

GRASSLAND BIRDS: COMMUNITY DYNAMICS, RESOURCE SELECTION, AND NEST  
SURVIVAL ON MIXED-GRASS PRAIRIE GRAZED BY NATIVE COLONIAL AND  
DOMESTIC HERBIVORES

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**Title**

Grassland birds: community dynamics, resource selection, and nest survival  
on mixed-grass prairie grazed by native colonial and domestic herbivores

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## ABSTRACT

Investigators surveyed avian and vegetation composition on- and off- black-tailed prairie dog (*Cynomys ludovicianus*; hereafter prairie dog) colonies to gain greater insight into community dynamics of grassland passerines. Few studies have investigated grassland bird community associations with prairie dogs, and of those limited studies aim to quantify nesting passerine habitat selection and nest success. The objective of this study was to identify community associations and factors that shape the community of grassland birds on grazed mixed-grass prairie, both on- and off-prairie dog colonies. Bird and vegetation communities, avian densities, nesting survival, and resource selection was investigated in relativity to a landscape occupied with prairie dogs. Individual species exhibited different selections in regards to different vegetation communities created by prairie dogs. This makes heterogeneity an important landscape component for maintaining diverse, robust bird and plant communities at the landscape scale.

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My undergraduate career took place at South Dakota State University in Brookings, South Dakota. I believe that SDSU provided me with a first class wildlife and fisheries education that is highly valued among professionals in this field. The opportunities that I received greatly influenced my desire to become a wildlife biologist and pursue research in avian ecology. I'd like to thank the many professors and friends for making my experience at SDSU an unforgettable one. Go Jackrabbits!

Pursuing my Master's at North Dakota State University in Fargo, ND has been a journey with many ups and downs. It is this program that I discovered a more thorough love for researching interactions between wildlife and habitat. I'd like to thank all my friends (Aaron, Alan, Alison, Erin, Garret, Jonathan, and Dan) who made time at NDSU the most gratifying experience both on campus in Fargo as well as in Hettinger. I would like to thank my thesis advisor, Dr. Benjamin Geaumont, for giving me the opportunity to work on this project and his continued guidance. I have benefited not only from his knowledge and academic assistance, but also for the opportunities he created for me out west. His enthusiasm for prairie conservation and hunting has greatly driven me to keep pursuing my dream as a research biologist.

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## **CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW**

### **An Explanation of Thesis Organization**

This thesis follows the format required for submission into Biological Conservation. The literature review is contained within Chapter One. Chapters Two and Three represent separate submissions for journal publication.

The pronoun “we” is used to give credit to my co-authors who provided their professional experience and guidance to help with the writing, analysis, and review. Each chapter is denoted with a footnote marker that explains the co-authors’ contributions to each proposed publication.

### **Introduction**

Across the western hemisphere grassland species compromise a very important ecological guild, and as researchers we find that these species are both fascinating ecologically and evolutionarily. With continued alteration of grassland landscapes, it becomes complicated to define grassland birds when many species occupy a range of habitats. Grassland birds may be defined as any species that has become adapted to and reliant on a character of grassland habitat for a portion of its life cycle whether it is breeding, migration, or wintering (Vickery et al., 1999). Within this ecological definition, two groups are used to classify how dependent species are on grassland habitats. Obligate grassland species consist of only 59 species across North America and Latin America, and are species that rely entirely on grassland habitats to live (Vickery et al., 1999). Facultative grassland birds include a much larger group of 97 species, but are more numerous because they utilize a much larger array of habitats throughout their life history (Vickery et al., 1999).

Grassland bird conservation must relate to historical dynamics and associations where ecological processes effectively maintained these distinctive grassland bird communities. The

need for beef production in the Great Plains is a pressing issue when trying to protect the grassland ecosystem and conservation should look at ways of advancing grassland bird friendly programs. Bird fauna across the mixed- and short-grass prairies selected for a variety of vegetative and landscape characteristics that were historically under intense grazing pressure by prairie dogs and bison (Vickery et al., 2000). North American conservation programs more recently have begun to model these bird-friendly grazing protocols aimed at changing management practices on private grasslands. By utilizing holistic management practices and rotational grazing and/ or with burning, conservation begins to provide many other environmental benefits not only to grassland birds.

### **Grassland Bird Declines**

North American grassland birds are one of the fastest and most consistently declining groups of species in the world due to habitat conversion, removal of native grazers, brood parasitism, suppression of fire, and other factors (McCracken, 2005). Many of these species are occupying artificial habitats across North America that never existed 200 to 300 years ago (Vickery et al., 1999). The loss and fragmentation of grassland ecosystems has been estimated to exceed over 80% since the mid-1800s, with a belief that this decline in grassland bird populations first began in the 19<sup>th</sup> century when the steel plow first broke prairie soil (Brennan and Kuvlesky, 2005). Van Auken (2009) also presented a second view of lost grasslands through the encroachment of woody species, converting approximately 220 and 330 million ha of grasslands to forested communities. Many species are dependent on remaining patches of grassland found across the Great Plains. It is suggested that for grasslands to support a diverse grassland community, tracts need to be at least 100 ha (Vickery et al., 1994). Species such as the grasshopper sparrow (*Ammodramus savannarum*) have declined over 70% in the last 25 years,

and species such as the western meadowlark (*Sturnella neglecta*) and lark sparrow (*Chondestes grammacus*) have declined over 85% since the late 1960's (Herkert, 1994). Some species such as bobolinks (*Dolichonyx oryzivorus*) and dickcissels (*Spiza americana*) have found ways to adapt to the modified landscapes. Grassland birds occupy many different ecosystems across the United States and North America.

The timing of haying grasslands in agricultural landscapes is a constant concern associated with grassland bird conservation. Haying earlier in the season is a bigger issue in landscapes more heavily fragmented by agriculture because cutting during the nesting season will lead to a higher rate of nest destruction, but producers are recommended to harvest grass hay to increase quality (Askins et al., 2007; Winter, 1998). The intensive management of hay fields is essentially an ecological trap for some birds. Nesting habitat is high quality during the breeding season, but instead acts as a population sink due to the early harvest (Seigel and Lockwood, 2010). Haying during the peak breeding season is known to cause destruction of nests for a multitude of grassland nesting species. Many management agencies across the United States have set regulations on when land such as ditches or Conservation Reserve Program can be cut to minimize disturbance during the peak hatching date. Bollinger (1995) found hayfields that were left idle longer had the most diverse breeding bird community, and had the least homogeneous vegetation.

Roughly 0.1% of northern tallgrass prairies remain due to conversion of grasslands to a more agriculture-dominated land (Brennan and Kuvlesky, 2005). Thus, the only remaining habitat for obligate tallgrass prairie grassland bird species is pastures and hayfields. Loss of prairie ecosystems is not the only contribution to the decline in grassland bird populations. Areas

where these birds winter and migrate are also being degraded. Consequently, many factors are contributing in some way to the declines in grassland bird populations.

Afforestation in the eastern United States has also been a contributing factor to declines of grassland birds. Many authorities argue that grassland birds in the east were never a significant portion of the native avifauna that habituated the area during early settlement (Brennan and Kuvlesky, 2005). This restoration method changes the amount of open habitat at the landscape scale, but creates more fragmentation outside the area where afforestation occurs. The increase of forest habitat creates negative effects beyond the forest boundary. This causes grassland birds to avoid these edges, because increasing fragmentation across the landscape may lead to higher rates of predation (Brennan and Kuvlesky, 2005).

Native habitats across the Great Plains have been severely fragmented over the last five decades. Habitat fragmentation and rangeland deterioration reduce the area of habitat, the size and proximity of habitat patches, and increases the amount of edges, but needs to be assessed in terms of different spatial scales (Tewksbury et al., 2006). All of these changes affect the bird populations by having negative impacts on nesting success, survival, and emigration/immigration rates. Edge, patch, and landscape scale is examined to quantify and measure what factors into nest survival of grassland birds. The scale-dependent level of fragmentation assessed by Stephens and authors (2003) showed an alternating effect on nesting success based on the predation sensitivity. Various grassland bird species have different ecological niche requirements, spatial patterns, and dispersal methods that are significantly impacted by habitat fragmentation. Research is still being conducted to assess the different impacts that each scale has on the landscape.

Recent developments in energy such as wind, oil, coal, and natural gas have increased the human footprint on the landscape and created more obstacles for birds. The lesser prairie-chicken (*Tympanuchus pallidicinctus*) needs at least 25 to 60 km<sup>2</sup> for a single lek, and wind farms can interfere with this requirement (Pruett et al., 2009). The development of wind farms has caused various species to avoid or change their movement and migration corridors. These corridors are important for maintaining genetic diversity, ecological processes, extirpation, immigration and emigration, and seasonal distributions (Pruett et al., 2009). Numerous studies on wind farms across the United States and the world have looked at mortality rates on avian species. Of roughly 5,000 documented fatalities at wind farm locations across the United States, it was found that small passerines were accountable for 62.5% of those deaths (Erickson et al., 2014). Power plants can cause deaths from acid rain which destroys nest sites, thins forest canopies, and alters the habitat (Sovacool, 2009). Mercury poisoning has been shown in research labs to reduce the reproductive and survival success of nestlings (Sovacool, 2009). Nuclear power plants and mining have similar effects on collision and mortality rates. The fossil-fuel facilities still lead the energy development industry with the most bird mortalities per year based upon gigawatt per hour. In 2006 it was found that over 7,000 birds were killed from wind farm collisions, roughly 327,000 deaths from nuclear power facilities, and 14.5 million avian deaths from fossil-fuel facilities (Sovacool, 2009).

Oil and natural gas extraction across the United States has impacted a multitude of migrating birds both offshore and on our grassland landscapes by causing habitat loss and decreasing reproductive success (Sauer and Peterjohn, 1999). Since 2001, we have seen oil extraction undergo rapid expansion in their techniques for production across the Bakken formations, with many of these new sites being in areas with high grassland bird diversity and

abundance (Sauer and Peterjohn, 1999). We begin seeing higher rates of fragmentation and increase in the amount of edge associated with well pad and access road construction. For sensitive species such as the Sprague's Pipit (*Anthus spragueii*), large expanses of habitat are lost when avoidance of well pads is at 350 m (Thompson et al., 2015). High noise levels from active well pads and lack of tall vegetation, contribute to lower densities of singing birds during the winter mating season in southern Texas (Lawson et al., 2011). Oil companies need to consider clustering numerous wells along corridors or on larger pads and use directional drilling to help reduce the footprint we are leaving on the landscape (Thompson et al., 2015).

### **Grassland Community Interactions**

Many vertebrates generally associated with black-tailed prairie dog (*Cynomys ludovicianus*; hereafter prairie dogs) colonies are species of special concern (Smith and Lomolino, 2004). There is a wide variety of birds and mammals, as well as other organisms that occupy prairie dog colonies. Before early European settlement, species associated with prairie dog colonies may have included bison (*Bison bison*), elk (*Cervus canadensis*), wolves (*Canis lupus*), pronghorn (*Antilocapra americana*), and grizzly bears (*Ursus arctos*). The burrows created by prairie dogs provide refuge for burrowing owls (*Athene cunicularia*), grasshopper mice (*Onychomys leucogaster*), and an abundance of other ground dwelling organisms (Pruett et al., 2010).

Many studies have evaluated whether or not avian community structure is influenced by prairie dogs. Avian species richness and abundance were highest on prairie dog colonies during summer months compared to off-colony locations (Smith and Lomolino, 2004). Avian and terrestrial predators rely on prairie dogs for food. Several threatened and endangered species rely on prairie dogs either as an important food or shelter source. There are certain species that are



positively and significantly associated with the bare ground and short vegetation associated with prairie dog colonies, which includes burrowing owls, killdeer (*Charadrius vociferus*), horned larks, upland sandpipers, and meadowlarks. Prairie dog colonies across the Great Plains also are home to mountain plovers (*Charadrius montanus*), long-billed curlews (*Numenius americanus*), and lesser prairie-chicken.

Prairie dogs, as a “keystone species” play an important role in the ecological communities that make up the Great Plains. They increase the biodiversity and heterogeneity of grassland ecosystems by creating distinct patches of habitat useful for a large, diverse avian community (Sierra-Corona et al., 2015). Prairie dog herbivory results in plant communities with greater concentrations of crude protein, greater live-to-dead ratio, and easier digestibility (Whicker and Detling, 1988). The increase in forage quality attracts many large bovine and ungulate herbivores. It's known that pronghorn preferentially select the center of prairie dog colonies for the forb/shrub dominated areas (Coppock et al., 1983; Detling and Whicker, 1988; Sharps and Uresk, 1990). Bison will use the younger, grass-dominated areas for grazing and resting, outer edges for foraging, and the older forb/shrub dominated areas for resting (Whicker and Detling, 1988). Bison tended to avoid areas of grassland that were not colonized and spent approximately 40% of the growing season on colonized patches (Whicker and Detling, 1988). Both mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) preferentially grazed prairie dog colonies during summer months (Lomolino and Smith, 2003). Since bison herds are not the size of what they were pre-settlement, cattle provide a great alternative to the loss of native grazers on grassland grazing systems.

