



Plant and Bird Community Dynamics in Mixed-Grass Prairie Grazed by Native and Domestic Herbivores[☆]



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ABSTRACT

Native colonial and large ungulate herbivores infrequently coexist on contemporary landscapes but frequently would have in the past, and understanding these interactions is important for conservation in working landscapes—those lands managed for biological and economic objectives. Although many factors contribute to grassland bird declines, consistent and long-term removal of native herbivores from western grasslands promotes homogenous landscapes that are now uniformly grazed by cattle (*Bos taurus*). This shift in grassland disturbance patterns limits habitat availability for specialized grassland species. We investigated vegetation and bird community dynamics in pastures grazed by domestic cattle and a native colonial herbivore, the black-tailed prairie dog (*Cynomys ludovicianus*). The study occurred in the northern mixed-grass prairie of the United States on four experimental pastures stratified by the proportion of prairie dog occupancy to create an ecological gradient. Vegetation and bird surveys were conducted from 2012 to 2015 on and off prairie dog colonies. Vegetation and bird communities were not different along the experimental pasture gradient but did differ relative to location on versus off town. Prairie dogs induced changes in the plant community with midstatured grasses like side-oats grama (*Bouteloua curtipendula*) and green needlegrass (*Nassella viridula*) being associated with off-colony sites while on-colony sites were associated with disturbance-tolerant species such as fetid marigold (*Dyssodia papposa*). The bird community responded to changes in vegetation structure resulting from prairie dogs with grasshopper sparrows (*Ammodramus savannarum*) being more abundant off colonies in areas with greater vegetation structure, while bird species with more complex life histories, such as the upland sandpiper (*Bartramia longicauda*), were associated with both on — and off — prairie dog colonies. Our findings demonstrate the importance of maintaining spatial heterogeneity in working landscapes and show that native colonial herbivores can help achieve this in the presence of herbivory by domestic cattle.

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Introduction

Temperate grasslands are found worldwide and cover ~46 million km² or nearly 27% of the Earth's terrestrial surface (Henwood, 1998). They 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 are 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 expansion of woody plants, overgrazing, and altered hydrology and erosion (Askins, 2000; Briggs et al., 2002; Brennan and Kuvlesky, 2005; Anderson, 2006). Conservation and management of temperate grasslands are necessary as 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). Effective conservation strategies need to be applicable in working grassland landscapes—those areas that are managed for biological and economic objectives (Polasky et al., 2005)—as conservation and livestock production must be able to coexist in order to preserve declining grassland-dependent organisms.

Grazing by domestic cattle (*Bos taurus*) is the most frequent land use of native grassland ecosystems worldwide (Allred et al., 2013). For example, grasslands in the western United States provide approximately 70% of the required annual forage for U.S. cattle (Fleischner, 1994) and are, therefore, an important driver of rural economies. A recent estimate indicated 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). Livestock herbivory has many direct ecological consequences on vegetation composition, structure, and function, which can influence community succession and multiple other ecological functions (Fleischner, 1994; Anderson, 2006). As a result, conservation planning commonly accounts for the influence of different

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grazing regimes on native flora and fauna, but limited research exists to inform conservation of grazing management when both domestic cattle and native colonial herbivores occupy the same landscapes.

Native colonial, burrowing herbivores were historically integral to grassland ecosystems worldwide but have largely been extirpated because of their perceived direct conflict with human activities (Davidson et al., 2012; Derner et al., 2006; Detling, 2006; Augustine and Baker, 2013). Many of these small native herbivores are referred to as “keystone species” or “ecosystem engineers” and play important roles in the composition and structure of grassland ecosystems (Smith and Lomolino, 2004). Specifically, black-tailed prairie dogs (*Cynomys ludovicianus*; hereafter prairie dogs) once inhabited large expanses of North American grasslands and have previously been referenced as a keystone species (Kotliar, 2000). Prairie dog herbivory changes the structural arrangement of grassland vegetation, and their continuous clipping can result in higher concentrations of crude protein and improved digestibility of forage for cattle and other herbivores (Whicker and Detling, 1988). In addition, the elaborate burrow systems created by prairie dogs provide refuge for many species including the prairie rattlesnake (*Crotalus viridis*) and black-footed ferret (*Mustela nigripes*; Sharps and Uresk, 1990). Similar to other burrowing herbivores worldwide, prairie dog populations have been targeted for removal because livestock producers perceive their burrows as potential hazards and believe their herbivory and clipping activities reduce forage availability for livestock (Hoogland, 1996). As a consequence, landowners often promote consistent persecution of prairie dogs through extensive poisoning of colonies and widespread shooting (Hoogland, 1996).

