x	x	
Asteraceae	Achillea	millefolium	x	x	x	x	x
Asteraceae	Ambrosia	psilostachya	x	x	x	x	x
Asteraceae	Artemisia	ludoviciana	x	x	x	x	x
Asteraceae	Bidens	bipinnata		x			
Asteraceae	Castilleja	indivisa				x	x

Table B.1 continued

Family	Genus	Species	Old Colony	New Colony	Burn	1-Year Post Burn	Control
Asteraceae	Chrysopsis	pilosa	x	x			x
Asteraceae	Cirsium	undulatum	x	x			x
Asteraceae	Coreopsis	grandiflora	x	x	x	x	x
Asteraceae	Coreopsis	tinctoria				x	
Asteraceae	Echinacea	angustifolia	x		x	x	x
Asteraceae	Erigeron	strigosus				x	x
Asteraceae	Gaillardia	pulchella					x
Asteraceae	Grindelia	squarrosa			x	x	x
Asteraceae	Gutierrezia	dracunculoides	x	x	x		x
Asteraceae	Helenium	amarum	x	x	x	x	x
Asteraceae	Iva	annua			x	x	
Asteraceae	Liatris	punctata		x	x	x	x
Asteraceae	Marshallia	caespitosa		x	x		x
Asteraceae	Packera	plattensis	x	x			

Table B.1 continued.

Family	Genus	Species	Old Colony	New Colony	Burn	1-Year Post Burn	Control
Asteraceae	<i>Pseudognaphalium</i>	<i>obtusifolium</i>	x	x	x	x	x
Asteraceae	<i>Pyrrhopappus</i>	<i>grandiflorus</i>	x				
Asteraceae	<i>Ratibida</i>	<i>columnifera</i>	x	x	x	x	x
Asteraceae	<i>Rudbeckia</i>	<i>hirta</i>					x
Asteraceae	<i>Thelesperma</i>	<i>filifolium</i>	x	x	x	x	x
Asteraceae	<i>Verbena</i>	<i>pumilia</i>	x	x			
Asteraceae	<i>Vernonia</i>	<i>baldwinii</i>			x		
Brassicaceae	<i>Dimorphocarpa</i>	<i>candicans</i>					x
Brassicaceae	<i>Lepidium</i>	<i>virginicum</i>	x	x	x	x	
Cactaceae	<i>Echinocereus</i>	<i>reichenbachii</i>					x
Cactaceae	<i>Opuntia</i>	<i>macrorhiza</i>			x		x
Caprifoliaceae	<i>Symphoricarpos</i>	<i>orbiculatus</i>			x	x	
Commelinaceae	<i>Tradescantia</i>	<i>ohiensis</i>			x	x	
Crassulaceae	<i>Sedum</i>	<i>nuttallianum</i>	x	x		x	

Table B.1 continued.

Family	Genus	Species	Old Colony	New Colony	Burn	1-Year Post Burn	Control
Cyperaceae	Carex	sp 1	x	x	x		
Cyperaceae	Carex	sp 2		x			
Cyperaceae	Carex	sp 3	x	x			x
Cyperaceae	Eleocharis	obtusa			x		
Cyperaceae	Fimbristylus	puberula	x	x	x		x
Cyperaceae	Scirpus	canadensis				x	
Cyperaceae	Scleria	ciliata	x	x	x	x	x
Euphorbiaceae	Croton	capitatus		x	x	x	x
Euphorbiaceae	Euphorbia	corallata			x		
Euphorbiaceae	Tragia	ramosa	x	x	x	x	x
Fabaceae	Astragalus	crassicaarpus	x	x	x	x	x
Fabaceae	Baptisia	bracteata				x	x
Fabaceae	Dalea	purpurea					x
Fabaceae	Medicago	lupina		x			

Table B.1 continued.

Family	Genus	Species	Old Colony	New Colony	Burn	1-Year Post Burn	Control
Fabaceae	Tephrosia	virginiana			x		x
Gentianaceae	Sabatia	campestris	x	x	x	x	x
Juncaceae	Juncus	marginatus			x	x	x
Krameriaceae	Krameria	lanccolata	x	x	x		x
Lamiaceae	Monarda	fistulosa				x	x
Linaceae	Linum	sulcatum		x		x	x
Malvaceae	Callirhoe	involuta			x		
Mimosaceae	Mimosa	quadrivalvis	x		x	x	x
Mimosaceae	Neptunia	lutea	x	x	x	x	x
Onagraceae	Oenothera	curtiflora	x	x		x	x
Onagraceae	Oenothera	serrulata		x			
Onagraceae	Oenothera	speciosa		x			x
Oxalidaceae	Oxalis	violaceae	x	x	x	x	
Oxalidaceae	Oxalis	stricta	x	x		x	

Table B.1 continued.