Many grassland bird species respond to livestock grazing based upon the modifications to vegetation structure created from livestock activity (Bock and Webb, 1984). Proper grazing

management can help increase suitable habitat for grassland nesting species. Species will respond differently to the intensity of grazing implemented to grassland. Some may benefit more from the reduced visual obstruction and increasing bare ground associated with less litter, whereas other species will benefit from low intensity grazing and prefer taller vegetation and more structure. Grazing will affect the densities of songbirds, and can increase biodiversity within larger pastures (Renfrew and Ribic, 2008; Perlut and Strong, 2010). Low-intensity, late-season grazing will help create a heterogeneous habitat mosaic that is attractive to a variety of species (Walk and Warner, 1999). The abundance and diversity will depend on the ecosystem (tallgrass vs. shortgrass prairie), and the intensity of grazing implemented. Grazing can have varying impacts on grassland bird populations whether it is from changes in the vegetation structure, available food resources, or predation pressure (Batáry et al., 2007).

There is a wide array of grassland birds that select for specific habitats on the prairies for nesting. The alteration in vegetation structure caused by grazers such as cattle or prairie dogs will affect the suitability of a specific site for nesting. The ferruginous hawk (*Buteo regalis*) is one of a few species of hawks that nests in grasslands. With the prairie dog being an important food source for ferruginous hawks, their nest selection focuses on grasslands in the vicinity of prairie dog colonies (Cook et al., 2003). Selection for nest sites varies heavily by species and the habitat that is most suitable for it. For example, Sprague's pipit selected nest sites with tall standing dense vegetation, and patch areas with higher litter cover and depth (Dieni and Jones, 2003). Grasshopper sparrows generally avoided areas that consisted of bare ground and low visual obstruction most correlated with areas off a prairie dog colony (Smith and Lomolino, 2004). Dieni and Jones (2003) found that western meadowlarks selected nest sites with high visual obstruction, tall stands of grass with greater litter cover. Western meadowlarks tend to be

generalists when selecting for nest sites and will nest both on and off prairie dog colonies (Augustine and Baker, 2013; Fuhlendorf et al., 2006; Knopf, 1996). Some species select solely for the larger percentages of bare ground that are correlated with prairie dog colonies. Killdeer, horned larks, and burrowing owls are a couple species that select for this open habitat type for nesting and brood rearing purposes (Smith and Lomolino, 2004). Nest selection may be influenced largely by the landscape and the influences that reciprocate to the patch and nest site levels. As scientists we need to consider both the patch and nest scale, and also look into how the landscape effects play a role in grassland bird habitat selections.

Two limiting factors that affect success of grassland bird nests are brood parasitism and predation (Tewksbury et al., 2006). A review conducted by Hartway and Mills (2012) found that cowbird and predator removals increased nest survival at 0.84 and 0.69, respectively, standard deviations greater than the control studies. Nest failures from parasitism and predation are heavily dependent on the composition and structure of the surrounding landscape (Tewksbury et al., 2006). Obligate grassland birds are highly susceptible to nest parasitism by a variety of species. The brown-headed cowbird (*Molothrus ater*) is the most common nest parasite in the grassland bird community. Davis and Sealy (2000) documented areas that were highly fragmented and had more edge tended to have increased numbers of brown-headed cowbirds. It is hypothesized, with increasing amounts of woody encroachment across portions of the west, ecosystem change may exert a very strong flux of parasitism rates on grassland song birds (Hovick and Miller, 2013). Hovick and Miller (2013) suggest that areas that would provide the most minimal risk of nest parasitism are grasslands void of tree and shrub cover.

Predation may affect types of grassland birds based upon individual similarities between nest characteristics, which may be a factor to consider when analyzing ecological communities

(Martin, 1993). There are many different nest predators of grassland songbirds. Small mammals such as thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*), weasels (*Mustela ermine*), mink (*Neovison vison*), and others are responsible for a large amount of predation events. A study in Minnesota, reported that grasshopper sparrows and western meadowlarks were found nesting in larger grassland patches where nest predation rates were lower (Herkert, 1994). Some cases have been documented where deer will also predate nests (Murray, 2015; Pietz and Granfors, 2000). Birds could reduce predation rates if they selected nesting locations that reduce visual, auditory, and olfactory cues that predators use to hunt their prey (Davis, 2005).

### **Conservation**

As conservationists and preservationists, strategies are needed to assess these population declines, and methods for stabilization need to be further researched to help recover grassland bird populations. When incorporating processes such as grazing, fire, and other disturbances, managers need to recognize how the intensity, timing, and seasonality can influence the outcome. These strategies must be focused on all the biomes grassland birds are part of including rangelands, prairies, agricultural lands, and forests. Managers should continue to provide incentives to keep federal conservation programs active in order to protect grasslands and focus on habitat restoration. Legislation and initiatives that benefit grassland bird species include the North American Waterfowl Management Plan, Permanent Cover Program, and Joint Ventures (McCracken, 2005). The United States Department of Agriculture (USDA) and other federal and state programs have voluntary enrollment for landowners that offer financial incentives to convert agricultural lands to grassland habitats. The Conservation Reserve Program (CRP) is currently the largest private land conservation program in the United States (Seigel and Lockwood, 2010). Programs like this are vital in protecting habitat for a variety of grassland

species. The North American model of wildlife management is a crucial tool that can be implemented to help stabilize and increase populations of grassland birds (Brennan and Kuvlesky, 2005).

One way to implement conservation to minimize impacts of nest predation is to manage for important habitat characteristics during the nesting season because it is a critical time for success and structuring the bird population (Martin, 1993). In order to help minimize parasitism and predation there needs to be a better understanding of what a species needs in regards to habitat, food resources, reproduction, and survival. By creating tracts of land that are connected and no longer fragmented, the amount of edge decreases therefore decreasing predation by generalist predators.

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## CHAPTER 2: PLANT AND BIRD COMMUNITY DYNAMICS IN MIXED-GRASS PRAIRIE GRAZED BY NATIVE AND DOMESTIC HERBIVORES<sup>1</sup>

### Abstract

Native colonial and domestic herbivores infrequently co-occur on the landscape, but understanding these interactions is important for conservation in working landscapes. While many factors have contributed to grassland bird declines, the consistent and long term removal of native herbivores from western grasslands has promoted homogenous landscapes that are now uniformly grazed by domestic cattle (*Bos taurus*). This shift in pattern of grassland structure limits the availability of habitat for specialized grassland species. To address this, we investigated bird and vegetation dynamics in landscapes grazed by domestic cattle and native colonial herbivores, the black-tailed prairie dog (*Cynomys ludovicianus*). This study took place in mixed-grass prairie on four experimental landscapes stratified by the proportion of prairie dog occupancy within a pasture. Bird and vegetation surveys were conducted from 2012-2015 along fixed-width belt transects located both on- and off-prairie dog colonies. We found varying composition and abundance of both birds and vegetation across experimental landscapes. Basal bare ground was the most important habitat variable associated with differing bird communities. Grasshopper sparrows (*Ammodramus savannarum*) were associated with greater vegetation structure commonly found at off-colony locations, while species such as the western meadowlark (*Sturnella neglecta*) and upland sandpiper (*Bartramia longicauda*) utilized both on- and off-prairie dog colony locations. Our findings demonstrate the importance of maintaining spatial

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<sup>1</sup> This chapter is co-authored by Wyatt Mack, Benjamin Geaumont, Amanda Lipinski, Torre Hovick, Ryan Limb, and Kevin Sedivec. Wyatt Mack (graduate student) was the main co-author responsible for collecting data, statistical analysis, interpreting statistical outputs, and synthesizing information for the completion of this chapter. Amanda Lipinski assisted with data collection and editing. Benjamin Geaumont and Kevin Sedivec provided insight and assistance on study design. Torre Hovick and Ryan Limb assisted with analysis of data in Distance and PC-ORD, respectively. Benjamin Geaumont, Kevin Sedivec, Ryan Limb, and Torre Hovick assisted through editing and review of the chapter and added professional insight for the chapter.

heterogeneity in working landscapes, and demonstrate that native colonial herbivores can help achieve this in the presence of herbivory by domestic grazers.

## **Introduction**

Temperate grasslands are found worldwide and occur on all continents of the globe except Antarctica (Henwood, 1998). They cover ~46 million km<sup>2</sup> or nearly 27% of the Earth's surface and are diverse areas that provide an array of ecological services such as provisioning of forage and nutrient cycling (Henwood, 1998). Few intact grassland landscapes remain, and those that do have been altered as a result of anthropogenic forces. Factors contributing to grassland loss and degradation include conversion to cropland, invasion of exotic vegetation, fire suppression and encroachment of woody plants, overgrazing, and altered hydrology and erosion rates (Askins, 2000; Briggs et al., 2002; Brennan and Kuvlesky, 2005; Anderson, 2006).

Conservation and management of temperate grasslands is necessary because people throughout these regions depend on them for their livelihood, primarily because of the forage they provide for grazing domestic livestock (Brennan and Kuvlesky, 2005). Therefore, research should focus on conservation efforts that can be applied in working grassland landscapes as conservation and production must be able to co-exist if we hope to conserve declining grassland-dependent organisms.

Livestock grazing by domestic cattle (*Bos taurus*) is the most frequent land use of native grassland ecosystems worldwide (Allred et al., 2013). Grasslands in the western United States provide approximately 70% of the required annual forage for cattle (Fleischner, 1994) and are therefore, important to the livelihood of many people. A recent estimate suggested 92 million cattle are raised for meat production in the United States annually and are predominantly from grasslands in states west of the Mississippi River (NASS, 2012). Moreover, livestock herbivory

has many ecological consequences on ecosystem composition, structure, and function, which disrupts succession by preventing seed establishment and decreasing water availability to biotic communities (Fleischner, 1994; Anderson, 2006). Furthermore, livestock production is an important economic engine throughout the Great Plains of North America and must be considered if conservation efforts are expected to be effective in grasslands.

Native colonial herbivores are essential to rangelands but have largely been eliminated because of their perceived competition with livestock (Derner et al., 2006; Detling 2006; Augustine and Baker, 2013). Despite confounding reports regarding competition between native burrowing herbivores and livestock, many livestock producers perceive the black-tailed prairie dog (*Cynomys ludovicianus*; hereafter prairie dogs) as a direct threat to their economic well-being (Hoogland, 1996). Prairie dogs are often referred to as “keystone species” and “ecosystem engineers” and play an important role in the composition and structure of grassland biomes (Smith and Lomolino, 2004). In addition to providing habitat for a variety of species, herbivory and continuous clipping by burrowing mammals can result in higher concentrations of crude protein within the plant community and result in more easily digestible forage for cattle and other grazing ungulates (Whicker and Detling, 1988). The elaborate burrow systems and holes associated with prairie dog colonies are often viewed as a potential cause of injury to livestock. These issues resulted in widespread persecution of prairie dogs with extensive poisoning and widespread shooting of colonies (Hoogland, 1996). These factors, coupled with the accidental introduction of sylvatic plague (*Yersinia pestis*) and habitat loss, have drastically diminished prairie dog populations throughout North America, resulting in an estimated 90-98% population decline (Knowles et al., 2002; Proctor et al., 2006). The large scale eradication of prairie dogs combined with the loss of other native herbivores (e.g., *Bison bison*) and disturbance processes

has severely limited the spatial and temporal heterogeneity of North American grasslands and replaced it with practices focused on uniform and even distribution of grazing cattle (Knapp et al., 1999). These landscape-level changes undoubtedly influenced the fauna and flora that are reliant on the inherent structural and compositional heterogeneity that historically occurred in grasslands of North America.

Grassland birds require a wide breadth of structural and compositional vegetation attributes within an ecosystem that were historically maintained by fire and herbivory (Knopf, 1996; Brennan and Kuvlesky, 2005). Prior to European settlement, this variation would have occurred at a range of scales primarily through the interaction of fire, a vast network of prairie dogs, and bison creating a variety of distinct habitat types (Askins, 1999). Certain species of birds such as burrowing owls (*Athene cunicularia*), killdeer (*Charadrius vociferus*), horned larks (*Eremophila alpestris*), and upland sandpipers (*Bartramia longicauda*) have been found to be positively influenced by prairie dog colonies (Augustine and Baker, 2013). Similar in response to prairie dogs presence, birds generally respond to livestock grazing based on the modifications to vegetation linked with livestock activity (Bock and Webb, 1984). The requirement for heterogeneous grasslands to maintain diverse bird communities suggests the need to develop management options that can meet these needs on existing grasslands.