The intentional removal of prairie dogs coupled with the accidental introduction of sylvatic plague (*Yersinia pestis*), which can wipe out entire colonies, has altered patterns and processes on rangeland of western North America (Knowles et al., 2002; Proctor et al., 2006). In addition, loss of other native herbivores (e.g., *Bison bison*) and disturbance processes (i.e., historic fire regimes) severely limits North American grassland spatial and temporal heterogeneity and promotes practices focused on uniform and even distribution of domestic cattle (Knapp et al., 1999). These landscape-level changes undoubtedly influence the fauna and flora that are reliant on the inherent structural and compositional heterogeneity resulting from both vegetation and soil disturbances that historically occurred in grasslands of North America (Knopf, 1996; Limb et al., 2010).

Grassland bird populations have undergone dramatic population declines over the past half century, and research in working landscapes is needed to improve their conservation (Sauer et al. 2013). Grassland birds are known to select nesting sites based on vegetation structure in grassland ecosystems (Knopf, 1996; Brennan and Kuvlesky, 2005; Fuhlendorf et al., 2006; Hovick et al., 2015). Before European settlement, this variation occurred at a range of scales maintained by fire, a vast network of prairie dogs, and bison herbivory (Knopf, 1996; Askins, 1999). Specialized bird species select for frequently disturbed sites, while other specialists select for infrequently disturbed areas and more generalized species occupy sites that fall somewhere in between the extremes of this structural gradient (Fuhlendorf et al., 2006; Augustine and Baker, 2013; Hovick et al., 2015). 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 while still encouraging economic gains for private livestock managers.

Few studies have evaluated how plant and bird communities are influenced by varied prairie dog abundance in working landscapes. Consequently, there is a need to evaluate the influence of co-occurring native and domestic herbivores on grassland vegetation and wildlife if long-term conservation of grassland-dependent organisms is going to be successful. In addition, because many ranchers have a negative perception of prairie dogs, there is conservation value in understanding if a minimum level of prairie dog abundance exists that can maximize ecological diversity while maintaining cattle production (Lamb et al., 2006). To examine this, we evaluated plant and bird community

dynamics across multiple pastures grazed by cattle and representing a gradient of prairie dog abundance (i.e., 0–75%). We hypothesized that plant and bird communities will differ across the gradient of prairie dog abundance as a consequence of consistent herbivory and clipping by prairie dogs and the resulting varied grassland structure (i.e., height and density). More specifically, we predict that the constant clipping and foraging activities on prairie dog towns in conjunction with cattle herbivory will result in a plant community that is shorter in stature and dominated by forbs relative to a more grass-dominated community at off-town locations where only cattle herbivory occurs (Baker et al., 2013). In addition, we expect that the prairie dog and cattle herbivory on town and cattle herbivory off town will create structural heterogeneity that will increase overall bird community diversity by creating a vegetation structure that is used by generalist and specialist grassland bird species (Augustine and Baker, 2013). To address this hypothesis, our objectives were to 1) quantify differences in plant and bird community composition on and off prairie dog colonies across pastures grazed by cattle along an ecological gradient of prairie dog occupancy and 2) quantify grassland breeding bird densities across this same ecological gradient.

Methods

Study Area

We examined plant and bird community dynamics from 2012 to 2015 on 1 420 ha of private and tribally owned land located in Corson County, South Dakota (SD) (Fig. 1). This property is centrally located on the Standing Rock Sioux Indian Reservation and is 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 is semiarid and characterized by cold winters (−8°C mean temperature) and hot summers (20°C mean temperature). The average rainfall is 440 mm of precipitation annually with the majority occurring during the growing season (South Dakota Climate and Weather, 2015). Precipitation and temperature data were collected at the McLaughlin, South Dakota Mesonet station in 2012 and from an on-site Mesonet weather station that was constructed in 2013 for the remainder of the study (South Dakota Mesonet SDSU). During this study, annual precipitation varied across study years ranging from 373 mm in 2012 to 525 mm in 2013. Annual precipitation was 5% above the 440 mm long-term average in 2014 (461 mm) and 3% below the long-term average in 2015 (427 mm). Annual variation in precipitation existed within each growing season (April–September; Appendix A). The average temperature during the growing season was consistent across yrs at 17°C, 16°C, 14°C, and 16°C for 2012–2015, respectively. The landscape is a mixture of rangeland and agricultural fields with perennial vegetation dominated by both mid-statured and short-statured C₃ and C₄ 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). Historic photos of the study site show the presence of prairie dogs dating back to pre-1938 with more recent photos indicating fluctuations in prairie dog occupancy (Geumont et al., 2016). Prairie dog colonies are dominated by shorter C₄ grasses including buffalo grass (*Bouteloua dactyloides* [Nutt.] J.T. Columbus) and blue grama. Common forb species off town include purple coneflower (*Echinacea angustifolia* DC.), scarlet globemallow (*Sphaeralcea coccinea* [Nutt.] Rydb.), and sagewort species (*Artemisia* spp.), while fetid marigold (*Dyssodia papposa* [Vent.] Hitchc.) commonly occurs at on-town locations. Plant nomenclature and abbreviations follow the U.S. Department of Agriculture (USDA) PLANTS Database (USDA-NRCS, 2017).