Family	Genus	Species	Old Colony	New Colony	Burn	1-Year Posts Burn	Control
Plantaginaceae	Collinsia	violaceae			x		
Plantaginaceae	Plantago	aristata	x	x	x	x	x
Plantaginaceae	Plantago	wrightiana	x	x	x	x	x
Poaceae	Agrostis	hyemalis		x			
Poaceae	Aristida	purpurea		x			x
Poaceae	Bothriochloa	laguroides		x	x	x	x
Poaceae	Bouteloua	curtipendula					x
Poaceae	Bouteloua	hirsuta		x	x	x	x
Poaceae	Bouteloua	rigidiseta	x	x	x		x
Poaceae	Bromus	japonicus		x	x	x	x
Poaceae	Buchloe	dactyloides	x	x	x	x	x
Poaceae	Chloris	verticillata	x	x	x		
Poaceae	Cynodon	dactylon		x	x		
Poaceae	Digitaria	cognata	x	x			

Table B.1 continued.

Family	Genus	Species	Old Colony	New Colony	Burn	1-Year Post Burn	Control
Poaceae	Elymus	canadensis		x	x	x	x
Poaceae	Eragrostis	curtipedicellata		x			x
Poaceae	Eragrostis	intermedia	x			x	x
Poaceae	Eragrostis	secundiflora	x	x			
Poaceae	Hordeum	pusillum		x	x		
Poaceae	Panicum	oligosanthes	x	x	x	x	x
Poaceae	Panicum	virgatum			x	x	x
Poaceae	Panicum	sphaerocarpon				x	
Poaceae	Paspalum	setaceum		x			
Poaceae	Schedonardus	paniculatus	x	x	x		
Poaceae	Schizachyrium	scoparium	x	x	x	x	x
Poaceae	Setaria	parviflora				x	x
Poaceae	Sorghastrum	nutans		x	x	x	x
Poaceae	Urochloa	texana		x			

Table B.1 continued.

Family	Genus	Species	Old Colony	New Colony	Burn	1-Year Post Burn	Control
Ranunculaceae	Anemone	caroliniana					x
Rubiaceae	Diodia	teres	x	x	x		x
Rubiaceae	Hedyotis	nigricans	x		x	x	x
Rubiaceae	Houstonia	nigricans			x		x
Solanaceae	Solanum	carolinensis		x			
Solanaceae	Solanum	elaeanifolium	x				x
Solanaceae	Solanum	rostratum	x			x	
Umbelliferae	Daucus	pusillus					x

VITA

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Pages in Study: 118

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Major Field: Natural Resource Ecology and Management

Scope and Method of Study: Restoring historic fire-grazing regimes and the declining keystone species the black-tailed prairie dog (*Cynomys ludovicianus*) are two management priorities in North America's grasslands. My study sought to investigate the relationship between these two elements of grassland ecology. Analysis included comparisons of prairie dog, bison, and cattle use of prairie dog colonies, burned grasslands, and mixed-grass prairie controls. In 2009 and 2010 I collected data on plant community characteristics and treatment use by prairie dogs and large ungulates at Wichita Mountains Wildlife Refuge, Oklahoma.

Findings and Conclusions: Prairie dogs responded positively to burn treatments in both years, with the strongest response occurring in 2009, when precipitation during the growing season was lowest. Vertical obstruction was significantly reduced within burned treatments and might explain the colonization of burns. There was no observed attempt to colonize unburned grasslands. Bison and cattle both selected disturbed sites and avoided unburned and uncolonized grasslands. However, there were differences in treatment use. Cattle preferred colonies for both loafing and grazing, while bison favored colonies for loafing and burn treatments for grazing. This likely is associated with differences in diet and the plant communities found in each treatment. While plant species diversity and richness varied between treatment types, cover types reflected intensity and length of disturbance. Forb cover and biomass increased with disturbance, with colonies and burns having a greater abundance of forbs than mixed-grass prairie controls. Conversely, graminoid cover and biomass were greatest within controls and lowest within colonies. It appears that prairie dogs and large ungulates can both benefit from restoring fire to the landscape. When applied to appropriate sites, fire can create valuable habitat for dispersing prairie dogs. This can aid in colony expansion and potentially improve conditions for both artificial and natural colony establishment. It also provides additional evidence that cattle utilize prairie dog towns for grazing and are not ecologically equivalent to bison.

ADVISER'S APPROVAL: Dr. R. Dwayne Elmore