Few studies aim to assess how bird and plant communities may be influenced by the declines of prairie dogs in a scenario that includes livestock herbivory. There is a need to evaluate the influence of co-occurring, native and domestic grazers on grassland birds because working grassland landscapes must be able to co-exist if we hope to aid in the conservation of grassland-dependent organisms. Therefore, we test the hypothesis that the simultaneous herbivory by native prairie dogs and domestic cattle will result in heterogeneous vegetation

structure and composition that creates a diverse avian community. To address this hypothesis our objectives were to: 1) quantify differences in plant and bird community composition across landscapes grazed by cattle with varying rates of prairie dog occupancy, 2) identify vegetation variables which may be driving habitat use by breeding birds, and 3) quantify grassland breeding bird densities across experimental landscapes with varying levels of prairie dog occupancy.

## **Methods**

### *Study Area and Field Methods*

We examined mixed-grass prairie dynamics on 1420 ha of private and tribally owned land located in Corson County, South Dakota (SD) USA, on the Standing Rock Sioux Indian Reservation, approximately 16 km southeast of McLaughlin, SD and 42 km northwest of Mobridge, SD (45° 44' 44.6" N, 100° 39' 43.6" W). The climate was semi-arid and characterized by cold winters and hot summers. This region receives 44 cm of precipitation on average with approximately 75% occurring during the growing season (South Dakota Climate and Weather, 2015). The 30-year mean annual winter (December-March) temperature was -8 °C and mean summer (June-August) temperature was 20 °C (South Dakota Climate and Weather, 2015). The study site lies in a landscape characterized by a mixture of rangeland and agricultural fields in a topographically diverse landscape. Vegetation is dominated by both mid- and short-statured C<sub>3</sub> and C<sub>4</sub> grasses including: western wheatgrass (*Pascopyrum smithii* (Rydb.) Á. Löve), Kentucky bluegrass (*Poa pratensis* L.), needle and thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), and blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths). Prairie dog colonies are dominated by shorter C<sub>4</sub> grasses including buffalo grass (*Bouteloua dactyloides* (Nutt.) J.T. Columbus) and blue grama. A variety of forbs commonly encountered in the region include purple coneflower

(*Echinacea angustifolia* DC.), scarlet globemallow (*Sphaeralcea coccinea* (Nutt.) Rydb.), fetid marigold (*Dyssodia papposa* (Vent.) Hitchc.), and sagewort species (*Artemisia* spp).

We delineated the study site into four experimental landscapes (200±7 ha) with varying prairie dog occurrence. Each landscape represented a different level (treatment) of prairie dog occupancy, with the four levels including 1) 0%, 2) 18%, 3) 40%, and 4) transitional. The transitional landscape originally was 75% occupied by prairie dogs, but during the second year of our study accidental poisoning of prairie dogs reduced occupancy to 24 ha or 11%.

Throughout the remainder of the study, prairie dogs were allowed to recolonize the area and had rebounded to 29% occupancy by 2015. We stocked each landscape with Angus steers from early-June to early-October at a rate to achieve 50% degree of disappearance. Stocking rates were calculated based on forage availability within each experimental landscape; 0% equivalent to 1.0 ha/Animal Unit Month (AUM), 18% equivalent to 1.3 ha/AUM, 40% equivalent to 1.6 ha/AUM, and transitional equivalent to 4.2 ha/AUM.

We sampled bird populations using fixed-width belt transects following standard distance sampling protocols (Bibby et al., 2000; Buckland et al., 2001; Hill et al., 2005). We randomly placed nine, 300 m transects in each experimental landscape, and with transects either entirely on- or off-prairie dog colonies. We conducted bird surveys one half hour before sunrise and concluded surveys by 0900 hours when winds were  $\leq 15$  km/hr with no precipitation. Each transect was surveyed three or four times annually during the breeding season (May-July) identifying all birds by sight or sound out to 100 m on either side of transect. Distance was measured from transect line with range finders (Leupold RX-1000 TBR).

Vegetation surveys were completed on a subset of the bird survey belt transects. We sample 21, 10x10 m plots along the length of each transect on alternating sides at 15 m intervals.

Within each 10x10 m plot, vegetative sampling was completed at six systematic sample points (Lipinski, 2014) and included maximum live vegetation height (cm), maximum standing dead vegetation height (cm), visual obstruction reading (VOR) using a modified Robel pole (cm) (Robel et al., 1970), basal cover of functional groups using a ten-pin frame (Evans and Love, 1957), and species composition and abundance using modified Daubenmire cover classes (grass, forb, shrub, sedge) (Daubenmire, 1959). Visual obstruction readings were recorded in centimeters to allow for fine scale measurements that better capture small variations in the short vegetation typical of prairie dog colonies.

### *Community Analyses*

We analyzed both bird and plant community data from all four years of the study using nonmetric multidimensional scaling (NMS) ordination in PC-ORD version 6. The avian and vegetation community composition represented the main matrix and the four experimental landscape and relative location on- and off-prairie dog colonies were supplementary variables. We used average avian abundance for each transect in the ordination and the “medium” setting on autopilot running with the Euclidean distance measurement to account for taxonomic and non-taxonomic data (McCune and Grace, 2002). Furthermore, we used multi-response permutation procedure (MRPP) implemented in PC-ORD to test for differences among bird and plant communities between each experimental landscape type and on- versus off- prairie dog colonies (McCune and Grace, 2002). Pearson correlation coefficients within the main matrix were used to assess which parameters were most strongly correlated with the principal axis. We considered variable sets to be strongly correlated if the corresponding  $r$  values  $\geq 0.5$ , which also allowed us to account for having small sample sizes (McCune and Mefford, 2011).

### *Bird Density Analyses*

We used program DISTANCE (version 6.2) to estimate a detection function for all bird species that had  $\geq 60$  observations over the four years of the study (Buckland et al., 2001; Thomas et al., 2010). Program DISTANCE combines a detection function and the total number of observations for each species to calculate a density estimate and confidence intervals (Augustine and Baker, 2013; Buckland et al., 2001; Thomas et al., 2009). For each of the eight species that had  $\geq 60$  observations, we fitted a model through conventional distance sampling (CDS). We designated the occupancy percentages of our four experimental landscapes as the strata (0%, 18%, 40%, and transitional) and fitted these to each species. For each individual species we examined the standard suite of models and the half-normal key with standard cosine expansion performed the best (Buckland et al., 2001). Standard errors are reported and a 95% CI used to determine differences in densities among landscapes.

## **Results**

### *Community Associations*

Occupancy rates of prairie dogs within the different landscapes affected both bird and plant communities (Figure 2.1). Multi-response permutation procedure confirmed that there were differences among landscapes and all but one comparison was significant (MRPP:  $p < 0.05$ ). There was no difference between bird and plant communities in the 18% and 40% experimental landscapes. Landscape centroids were different when comparing on- and off-colony communities, indicating differences in composition of communities. Within-cluster homogeneity was greater when transects were clustered on- versus off-prairie dog colony ( $A = 0.137$ ) than when clustered within each experimental landscape ( $A = 0.063$ ), indicating that these groups are significantly more homogenous than others with values closest to 1.0 being most significant.



Vegetation characteristics and bird species were strongly correlated with the principal axis in both directions, with axis 1 and axis 2 accounting for 52% and 31% of the variability. Axis 1 was positively correlated with basal bare ground ( $r = 0.92$ ) and negatively correlated with maximum live vegetation height ( $r = -0.78$ ), VOR ( $r = -0.64$ ), and litter depth ( $r = -0.62$ ). Axis 2 was positively correlated with maximum dead vegetation height ( $r = 0.69$ ) and negatively correlated with percent litter cover ( $r = -0.90$ ).

The differences in both avian and plant communities between on- and off- colony sites were primarily associated with the variation in basal bare ground, visual obstruction, and maximum height of live vegetation. Grasshopper sparrow (*Ammodramus savannarum*) was negatively correlated ( $r = -0.76$ ) and horned lark positively correlated ( $r = 0.69$ ) with bare ground. Both native and nonnative plant species were strongly correlated with axis 1 (Table 2.1).

Kentucky bluegrass and needle and thread were negatively correlated with axis 1 ( $r = -0.51$  and  $r = -0.65$ , respectively). Fetid marigold, a common forb on prairie dog colonies was positively correlated with axis 1 ( $r = 0.55$ ) while purple coneflower, a common forb located off colonies, was negatively correlated with axis 1 ( $r = -0.62$ ). Western wheatgrass was the only grass negatively correlated with axis 2 (Table 2.1;  $r = -0.58$ ).

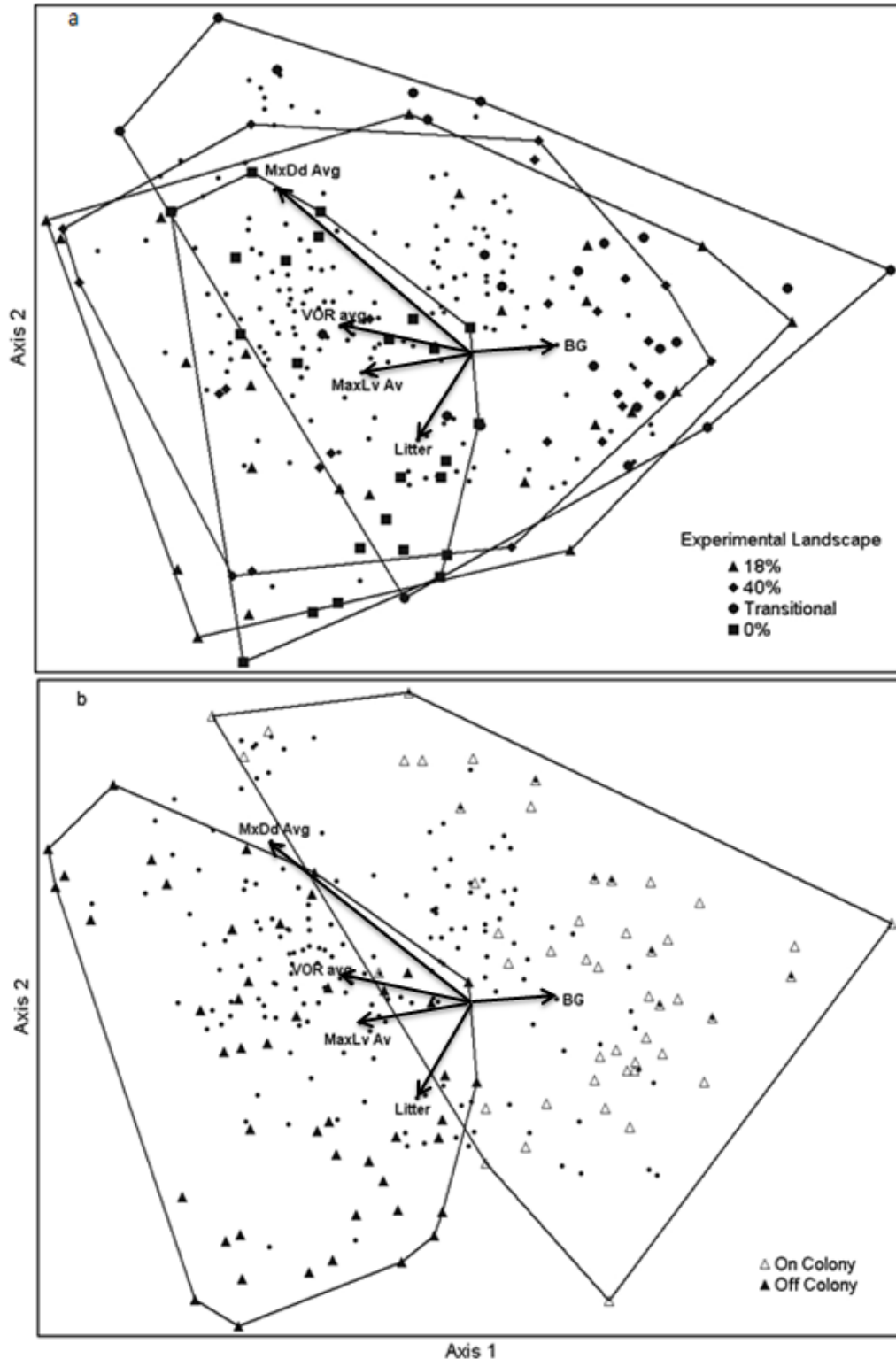


Figure 2.1. Nonmetric multidimensional scaling ordination examining differences in bird and plant communities on (a) experimental landscapes with 1) 18% 2) 40% 3) transitional and 4) 0% of pasture area colonized by prairie dogs and (b) on and off prairie dog colonies. Each shape represents a belt transect and background points are individual variables.

Table 2.1. Plant species strongly correlated ( $r \geq 0.5$ ) with the principal and secondary NMS ordination axes.