Before the onset of our study, we mapped prairie dog boundaries with a global positioning system by walking the entire research area. We partitioned the study site into four experimental pastures (200 ± 7 ha) on the basis of varying levels of prairie dog occurrence to create

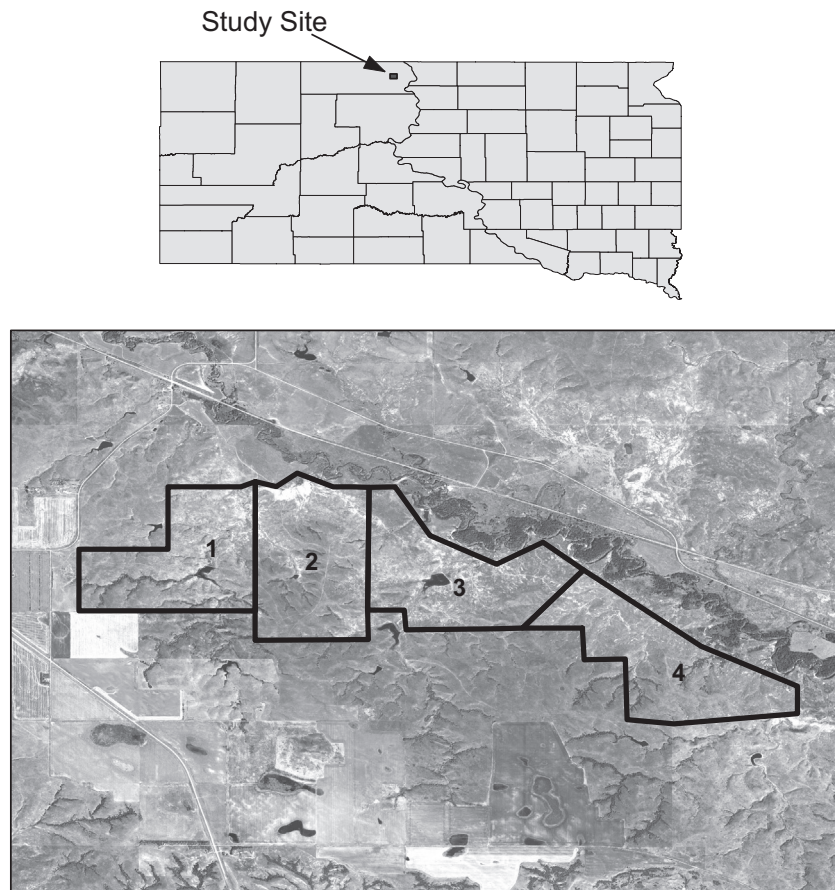


Figure 1. Map of study location and pasture layout in Corson County, South Dakota, USA used to assess the effects of black-tailed prairie dog and livestock herbivory on the plant and bird communities. Experimental pastures were stratified by the proportion of the pasture area colonized by prairie dogs with 1) 18% 2) 40% 3) transitional and 4) 0% of pasture area colonized by prairie dogs.

an ecological gradient in which prairie dog occupancy varied across sites. The proportion of each pasture occupied by prairie dogs was based on the concurrent needs of livestock research at the study site (Olson et al., 2016), and both landscape size and configuration were determined partially by the ability of the site to create the desired ecological gradient of prairie dog occupancy (i.e., roughly increments of 25%). We defined prairie dog occurrence as the percentage of each experimental pasture occupied by prairie dogs on the basis of actual observations or signs of prairie dog activity (burrows, clipping, fresh scat, etc.). Each pasture represented a different level of prairie dog occurrence across the gradient (percent pasture occupied by prairie dogs), with the four levels including 1) 0%, 2) 18%, 3) 40%, and 4) 75%.

A variety of soil series occurred at our site with most being present in all pastures (Barth, 2012; Field et al., 2016; Soil Survey Staff et al., 2018). Wayden, Dupree, Cabba, and Hurley series soils are the dominant series across pastures (Soil Survey Staff 2018). Wayden, Dupree, Cabba, and Hurley series soils are associated with shallow clayey, dense clayey, shallow loamy, and thin claypan ecological sites, respectively (Barth, 2012; Field et al., 2016; Soil Survey Staff et al., 2018). These commonalities in soils and associated plant communities across pastures were intentional because in addition to livestock requirements, soils and other plant-related research objectives were also considered during pasture design. A more thorough evaluation of the effect of prairie dogs and livestock herbivory on key soil parameters and vegetation based on ecological sites at the study location are presented elsewhere (Barth, 2012; Barth et al., 2014; Field, 2017).