Species	Axis 1	Axis 2
<i>Carex spp.</i>	-0.66	—
<i>Hesperostipa comata</i>	-0.64	—
<i>Amorpha canescens</i>	-0.63	—
<i>Echinacea angustifolia</i>	-0.62	—
<i>Artemisia dracunculoides</i>	-0.59	—
<i>Pascopyrum smithii</i>	—	-0.58
<i>Bouteloua curtipendula</i>	-0.55	—
<i>Bromus inermis</i>	-0.55	—
<i>Psoralea argophylla</i>	-0.55	—
<i>Schizachyrium scoparium</i>	-0.54	—
<i>Nassella viridula</i>	-0.54	—
<i>Artemisia frigida</i>	-0.52	—
<i>Poa pratensis</i>	-0.51	—
<i>Symphoricarpos occidentalis</i>	-0.50	—
<i>Conyza canadensis</i>	—	0.50
<i>Ratibida columnifera</i>	—	0.51
<i>Solidago missouriensis</i>	—	0.51
<i>Sphaeralcea coccinea</i>	—	0.53
<i>Dyssodia papposa</i>	0.55	—

### *Bird Density*

We calculated density estimates for eight mixed-grass prairie bird species while accounting for imperfect detection (Figure 2.2). We found that western meadowlarks were the most common bird species at our research site with similar densities across all four experimental landscapes. Additionally, mourning doves (*Zenaida macroura*) had similar densities among experimental landscapes and were present across the entire study area. Horned larks and lark sparrows (*Chondestes grammacus*) had greater densities within landscapes occupied by prairie dogs. The eastern kingbird (*Tyrannus tyrannus*) was consistently seen in landscapes with larger

woody ravine habitat. The density of grasshopper sparrows decreased as prairie dog occupancy increased, and grasshopper sparrow density was four times greater in the landscape void of prairie dogs when compared to the transitional landscape. The upland sandpiper and the brown-headed cowbird (*Molothrus ater*) showed no clear pattern across experimental landscapes.

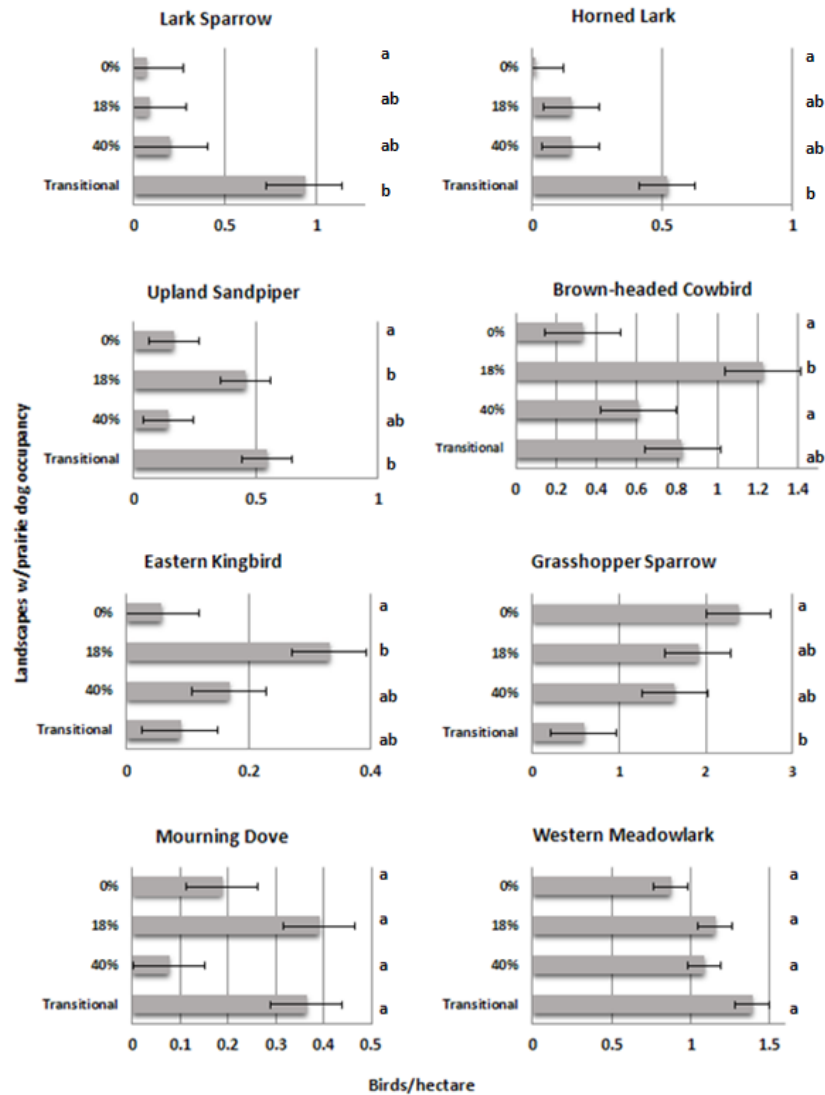


Figure 2.2. Program Distance density estimates for 8 bird species on each experimental landscape colonized by prairie dogs. The y-axis represents each experimental landscape and the x-axis is equal to the density of birds per hectare (*error bars, 95% CI; letters indicate differences among landscapes at the 95% confidence level*).

## **Discussion**

Conservation in working landscapes should try to incorporate native grazers in conjunction with domestic cattle to benefit grassland diversity. Studies of how prairie dogs alter grassland bird and plant communities have primarily focused on how prairie dog disturbance supports such communities, but fail to evaluate the simultaneous relationship on how grazing by domestic and natural herbivores influences these communities (Augustine and Baker, 2013). By assessing vegetation and avian community in areas colonized and uncolonized by prairie dogs, our findings show that certain species of grassland birds selected for sites on- or off- prairie dog colonies almost exclusively, while other more generalized species used all sites. Rangelands occupied with low to moderate amounts of prairie dogs can create a valuable resource for domestic cattle because prairie dogs create vegetation with higher digestibility and protein concentrations for cattle consumption (Detling, 2006). Areas used by cattle and void of prairie dogs generally had little bare ground, relatively elevated structure and tall vegetation greatly contrasting with vegetation characteristics located on colonies; attracting a much different group of grassland birds (Figure 2.3). Management and conservation of prairie dog colonies requires more thorough consideration when these landscapes increase grassland heterogeneity by altering vegetative structure, which allows many species to inhabit and utilize these areas (Fuhlendorf et al., 2006; Knopf, 1996).

Prairie dog colonies continue to influence species assemblages and community structure, creating ecological interactions important in working landscapes across the entirety of the Great Plains (Smith and Lomolino, 2004). Community analysis shows the contrast in bird and plant communities in relationship to the simultaneous grazing by a colonial herbivore and domestic herbivory within each landscape. Similarly, native and domestic herbivory increases landscape

heterogeneity, manipulating vegetative communities and providing habitat for a diverse avian community (Barko et al., 1999). We found greater forb abundance on-colony and consistently greater graminoids abundance off-colony, which is consistent with other results assessing vegetation composition on mixed-grass prairie and the effects ungulates and prairie dogs have on a community (Fahnestock et al., 2003). We suggest prairie dogs may preserve native communities, because our findings show that Kentucky bluegrass was absent from prairie dog grazed areas. This is important in this region because encroachment by introduced species like Kentucky bluegrass has led to a loss in ecosystem services (Toledo et al., 2014).

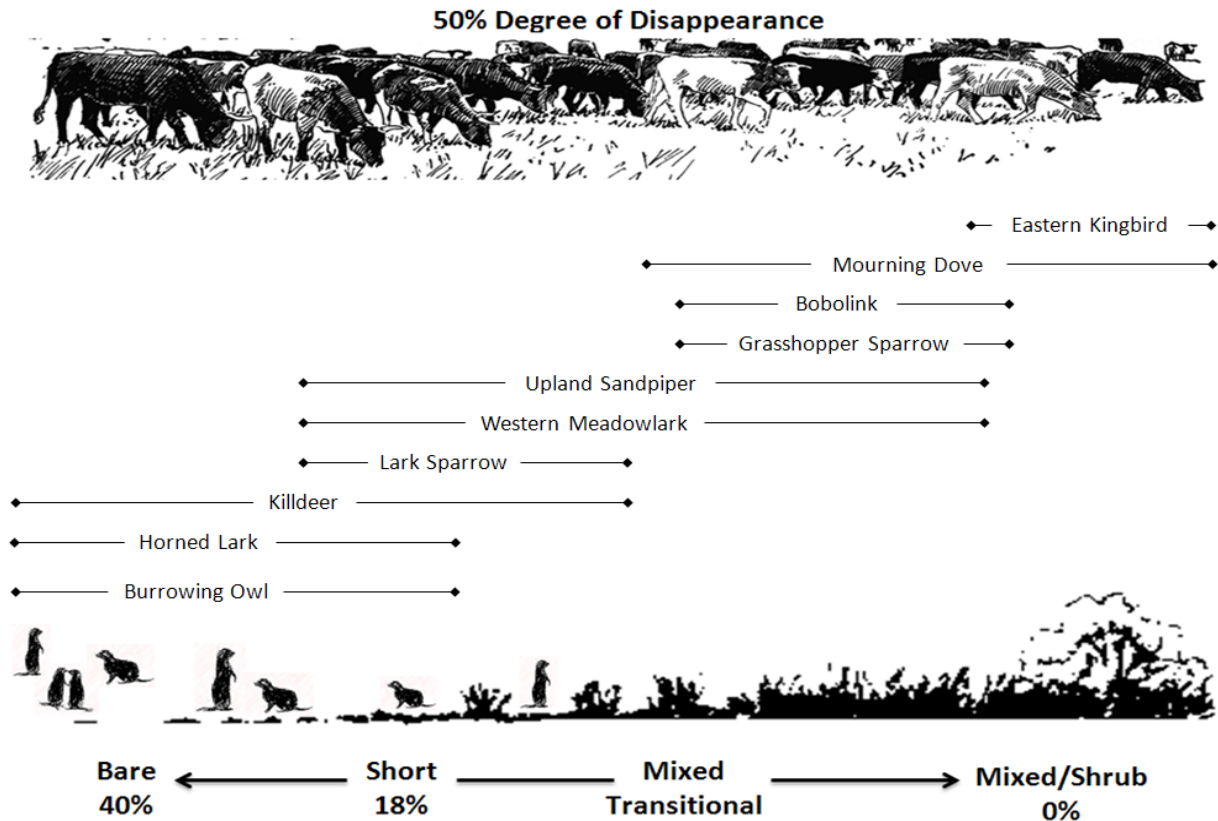


Figure 2.3. Illustration of how grazing by domestic and native herbivores affect avian species distributions across grassland landscapes with varying levels of prairie dog occupancy (Modified from Knopf, 1996).

Having a working landscape where prairie dog colonies existed, added increased habitat heterogeneity and avian diversity. We found horned larks and lark sparrows on landscapes consisting of short vegetation with ample bare ground typically occupied by prairie dogs, which is consistent with results found in Arizona where the sparrows were observed in areas with short grass and bare ground patches (Bock and Webb, 1984). Species such as mourning doves, western meadowlarks, upland sandpipers, and cowbirds showed minimal association with a specific landscape location presumably because they utilize the vegetation communities found on- and off-colony during the same breeding season for nest-site selection, foraging, and loafing (Knopf, 1996; Fuhlendorf et al., 2006; Augustine and Baker, 2013). We observed that all species except the eastern kingbird and grasshopper sparrow had high response to the transitional landscape, suggesting that type of temporal variation from dramatic changes in prairie dog occupancy creates long-term diversity in the landscape. Spatially, our findings show that with the occurrence of prairie dogs and domestic herbivores, a much more diverse bird and plant community interacts on the landscape in comparison to a landscape unoccupied by prairie dogs.

Population densities for the eight most detected bird species at our site were likely influenced by vegetation features required by species specific life history characteristics. Vegetation features, invertebrate abundance, prey diversity, and seed availability can influence avian densities and species specific habitat use (Agnew et al., 1986). Landscapes that consisted of higher forb and grass cover, moderate to low litter cover, and void of woody cover were areas where western meadowlark detections occurred. The western meadowlark had the greatest density of the eight species, but we found no difference in densities across the landscapes. Numerous studies have reported western meadowlarks to commonly be associated with prairie dog colonies, and likely to have increasing on-colony densities into the later summer months

when dense vegetation is more available to conceal nests (Agnew et al., 1986; Barko et al., 1999; Goguen, 2012). Our results show that grasshopper sparrows require greater vegetation structure and were often found on transects further away from areas occupied by prairie dogs. Although lower in numbers, grasshopper sparrows were detected on prairie dog colonies possibly utilizing these areas for foraging. Results from population studies show that upland sandpipers and grasshopper sparrows require tracts of undisturbed grassland where vegetation was more structured (Herkert, 1998; Weins, 1969; Dechant et al., 2003). Patterns of abundance between individual species may more likely respond to habitat structure and resource availability as ecosystems change as a whole (Goguen, 2012).

## **Conclusion**

Our findings provide strong support that burrowing herbivores and domestic grazers create dynamic vegetation communities that benefit specialized grassland bird species through increased structural heterogeneity. In our study, the contrast created by the ecological behavior of prairie dogs with cattle herbivory resulted in a heterogeneous landscape with high botanical diversity that provided diverse habitat conditions for many different bird species. Findings from our study will allow grassland managers to use these results to effectively make management recommendations for maintaining a level of prairie dog occupancy that will create a diverse bird and plant community without eliminating other species, while still sustaining grazing by domestic herbivores. Colonies represent important islands of unique habitat scattered across the western landscapes, yet they continue to disappear when not properly protected. Conservation of prairie dogs should look past the single species, but instead be seen as conserving many communities of plants and animals that are dependent on these ecosystems.



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**CHAPTER 3: GRASSLAND BIRD RESOURCE SELECTION AND NESTING  
SURVIVAL ON MIXED-GRASS PRAIRIE GRAZED BY NATIVE COLONIAL AND  
DOMESTIC HERBIVORES<sup>2</sup>**

**Abstract**

Few studies have investigated grassland bird community associations with black-tailed prairie dogs (*Cynomys ludovicianus*), and of those limited studies few aim to quantify nest-site selection and nest success. We studied nest-site selection and nesting success of four grassland obligate passerine species in northern mixed-grass prairie grazed by native colonial and domestic herbivores that included: western meadowlark (*Sturnella neglecta*), grasshopper sparrow (*Ammodramus savannarum*), lark sparrow (*Chondestes grammacus*), and upland sandpiper (*Bartramia longicauda*). We quantified habitat features at sites chosen for nesting and compared selected sites from what was available at multiple scales (nest, 100m, 250m, and 500m) during the breeding seasons of 2012-2016. Nest survival rates and resource selection function (RSF) were analyzed using Program Mark (v8.0) and Program R (v3.3.1), respectively. Western meadowlarks, grasshopper sparrows, and lark sparrows built their nests in areas with greater litter depth than what was available at random points. Additionally, we found that woody cover and edge play an important role in resource selection in a grassland landscape. Individual species exhibited a nesting gradient in regards to a landscape occupied with prairie dogs, where some species nested only in grassland unoccupied by prairie dogs (e.g., grasshopper sparrow) and others were more generalized and nested on- or off-colony (e.g., western meadowlark). Based on

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<sup>2</sup> This chapter is co-authored by Wyatt Mack, Benjamin Geaumont, Amanda Lipinski, Torre Hovick, and Kevin Sedivec. Wyatt Mack (graduate student) was the main co-author responsible for collecting data, statistical analysis, interpreting statistical outputs, and synthesizing information for the completion of this chapter. Amanda Lipinski assisted with data collection and editing. Benjamin Geaumont provided insight and assistance on study design. Torre Hovick and Ben Geaumont assisted with analysis of data with resource selection functions and program MARK, respectively. Benjamin Geaumont, Kevin Sedivec, and Torre Hovick assisted through editing and review of the chapter and added professional insight for the chapter.

our top nest survival models, daily survival rates varied from 0.94 for lark sparrows, 0.95 for western meadowlarks and grasshopper sparrows, and 0.98 for upland sandpipers. Time specific variables (nest age and year) and parasitism by the brown-headed cowbird (*Molothrus ater*) significantly affected nest survival, with vegetation and landscape variables accounting for additional variation. Our findings show that vegetative parameters at the nest-site play a hefty role in nest selection and survival, and validate the need for increased heterogeneity across working landscapes. Assessing how nest-site and landscape characteristics affect avian species will provide a better understanding for how prairie dogs create favorable nesting conditions while still sustaining grazing by domestic herbivores.

## **Introduction**

Since the late 1800s, the Great Plains have been reshaped by the removal of expansive herds of bison (*Bison bison*), replacement with domestic livestock through the installation of large agriculture operations resulting in vast land conversions, and continuous efforts to eradicate colonial herbivores. These changes have created a fragmented landscape, confined grazing, and reduced fire. Historically, grazing behavior of native herbivores helped regulate a level of disturbance that sustained grassland bird and colonial herbivore populations (Brennan and Kuvlesky, 2005). Current management of the remaining fragmented landscapes may not be adequate to maintain the thriving, diverse ecosystem that historically existed.

The black-tailed prairie dog (*Cynomys ludovicianus*; hereafter prairie dog) is considered a “keystone modifier” and plays an important role in ecological communities. Prairie dogs are burrowing, colonial rodents native to North American grasslands (Hoogland, 1995). Large reductions in population from lost habitat, eradication programs and sylvatic plague (*Yersinia pestis*) have decreased populations by 98% (Barko et al., 1999; Hassien, 1976; Miller et al.,

1994; Shaw et al., 1993). The removal or loss of prairie dogs can subsequently result in changes in energy flow, loss of vegetative structure that affects habitat flow and trophic interactions, and the disappearance of other species that rely heavily on successional resources (Mills et al., 1993). The eradication of prairie dogs coupled with the loss of the American bison and their replacement by cattle, has altered the heterogeneity of the grassland ecosystem (Knapp et al., 1999). Despite their limited occurrence across the landscape, populations of prairie dogs continue to increase biodiversity and heterogeneity in grasslands and create biological niches useful for a large, diverse avian community (Sierra-Corona et al., 2015).

Livestock grazing involves harvesting vegetation for forage, but can ultimately be used to construct a mosaic of grass species and structure that provides grassland bird habitat (Henderson and Davis, 2014). Livestock production has become the primary use of the remaining grasslands across the western United States and much of the world, with current management actions confining prairie dog populations (Allred et al., 2013). With livestock grazing being the primary use of our grasslands, native colonial herbivores interacting with livestock on a working landscape remains a critical component of grassland bird conservation in the plains (Bock and Webb, 1984).

The alteration in vegetation structure that results from herbivory can affect use by grassland nesting birds. Assessing how avian species are affected by a landscape influenced by the disturbance of prairie dogs will shed light on how vegetation characteristics influence nesting behaviors. Each species perceives differences in its environment at multiple scales suggesting the need to determine how vegetation structure and landscape characteristics influence grassland heterogeneity (Bleho, 2009). Some avian species selected areas with larger percentages of bare ground and shorter vegetation, while others, such as the grasshopper sparrow and upland

sandpiper, rely on grassland patches with greater availability of tall dense vegetation and greater litter cover in landscapes occupied by prairie dogs (Augustine and Baker, 2013; Barko et al., 1999; Bleho, 2009). Landscapes act as filters, and if woody cover becomes too great at large scales, than fine spatial scale management in remaining grasslands becomes useful for a limited suite of species (Sandercock et al., 2015). Understanding the importance of spatial scales in individual nest site selection can have a positive impact on how we manage for greater grassland bird diversity in working landscapes.

Limited studies have assessed the need to understand how grassland birds use the landscape for nesting in areas that are occupied by native grazers and prairie dogs while continuing management for cattle production. Therefore, on-going declines and future conservation of grassland birds create the need to investigate and quantify the relationships between prairie dogs and how grassland birds use these types of working landscapes for nesting. To address this our objectives were to: 1) assess nesting survival rates and identify factors that contribute to nest success of grassland birds, and 2) evaluate which habitat features are selected by nesting species at both a micro (nest-site) and landscape scale. We quantified vegetation characteristics at the nest site and landscape scale to determine whether these characteristics influence overall nest survival and nest site selection for four grassland bird species common to the Northern Plains (western meadowlark [*Sturnella neglecta*], upland sandpiper [*Bartramia longicauda*], lark sparrow [*Chondestes grammacus*], and grasshopper sparrow [*Ammodramus savannarum*]).



## Materials and Methods

### *Study Area*

We collected data on private and tribally owned mixed-grass prairie located in the Standing Rock Sioux Indian Reservation near Mahto, South Dakota (SD), USA (45° 44' 44.6" N, 100° 39' 43.6" W). The climate is considered semi-arid and characterized by having cold winters and hot summers. The study area receives an average annual precipitation of 44 cm with approximately 75 percent occurring during the growing season (South Dakota Weather and Climate, 2015). The 30-year mean annual winter (December-March) temperature is -8 °C and a mean summer (June-August) temperature of 20 °C (South Dakota Weather and Climate, 2015). The study site lies in a landscape characterized by a mixture of rangeland and agricultural fields in a topographically diverse landscape. Woody vegetation is found in areas of concentrated moisture such as draws and bottomlands. The region consists of mixed-grass prairie dominated by mid-height cool season (C<sub>3</sub>) grasses such as western wheatgrass (*Pascopyrum smithii* (Rydb.) Á. Löve) and green needlegrass (*Nassella viridula* (Trin.) Barkworth). Prairie dog colonies are dominated by shorter warm season (C<sub>4</sub>) grasses, including buffalo grass (*Bouteloua dactyloides* (Nutt.) J.T. Columbus) and blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths). A variety of forbs commonly encountered in the region include purple coneflower (*Echinacea angustifolia* DC.), scarlet globemallow (*Sphaeralcea coccinea* (Nutt.) Rydb.), fetid marigold (*Dyssodia papposa* (Vent.) Hitchc.), bushy knotweed (*Polygonum ramosissimum* Michx.), and sagewort species (*Artemisia* spp). The dominant soil map units on the study site were Cabba-Reeder loams, Reeder-Cabba loams, and Wayden-Cabba complexes on topography of rolling hills with relatively flat lowlands (0 to 70% slope) (USDA-NRCS, 2014).

### ***Treatment Design***

We delineated the study site into four experimental landscapes (200±7 ha) with varying degrees of prairie dog occurrence. Each landscape represented a different treatment, with the four levels of prairie dog occupancy including 1) 0%, 2) 18%, 3) 40%, and 4) transitional. The transitional landscape originally was 75% occupied by prairie dogs, but during the second year of our study accidental poisoning of prairie dogs reduced occupancy to 24 ha or 11%. Although the transitional treatment dropped from 75% to 11% prairie dog occupancy, the vegetation community, bare ground and litter levels present during the study period was caused by the 75% occupancy level. Throughout the remainder of the study, prairie dogs were allowed to recolonize the area and rebounded to 29% occupancy by 2015. Each landscape was stocked with Angus steers to achieve a targeted 50% degree of disappearance of vegetation. Stocking rates were calculated based on forage availability within each pasture; 0% equivalent to 1.0 ha/Animal Unit Month (AUM), 18% equivalent to 1.3 ha/AUM, 40% equivalent to 1.6 ha/AUM, and transitional equivalent to 4.2 ha/AUM. Cattle grazed each pasture from early-June to early-October.

### ***Field Methods***

We established six, 16 ha study plots to focus nest searching in areas occupied and unoccupied by prairie dogs. Half of the study plots (3) were randomly placed on prairie dog colony, while the other half (3) randomly placed off-colony across the landscapes. The 18% and 40% pastures each had two study plots with one located both on- and off-colony, the transitional pasture had one study plot on-colony, and the 0% pasture had one study plot. Nests were also located incidentally while conducting other field operations within the entire study site. When nests were found, their location relative to prairie dog colonies (on or off colony) was recorded. Additional time was spent observing behaviors of adults to determine locations of nests

throughout the study site (Winter et al., 2003). Nest searching and monitoring was conducted from early May to August, 2012-2016. Nest searches occurred between 0700 and 1500 (MST) by flushing adults from the nest using a 31 m rope with aluminum cans attached at every 2.5 m (Koford, 1999). Nests were marked with surveyor flags 3 m away towards a distinct landmark and inspected every 4–6 days until the young fledged or the nest failed (Churchwell et al., 2008). Parasitism by brown headed cowbirds was monitored and we recorded whether a cowbird chick hatched and fledged. Incubation was considered successful if at least one host egg hatched, and fledging was considered successful if at least one chick fledged.

#### *Nest-Site Measurements*

We evaluated vegetative characteristics at nest sites and a matching random point (within 100 m of the nest) following the completion of each nesting attempt to allow minimal disturbance (Lusk et al., 2003). The vegetative sampling design was adapted from the breeding biology research and monitoring database (BBIRD) protocol from University of Montana (Martin et al., 2014). Vegetation measurements were conducted at the nest bowl, 2.5 m, and 5 m distances in all cardinal directions for a total of nine sampling locations. Visual obstruction was assessed using a modified Robel pole (Robel et al., 1970), maximum vegetation height (cm) was measured with the Robel pole, bare ground basal cover was estimated using a 10 pin-point frame (Evans, 1957), and litter depth (cm) was estimated at the nest, 2.5 m, and 5.0 m intervals. Visual obstruction readings were recorded in centimeters to allow for fine scale measurements that better capture small variations in the short vegetation of prairie dog colonies (change in increment was the modification to Robel et al., (1970) protocol). Canopy cover estimates of vegetation functional groups (grass, forb, shrub, and sedge) and litter was determined using a 20x50 cm frame centered over the nest bowl and at the random point (Daubenmire, 1959).

Variable measurements were averaged across common distances to obtain one value for analyses.

### Landscape Measurements

We used a geographic information system approach with ArcGIS (v10.3) to evaluate landscape characteristics in relation to nest site location (used) and at one random point (available) per nest (Hovick et al., 2015). We randomly distributed one point within a 250 m radius of each nest representing a realistic area (within home range) available for nest selection which is similar to what has been justified for other grassland species (Hovick et al., 2015). The amount of woody plant cover was quantified within 100 m, 250 m, and 500 m buffers of nest and random points. Woody cover was considered any tall woody vegetation (> 2 m, shrubs and trees) found in areas of concentrated moisture such as draws and bottomlands. For nests located off-colony, distance to the nearest edge of prairie dog colony was measured and recorded. Distance to edge of prairie dog colony was measured for nests located on-colony. Distance to nearest fence and woody cover was calculated for each individual nest (Table 3.1).

Table 3.1. Summary for variables used to examine nest survival and resource selection models of four mixed-grass prairie grassland avian species on mixed-grass prairie in the northern plains, SD, USA.

Parameter/Classification	Definition
<i>Landscape (Macro)</i>	
Edge	Distance from nest (m) to the nearest colony edge
Fence	Distance from nest (m) to the nearest fence
WoodyDistance	Distance from nest (m) to the nearest woody habitat
Woody250	Woody vegetation per hectare measured in 250-m radius of the nest
Woody500	Woody vegetation per hectare measured in 500-m radius of the nest
<i>Nest-site (Micro)</i>	
BareGround	Bare ground cover at nest, 2.5-m, and 5-m radius using point sampling
%Forb	Forb canopy cover in 1-m <sup>2</sup> quadrat at the nest
%Grass	Grass canopy cover in 1-m <sup>2</sup> quadrat at the nest
%Shrub	Shrub canopy cover in 1-m <sup>2</sup> quadrat at the nest
%Sedge	Sedge canopy cover in 1-m <sup>2</sup> quadrat at the nest
LitterDepth	Litter depth (cm) in 1-m <sup>2</sup> quadrat at the nest, 2.5-m, and at 5-m
MxhtNest	Tallest piece of vegetation (cm) at the nest, 2.5-m, and at 5-m
VOR	Visual obstruction readings (cm) at nest, 2.5-m, and 5-m radius
<i>Biological/Temporal*</i>	
Age	How survival changed as the nest aged (Dinsmore et al., 2002)
In season trend	How survival changed within the nesting season
ParasiteHatch	Presence of a cowbird nestling (Hovick et al., 2011)
Parasitized	Presence of a cowbird egg (Tewksbury et al., 2006)
Year	The year the nest was monitored

\*Biological/Temporal variables were only used during survival analysis

### ***Statistical Analysis***

#### ***Resource Selection***

We used the resource selection function package in program R to determine nest-site selection (Boyce et al., 2002; R Development Core Team, 2014). Resource selection function (RSF) allow us to investigate habitat selection by comparing available vegetation characteristics to areas of use, and allows one to assess the impact of landscape and vegetation features on species specific nest-site selection. A binomial generalized linear model was implemented for use versus availability sampling design. Prior to analysis, we standardized all vegetation and

landscape variables by calculating  $z$ -scores and used correlation coefficients among all variables to determine which were highly correlated ( $r > 0.6$ ; Gelman and Hill, 2007). When variables were highly correlated, we chose to retain the variable with the most biological relevance based on the literature or observations during field work. Akaike's Information Criteria (AIC) adjusted for small sample size (AIC<sub>c</sub>) and model weights ( $w_i$ ) were used to evaluate models, allowing us to identify the best model that accounts for the most variation among variables (Burnham and Anderson, 2002). We considered models within 2  $\Delta$ AIC points of the top model to be supported (Burnham and Anderson, 2002).

In an attempt to reduce the overall model set, we followed a two-step approach during analyses. First, we ran single variable models and compared them to one another and against the null model. We kept those variables that were better than the null model and within 2  $\Delta$ AIC<sub>c</sub> units of the top model for final analysis. Second, we used all variables retained during the single variable analyses and developed a best model set. The best model set included models consisting of all possible single and combinations of retained variable models.

### Survival Analysis

We used Program MARK (v8.0) to model daily survival rates of nests to quantify the effects of vegetation, landscape characteristics, and biological variables have on survival of nesting grassland passerines nests (White and Burnham, 1999; Table 3.1). We created encounter histories for all nests monitored in our five-year study (2012-2016) where we had data for nesting fates and dates of monitoring. We standardized the nesting season for each species based on the first and last day we monitored a nest during the study (White and Burnham, 1999). We constructed groups based on year and nesting stage. We followed a similar approach in nest survival analyses as taken in the RSF. We ran single variable models and compared them to each

other and the constant model. We used  $AIC_c$  to compare models and calculated Akaike's weights as an indication of support for each model (Burnham and Anderson, 2002). We retained variables that were better than the constant model and within  $2 \Delta AIC_c$  units of the top model. We then used all variables retained during the single variable analyses and developed models that included all single variable and combinations of retained variables. We considered all models within  $2 \Delta AIC$  points of the top model as supported (Burnham and Anderson, 2002).

## **Results**

Vegetation and landscape characteristics were quantified at 188 nests over the five year study. Western meadowlark nests had the highest sample size ( $n = 77$ ), followed by grasshopper sparrow ( $n = 51$ ), lark sparrow ( $n = 31$ ), and upland sandpiper ( $n = 29$ ).

### ***Resource Selection***

Litter depth was an important attribute at nest sites of western meadowlarks, grasshopper sparrows, and lark sparrows (Table 3.2). These species selected sites with greater litter depth surrounding the nest relative to what was available (Figure 3.1). Of the landscape characteristics quantified, woody cover or distance to the nearest prairie dog colony border (edge) influenced nest selection for all species except the upland sandpiper (Table 3.2). On a landscape occupied by prairie dogs, the western meadowlark tended to avoid the habitat transition (edge) onto prairie dog colonies (Figure 3.1). Both western meadowlarks and grasshopper sparrows selected against woody cover on the landscape. Western meadowlarks avoided woody cover within 250 m of the nest, but grasshopper sparrows selected nest sites that maximized distance from woody cover ( $\beta = 0.39$ ,  $SE = 0.22$ ,  $CI = -0.02$  to  $0.86$ ,  $\Sigma w_i = 0.33$ ; Figure 3.1). Our best model for nest-site selection of the upland sandpiper included bare ground at the 2.5 m scale. The upland sandpiper

selected nest sites that minimized the amount of bare ground within 2.5 m of the nest (Figure 3.1). The null model was supported in the top model set for upland sandpiper (Table 3.2).

Table 3.2. Resource selection models investigating the influence of vegetation and landscape characteristics on grassland bird nest site selection in working landscapes grazed by native colonial and domestic herbivores in northcentral South Dakota, USA, 2012-2016. Models include the best model (lowest Akaike’s Information Criteria adjusted for small sample sizes (AICc) value), candidate models within two  $\Delta AIC_c$  points of best model, and null models. The number of parameters ( $k$ ), AICc weights ( $w_i$ ), and deviance for each model are provided.

Species	Model <sup>a</sup>	$\Delta AIC_c^b$	$k$	$w_i$	Deviance
Western Meadowlark	Edge + Woody250 + LitterDepth	0.0	4	0.62	175.16
	Woody250 + LitterDepth	1.3	3	0.32	178.67
	Null	31.9	1	<0.001	213.49
Grasshopper Sparrow	LitterDepth + WoodyDistance	0.0	3	0.65	120.60
	LitterDepth	1.2	2	0.35	123.98
	Null	16.6	1	<0.001	141.40
Lark Sparrow	LitterDepth	0.0	2	0.99	69.22
	Null	24.8	1	0.01	85.95
Upland Sandpiper	BareGround2.5	0.0	2	0.34	77.51
	Null	0.8	1	0.23	80.41

<sup>a</sup>Edge = distance to nearest habitat transition (m), Woody250 = woody cover within 250m of nest (ha), LitterDepth = litter depth at nest (cm), WoodyDistance = Distance to woody cover (m), BareGround 2.5 = percent bare ground within 2.5 m of nest

<sup>b</sup>AICc for best model: western meadowlark = 183.16, grasshopper sparrow = 126.60, lark sparrow = 62.90, and upland sandpiper = 81.51.



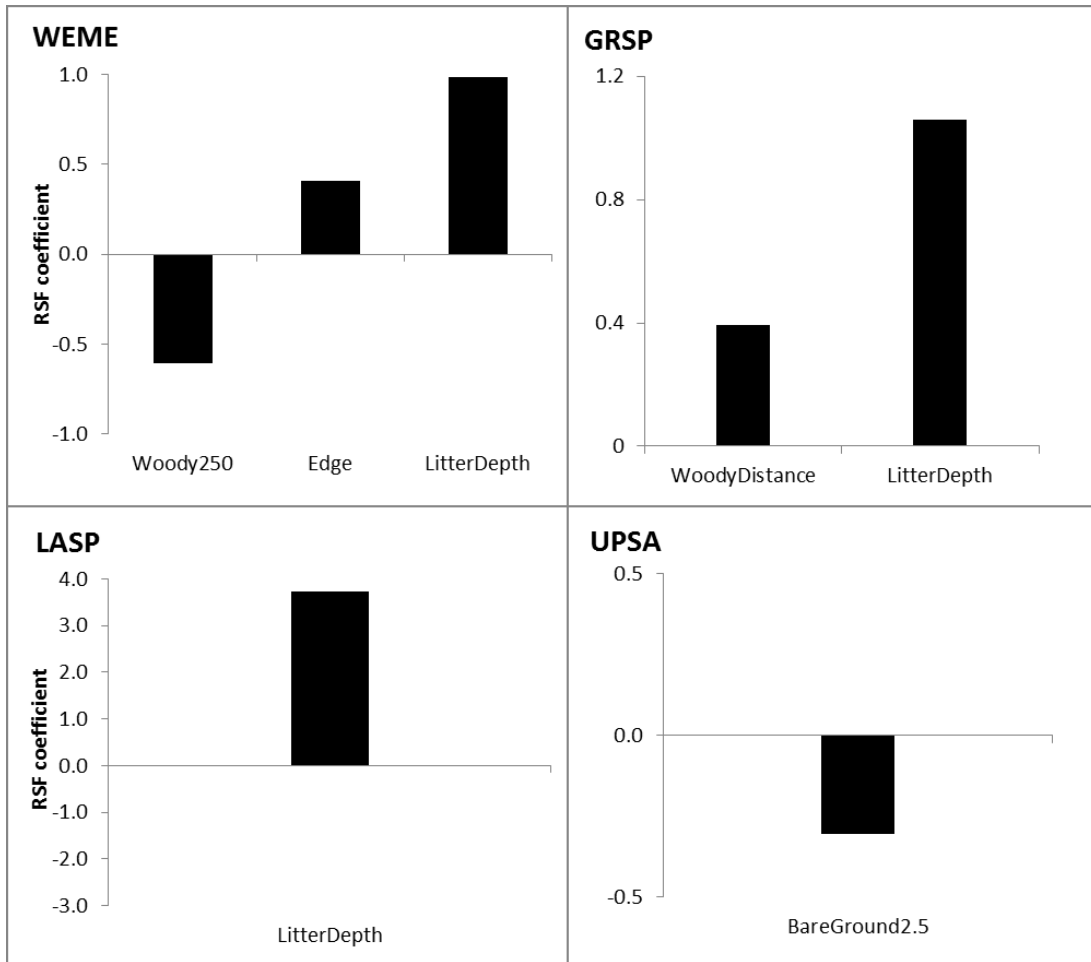


Figure 3.1. Standardized coefficients from resource selection functions describing western meadowlark (WEME), grasshopper sparrow (GRSP), lark sparrow (LASP), and upland sandpiper (UPSA) nest site selection. Bars extending upward indicate maximized use while downward bars indicate minimized use. (Woody250 = woody cover within 250 m of nest [ha], Edge = distance to nearest habitat transition [m], LitterDepth = litter depth at nest [cm], WoodyDistance = distance to woody cover [m], BareGround 2.5 = percent bare ground within 2.5 m of nest)

### *Nest Survival*

We did not find any common vegetation or landscape characteristics that influenced nest survival among all species when comparing our best model sets (Table 3.3). For grasshopper sparrows, eight models were more supported than the constant model, all of which contained the nest age variable (Table 3.3). The DSR for grasshopper sparrow nests increased as the nest aged ( $\beta = 0.02$ , CI = 0.003 to 0.05; Table 3.4). Other covariates included in the top model set for

grasshopper sparrows all included zero in the 95% confidence interval (Table 3.4). The hatching of a brown-headed cowbird egg negatively influenced DSR of western meadowlark and lark sparrow nests (Table 3.3). We observed 30% and 74% brood parasitism on western meadowlarks and lark sparrows; respectively, while upland sandpipers were not common hosts of nest parasites (Table 3.4). Survival analysis indicated that nesting success for grasshopper sparrows was not influenced by whether a parasite hatched despite having 33% of nests parasitized by cowbirds. Our results further indicated that DSR of western meadowlark nests increased as the height of the vegetation surrounding the nest increased (Figure 3.2). There was a year effect on the DSR of upland sandpiper nests ( $\beta = 1.45$ , CI = 0.13 to 2.77), and DSR increased as forb cover surrounding a nest increased (Figure 3.2). Other covariates were included in supported models for all species, but the 95% CI of the parameter estimates included zero (Tables 3.3 and 3.4).

The constant DSR for western meadowlark nests was 0.95. When exponentiated over the 26-day nesting period, western meadowlark nests in our working landscape have a 26.4% chance of surviving. For grasshopper sparrow analysis, we calculated a constant DSR of 0.95, and when exponentiated over the 20-day nesting period the nests had a 35.8% chance of surviving. Constant DSR for lark sparrow nests was 0.94, and when exponentiated over the 22-day nesting period equaled a nest success of 25.6%. Constant DSR for the upland sandpiper nests was 0.96, which based on a 29-day incubation period equates to a nest success of 30.6%.

Table 3.3. Nest survival models for four mixed-grass prairie grassland avian species in northcentral South Dakota, USA, 2012-2016. Models include the best model (Akaike's Information Criteria adjusted for small sample sizes (AICc) lowest AIC<sub>c</sub> value), candidate models within two  $\Delta$ AIC<sub>c</sub> points of best model, and null (constant survival) models. The number of parameters ( $k$ ), AIC<sub>c</sub> weights ( $w_i$ ), and deviance for each model are provided.

Species	Model <sup>a</sup>	$\Delta$ AIC <sub>c</sub> <sup>b</sup>	$k$	$w_i$	Deviance
Western Meadowlark					
	MxhtNest + ParasiteHatch	0.00	3	0.66	164.79
	Year + MxhtNest + ParasiteHatch	1.28	7	0.34	157.94
	Constant survival	15.41	1	0.00	184.23
Grasshopper Sparrow					
	Age + MxhtNest	0.00	3	0.17	119.24
	Age + %Grass + WoodyDistance	0.60	4	0.13	117.81
	Age + MxhtNest + %Grass	0.66	4	0.12	117.87
	Age + MxhtNest + WoodyDistance	0.69	4	0.12	117.90
	Age	0.73	2	0.12	122.00
	Age + WoodyDistance	0.78	3	0.11	120.02
	Age + MxhtNest + %Grass + WoodyDistance	0.88	5	0.11	116.04
	Age + %Grass	1.07	3	0.10	120.32
	Constant survival	4.15	1	0.02	127.44
Lark Sparrow					
	ParasiteHatch + LitterDepth2.5 + %Grass	0.00	4	0.29	67.84
	ParasiteHatch + %Grass	0.51	3	0.23	70.41
	LitterDepth2.5 + %Grass	0.84	3	0.19	70.74
	ParasiteHatch + LitterDepth2.5	0.91	3	0.18	70.81
	ParasiteHatch	2.01	2	0.11	73.96
	Constant survival	8.40	1	0.00	82.38
Upland Sandpiper					
	Year + %Forb	0.00	3	0.46	22.97
	Year + %Forb + Edge	1.79	4	0.19	22.70
	Year + %Grass + %Forb	1.87	4	0.18	22.78
	Year + VOR5 + %Forb	2.00	4	0.17	22.92
	Constant survival	14.73	1	0.00	41.77

<sup>a</sup>MxhtNest = maximum vegetation height at nest (cm), ParasiteHatch = brood parasitism, Edge = distance to nearest habitat transition, Age = nest age, LitterDepth2.5 = litter depth within 2.5 m of nest (cm), WoodyDistance = Distance to woody cover (m), %Grass = percent cover of grass at nest and within 2.5 m of nest, %Forb = percent cover forb at nest, VOR5 = visual obstruction within 5 m of nest (cm).

<sup>b</sup>AIC<sub>c</sub> for best model: western meadowlark = 170.82, grasshopper sparrow = 125.30, lark sparrow = 75.99, and upland sandpiper = 29.05.

Table 3.4. Parameter estimates ( $\beta$  and 95% confidence intervals [CI]) for variables influencing daily nest survival (logit scale) of four grassland songbird species in northcentral South Dakota, USA.

Variable	Western Meadowlark	Grasshopper Sparrow
	$\beta$ (95% CI)	$\beta$ (95% CI)
MxhtNest <sup>a</sup>	0.04 (0.02, 0.07)	0.01 (-0.01, 0.05)
ParasiteHatch	-1.14 (-2.14, -0.13)	----
Year	2.04 (0.33, 3.76)	----
%Grass	----	-0.01 (-0.01, 0.00)
Age	----	0.02 (0.00, 0.05)
WoodyDistance	----	-0.01 (-0.01, 0.00)
Intercept	3.00 (2.67, 3.34)	2.88 (2.49, 3.28)
	Lark Sparrow	Upland Sandpiper
ParasiteHatch	-1.58 (-3.10, -0.05)	----
Year	----	1.45 (0.13, 2.77)
LitterDepth (2.5m)	-2.18 (-4.75, 0.39)	----
%Grass	0.05 (-0.01, 0.10)	----
%Forb	----	0.09 (0.01, 0.16)
Intercept	2.74 (2.27, 3.23)	3.89 (3.08, 4.70)

<sup>a</sup>MxhtNest = maximum vegetation height at nest (cm), ParasiteHatch = brood parasitism, LitterDepth = litter depth at 2.5 m radius (cm), %Grass = percent cover grass at nest, %Forb = percent cover forb at nest

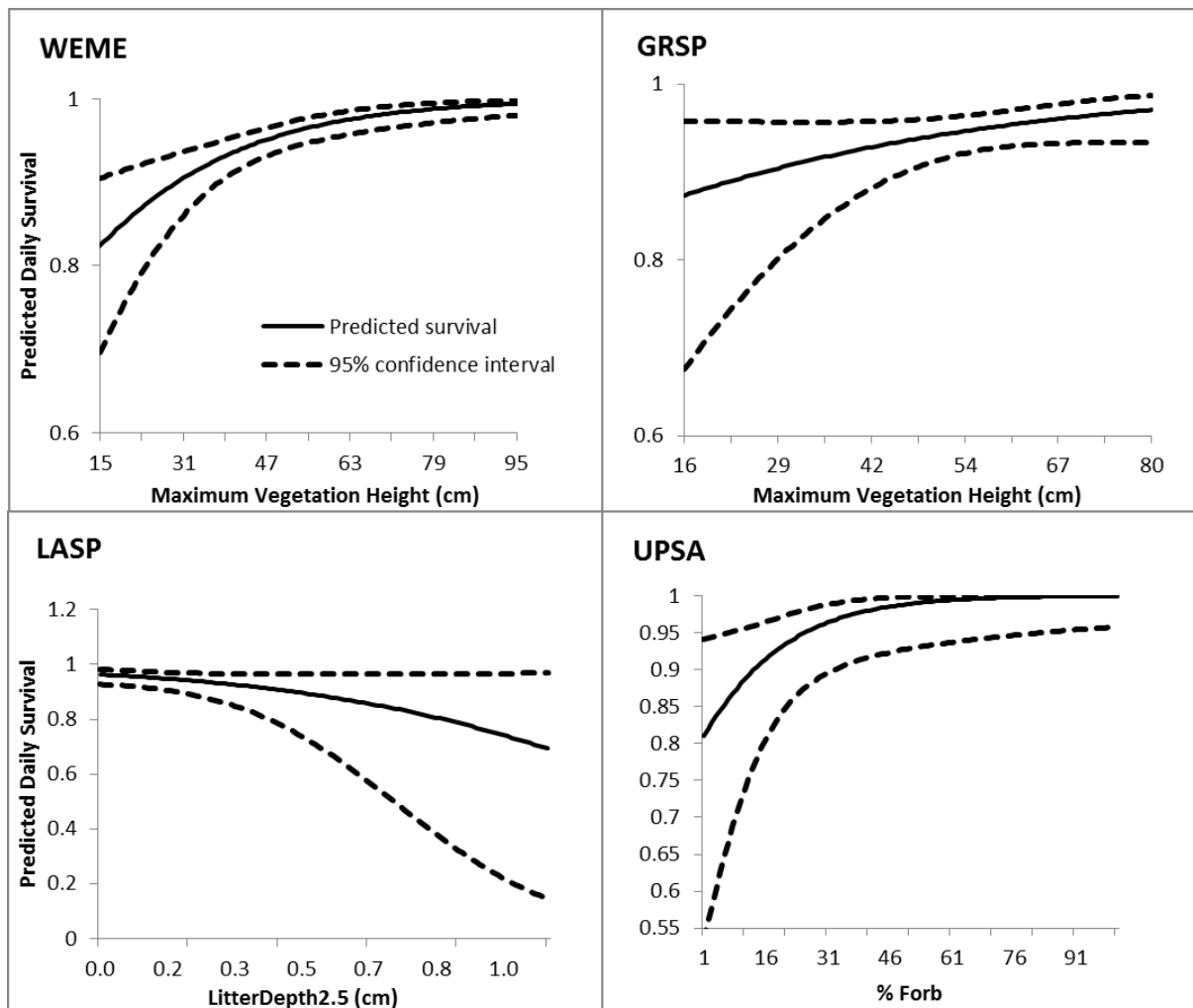


Figure 3.2. Logistic regression curve showing predicted daily survival rate as a function of various vegetation factors for four grassland songbird species in northcentral South Dakota, USA, 2012-2016. (Abbreviations WEME = western meadowlark, GRSP = grasshopper sparrow, LASP = lark sparrow, and UPSA = upland sandpiper, LitterDepth2.5 = depth of litter at 2.5m from the nest).

## Discussion

Prairie grassland bird species evolved with both colonial and nomadic herbivores where periodic disturbance helped maintain diversity within prairie landscapes (Fondell and Ball, 2003; Knopf, 1996; Vickery et al., 1999). This interaction of native colonial species and domestic grazers common in today's working landscapes has affected the types of species that successfully coexist based on nest-site characteristics offered by the landscape within this study.

Landscape and nest-site spatial scales play important roles when species select sites for nesting and survival of the nest. Thus, selection pressures should lead species to place nests in areas where vegetation is most concealing, and nests will have the greatest chances of survival.

Conservation efforts at the landscape level may better aid in increasing the densities of grassland passerines, and managing for vegetative structure at the nest-site will benefit nesting survival.

Many grassland species show area-sensitivity to distinct features of the landscape, whether it be edges of patches, areas of woody cover, water, or fence lines. Our results indicated that the western meadowlark, grasshopper sparrow, and lark sparrow avoided both edge between on and off prairie dog colonies and woody cover when selecting for nesting resources. The lark sparrow was more selective to the habitat transition between prairie dog colony and off colony areas where vegetation was shorter with patches of bare ground. Other work found that lark sparrows were frequently observed in disturbed areas common to a landscape occupied with prairie dogs (Bock et al., 1984, Bock and Webb, 1984; Lusk et al., 2003).

Our study site is strewn with extensive draws of woody cover, which affected nest-site selection for the grasshopper sparrow and western meadowlark. The western meadowlark selected areas with reduced woody cover within 250 m of the nest, and grasshopper sparrows maximized the distance from woody cover (Figure 3.1). These are common findings for both the western meadowlark and grasshopper sparrow, but our findings may provide new insight in landscape specific demography for passerines nest-site selection when managing landscapes occupied by prairie dogs (Bock and Webb, 1984; Dechant et al., 2002; Sample 1989; Weins, 1986).

Beyond landscape characteristics, grassland birds have been found to favor a more diverse plant community with greater vegetation structure at the nest-site, which may facilitate

higher nest survival (Sandercock et al., 2015; Towne et al., 2005). We began by assessing how vegetation structure, percent cover, and litter depth influence species specific resource selection. Our findings show that nest-site, vegetative parameters play the biggest role in both nest selection and survival. Structure of the vegetation in regards to visual obstruction and maximum height of vegetation around the nest has consistently been one of the most important features that affect the trend of increasing nest survival (Fondell and Ball, 2004; Lusk et al., 2003; Sandercock et al., 2015). In opposition to these earlier findings, we found very little support that VOR effected nest site selection or survival at our study sites, possibly due to the simultaneous grazing occurring on the landscape between prairie dogs and domestic livestock. Despite the lack of support for models containing VOR, maximum vegetation height was found to be an important factor effecting the DSR of western meadowlarks. Similar to many studies, we found that litter depth and bare ground are significant in regards to nest-site selection among all species (Davis, 2005; Lusk et al., 2003).

Specific factors such as age of nest and year appear to be strong factors that affect nest survival of some species. Many others have established models indicating that age and year have strong effects when assessing grassland passerine nest survival (Davis, 2005; Grant et al., 2005). Previous studies on area requirements and nesting success found that species tended to avoid extensive woody vegetation and edge (Johnson and Igl, 2001; Sample, 1989). Our estimated nest survival rates in a landscape grazed by both domestic and native colonial grazers were within the range of previously reported studies for grassland species nesting in undisturbed grasslands (Churchwell et al., 2008; Davis, 2005). We found grasshopper sparrow nesting success in prairie dog occupied landscapes to be greater compared to studies looking at Conservation and Wetland Reserve Program, and tallgrass prairie sites (Stauffer et al., 2011). Parasitism by the brown-

headed cowbird had a large influence on DSR for both lark sparrows and western meadowlarks, which may largely result from these species nesting in areas of short vegetation (Goguen and Mathews, 2001).

## **Conclusions**

Our findings suggest that mixed-grass prairie located in working landscapes should be managed for heterogeneity as different species were affected by different landscape and vegetative attributes. Species seek different characteristics based on individual requirements and are still able to coexist with one another on a landscape full of biological diversity created by prairie dog activities and cattle herbivory. Our findings provide strong support that native burrowing herbivores and domestic cattle create dynamic vegetation communities that benefit nesting grassland bird species through increased structural heterogeneity. By maintaining prairie dogs while still sustaining livestock production, we can better provide habitat heterogeneity, which is crucial for grassland bird conservation.

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## CHAPTER 4: GENERAL CONCLUSION

Throughout the course of the study, we made great progress towards collecting a complex dataset assessing bird and vegetation communities associated with grazed mixed-grass prairie occupied by black-tailed prairie dogs. A grazing community perspective between domestic herbivores and prairie dogs will help to better inform both producers and managers about the complex interactions occurring on these landscapes. Throughout the course of the five-year project, we completed nearly 500 bird surveys; sampled vegetation on 196 transects at more than 4,000 plots, and monitored over 240 nests. The analysis contained within this thesis will provide better insight on how to manage grazed rangelands at both the landscape and micro levels when accounting for prairie dog occupancy.

We made great strides towards understanding how prairie dogs influence the vegetation and avian communities in a landscape that sustains cattle production. Through vegetation sampling at nest sites and along transects, we have developed a better list of vegetation that arises when prairie dogs are present compared to undisturbed grasslands. We found that bare ground, decreasing litter depths, and short vegetation provided important structure for grassland birds such as horned larks and brown-headed cowbirds. Across the prairie dog colony, we found distinct patches of vegetation that provided the structure required for passerines such as western meadowlarks and lark sparrows to utilize for nesting. The landscape off a prairie dog colony also provided the necessary requirements for grasshopper sparrows and upland sandpipers to thrive. By surveying these prairie dog occupied landscapes, we have confirmed previously reported relationships between grassland birds, vegetation, and prairie dogs, while presenting new findings.

We begin to shed new light on the effect grazers (predominantly cattle) can play in creating a heterogeneous landscape while maintaining some occupancy level of prairie dogs. By assessing and quantifying landscape scale characteristics such as woody cover and habitat transitions, we were able to get a glimpse at the selection made by individual species for nesting. We found that landscape characteristics were a larger influence when species selected a nesting site, but micro-scale features were more influential to the overall survival of the nest. These findings help to reinforce the need for considering heterogeneity at multiple scales on working landscapes.

A brief summary of the extensive work that occurred at our research site can be found in the December 2015 issue of *Rangelands* titled “*Incorporating Rangeland Management on Tribal Lands: An Example from the Northern Great Plains*”, and covers research aspects ranging from exploring the roles of a land grant college, investigating use of ecological sites for managing wildlife and livestock, and assessing how prairie dog colonized rangelands influence the wildlife and vegetation communities. Allowing prairie dogs to play their role in the ecosystem doesn't need to be considered as a conflict of interest to landowners and producers. Managers can effectively implement individual management plans that consider impacts on soil health, hydrology, wildlife and vegetation, and livestock operations. Our research provides a brief insight that will help aid the people of the Standing Rock Indian Reservation as they strive to sustain an ecologically safe, and natural grazing operation.

## APPENDIX

Table A.1. Four-letter Alpha codes and common names of 36 bird species, and their detection totals during grassland bird surveys (\* indicates grassland obligate species analyzed).

4-letter code	Common name	Total Observations	4-letter code	Common Name	Total Observations
AMGO	American goldfinch	75	GRCA	Grey catbird	34
BAEA	Bald eagle	3	GRSP	Grasshopper sparrow*	932
BANS	Bank swallow	10	HOLA	Horned lark*	196
BARS	Barn swallow	77	KILL	Killdeer	39
BBMA	Black-billed magpie	50	LASP	Lark sparrow*	164
BHCO	Brown-headed cowbird*	691	MODO	Mourning dove*	206
BLGR	Blue grosbeak	26	NOFL	Northern flicker	37
BOBO	Bobolink	40	RHWO	Red-headed woodpecker	9
BRBL	Brewer's blackbird	33	RNEP	Ring-necked pheasant	20
BRTH	Brown thrasher	88	RWBL	Red-winged blackbird	161
CHSP	Chipping sparrow	9	SPTO	Spotted towhee	65
CCSP	Clay-colored sparrow	20	STGR	Sharp-tailed grouse	20
CLSW	Cliff swallow	74	TUVU	Turkey vulture	11
COGR	Common grackle	16	UPSA	Upland sandpiper*	280
DICK	Dickcissel	24	VESP	Vespers sparrow	16
EAKI	Eastern kingbird*	153	WEKI	Western kingbird	24
FISP	Field sparrow	14	WEME	Western meadowlark*	995
GOEA	Golden eagle	5	YEWA	Yellow warbler	94

Table A.2. Four-letter Alpha codes and common names of bird species detected during grassland bird surveys on mixed-grass prairie in north-central South Dakota during the 2012-2015 breeding seasons.

<b>4-letter code</b>	<b>Common name</b>	<b>4-letter code</b>	<b>Common name</b>
AMGO	American goldfinch	GOEA	Golden eagle
AMKE	American kestrel	GRCA	Gray catbird
AMRO	American robin	GRSP	Grasshopper sparrow
BAEA	Bald eagle	HOLA	Horned lark
BANS	Bank swallow	KILL	Killdeer
BARS	Barn swallow	LASP	Lark sparrow
BBMA	Black-billed magpie	LEFL	Least flycatcher
BEVI	Bell's vireo	MODO	Mourning dove
BHCO	Brown-headed cowbird	NOFL	Northern flicker
BLGR	Blue grosbeak	NOHA	Northern harrier
BOBO	Bobolink	OROR	Orchard oriole
BRBL	Brewer's blackbird	RHOW	Red-headed woodpecker
BRTH	Brown thrasher	RNEP	Ring-necked pheasant
BUOW	Burrowing owl	RWBL	Red-winged blackbird
CCSP	Clay-colored sparrow	SAVS	Savannah sparrow
CEDW	Cedar waxwing	SPTO	Spotted towhee
CLSW	Cliff swallow	STGR	Sharp-tailed grouse
CHSP	Chipping sparrow	TRES	Tree swallow
COGR	Common grackle	TUVU	Turkey vulture
DICK	Dickcissel	UPSA	Upland sandpiper
EAKI	Eastern kingbird	VESP	Vesper sparrow
EUST	European starling	WEKI	Western kingbird
FEHA	Ferruginous hawk	WEME	Western meadowlark
FISP	Field sparrow	YEWE	Yellow warbler
FRGU	Franklin's gull		



Table A.3. Alphabetical list of plant species detected during vegetative surveys on fixed width belt transects and nesting sites coinciding with black-tailed prairie dog range on mixed-grass prairie in north-central South Dakota, USA.

<i>Achillea millefolium</i>	<i>Cirsium flodmanii</i>	<i>Kochia scoparia</i>	<i>Psoralea esculenta</i>
<i>Agropyron cristatum</i>	<i>Cirsium undulatum</i>	<i>Koeleria macrantha</i>	<i>Ratibida columnifera</i>
<i>Agropyron intermedium</i>	<i>Cirsium vulgare</i>	<i>Lactuca serriola</i>	<i>Ratibida pinnata</i>
<i>Agrostis scabra</i>	<i>Convolvulus arvensis</i>	<i>Lactuca tatarica</i>	<i>Rosa acicularis</i>
<i>Amaranthus alba</i>	<i>Conyza canadensis</i>	<i>Liatris punctata</i>	<i>Rosa arkansana</i>
<i>Amelanchiver spp</i>	<i>Conyza ramosissima</i>	<i>Linum rigidum</i>	<i>Rosa woodii</i>
<i>Ambrosia artemisiifolia</i>	<i>Dalea candida</i>	<i>Lotus unifolius</i>	<i>Rumex aquaticus</i>
<i>Amorpha canescens</i>	<i>Dalea purpurea</i>	<i>Lupinus Spp</i>	<i>Salsola kali</i>
<i>Amorpha fruticosa</i>	<i>Descurainia sophia</i>	<i>Lygodesmia juncea</i>	<i>Schedonnardus paniculatus</i>
<i>Andropogon gerardii</i>	<i>Dicanthelium spp</i>	<i>Medicago lupulina</i>	<i>Schizachyrium scoparium</i>
<i>Anemone canadensis</i>	<i>Dichanthelium oligsanthes</i>	<i>Medicago sativa</i>	<i>Setaria viridis</i>
<i>Anemone patens</i>	<i>Digitaria ischaemum</i>	<i>Melilotus officinalis</i>	<i>Solanum rostratum</i>
<i>Antennaria neglecta</i>	<i>Distichlis spicata</i>	<i>Mentha spp</i>	<i>Solanum triflorum</i>
<i>Antennaria parvifolia</i>	<i>Dyssodia papposa</i>	<i>Monarda fistulosa</i>	<i>Solidago missouriensis</i>
<i>Aristida purpurea</i>	<i>Echinacea angustifolia</i>	<i>Muhlenbergia cuspidata</i>	<i>Solidago mollis</i>
<i>Artemisia absinthium</i>	<i>Elymus canadensis</i>	<i>Munroa squarrosa</i>	<i>Solidago spp</i>
<i>Artemisia cana</i>	<i>Elymus trachycaulus</i>	<i>Nassella viridula</i>	<i>Spartina pectinata</i>
<i>Artemisia dracunculoides</i>	<i>Erigeron annuus</i>	<i>Opuntia fragilis</i>	<i>Sphaeralcea coccinea</i>
<i>Artemisia frigida</i>	<i>Erigeron divergens</i>	<i>Opuntia macrorhiza</i>	<i>Sporobolus compositus</i>
<i>Artemisia ludoviciana</i>	<i>Erigeron strigosus</i>	<i>Oxalis stricta</i>	<i>Sporobolus cryptandrus</i>
<i>Asclepias pumila</i>	<i>Eriophyllum spp</i>	<i>Packera plattensis</i>	<i>Sporobolus spp</i>
<i>Asclepias speciosa</i>	<i>Escobaria vivipara</i>	<i>Panicum spp</i>	<i>Symphoricarpos occidentalis</i>
<i>Asclepias sullivantii</i>	<i>Galium boreale</i>	<i>Panicum virgatum</i>	<i>Symphytotrichum ericoides</i>
<i>Aster novae-angliae</i>	<i>Gaura coccinea</i>	<i>Pascopyrum smithii</i>	<i>Taraxacum officinale</i>
<i>Astragalus crassicaarpus</i>	<i>Geranium maculatum</i>	<i>Phalaris arundinacea</i>	<i>Thlaspi arvense</i>
<i>Bouteloua curtipendula</i>	<i>Glycyrrhiza lepidota</i>	<i>Pblox hoodia</i>	<i>Thynopyrum intermedium</i>
<i>Bouteloua dactyloides</i>	<i>Gnaphalium palustre</i>	<i>Physalis heterophylla</i>	<i>Toxicodendron radicans</i>
<i>Bouteloua gracilis</i>	<i>Grindelia squarrosa</i>	<i>Plantago patagonica</i>	<i>Tradescantia bracteata</i>
<i>Bromus inermis</i>	<i>Gutierrizia sarothrae</i>	<i>Poa pratensis</i>	<i>Tragopogon dubius</i>
<i>Bromus tectorum</i>	<i>Hedeoma hispida</i>	<i>Polygala alba</i>	<i>Trifolium repens</i>
<i>Cactaceae spp</i>	<i>Helianthus pauciflorus</i>	<i>Polygala verticillata</i>	<i>Urtica dioica</i>
<i>Calamovilfa longifolia</i>	<i>Hesperostipa comata</i>	<i>Polygonum aviculare</i>	<i>Verbena bracteata</i>
<i>Carduus nutans</i>	<i>Hesperostipa spartina</i>	<i>Polygonum erectum</i>	<i>Vicia americana</i>
<i>Carex spp</i>	<i>Hordeum jubatum</i>	<i>Potentilla spp</i>	<i>Vicia spp</i>
<i>Chamaesyce maculata</i>	<i>Hordeum pusillum</i>	<i>Prunus americana</i>	<i>Yucca glauca</i>
<i>Cirsium arvense</i>	<i>Kali tragus</i>	<i>Psoralea argophylla</i>	<i>Xanthium strumarium</i>

Table A.4. Total pasture area in hectares and extent of each pasture occupied by prairie dogs, with stocking rates and utilizations on study site near Mahto, South Dakota, USA.

<b>Pasture</b>	<b>Prairie Dog Colony (%)</b>	<b>Acreage (ha)</b>	<b>Stocking rate (ha/AUM)</b>	<b>Utilization</b>
1	18	193	1.3	55
2	40	207	1.6	48
3	Transitional	208	4.2	58
4	0	204	1.0	49