We monitored prairie dog occurrence annually throughout the study by mapping town boundaries based on prairie dog activity each fall with a GPS. The pasture that originally had 75% occupancy underwent a major, unplanned reduction in prairie dogs during yr 2

when poisoning reduced occupancy within the pasture to 11%. Throughout the remainder of the study, prairie dogs recolonized the “transitional” pasture and it rebounded to 29% occupancy by 2015. Prairie dog occurrence remained within 3% of their original area within the other three experimental pastures. We stocked each pasture with Angus steers from early June to early October at a moderate stocking rate. Stocking rates were calculated on the basis of forage availability within each pasture while accounting for reductions in available forage in the areas occupied by prairie dogs: 0% equivalent to 1.0 ha • animal unit month (AUM)⁻¹, 18% equivalent to 1.3 ha • AUM⁻¹, 40% equivalent to 1.6 ha • AUM⁻¹, and transitional (originally 75% prairie dog occupancy) equivalent to 4.2 ha • AUM⁻¹.

Data Collection

We collected plant and bird data along six randomly placed, 300-m permanent transects in each pasture with three on prairie dog towns and three off, with the exception of the unoccupied pasture, where all transects were located off town. We completed vegetation surveys once per year during the peak of the growing season (June–July) by placing twenty-one 10 × 10 m plots along the length of each sampled transect on alternating sides at 15-m intervals. Within each 10 × 10 m plot, two 10-m transects were established at 2.5 m and 7.5 m. Along each transect at 0 m, 5 m, and 10 m, we recorded vegetation characteristics that 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; Lipinski, 2014), and species composition and abundance using a Daubenmire frame (Daubenmire, 1959). We estimated cover for all species, bare ground and litter. 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.

We sampled the 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 orientated plant and bird transects entirely on and off prairie dog colonies and distributed transects > 250 m apart and > 100 m from edges to help avoid edge effects and limit double counting during bird surveys. Transect orientation varied in an effort to avoid fence edges and woody cover, but also to ensure transects were entirely on or off prairie dog colonies. We conducted bird surveys beginning 1 half-h before sunrise and concluded by 0 900 h when winds were ≤ 15 km/h with no precipitation. Each transect was surveyed three or four times annually during the breeding season (May–early July) identifying all birds by sight or sound out to 100 m on either side of transect. Distances to birds were measured from transect line with range finders (Leupold RX-1000 TBR).

Data Analyses

We assessed annual variation in vegetation and bird community composition on the basis of differences in pastures and relative to position, either on or off prairie dog towns using nonmetric multi-dimensional scaling (NMS) ordination (PC-ORD version 6). We conducted the study from 2012 – 2015 and treated each year as a replicate. We used NMS because it handles non-normal data well (McCune and Grace, 2002). Both vegetation and avian community composition represented the main matrix, and the four pastures and relative location on and off prairie dog town were supplementary variables. Because we sampled birds along transects more than once per breeding season, we used the maximum abundance for each species ascertained annually for analyses. In addition, we used observed maximum abundances as others have done, rather than detection-corrected density estimates, so that we could include additional species in our community assessment that did not meet the criteria laid out for estimating density using program DISTANCE (Acevedo and Restrepo, 2008; Mabry et al., 2010). However, in doing so we recognize the potential exists for a nondetection bias toward some secretive birds given the spatially heterogeneous vegetation conditions that occur on the site. Furthermore, we chose to use NMS because one of our objectives was a joint analysis of both vegetation and bird community data and no hierarchical model analogs that account for detection in NMS exist. We omitted birds from the community analyses that were not obligate or facultative grassland birds and likely were responding more to the presence of landscape features in the area than to management or prairie dogs. For analysis, we averaged vegetation characteristics and composition across transects within respective pastures and by their location on or off town. We used the “medium” setting on autopilot running with the Euclidean distance measurement to account for taxonomic and nontaxonomic data (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 were ≥ 0.5 (McCune and Mefford, 2011). We used the multiresponse permutation procedure (MRPP) in PC-ORD to test whether plant and bird communities differed across the ecological gradient (pastures) and between on- versus off-town locations. In addition to NMS, we used the Species Indicator Analysis function to calculate an indicator value (IV) for species that show a strong affinity for either on- or off – prairie dog towns (McCune and Grace, 2002). The indicator value is based on abundance and frequency of a particular species and can range from 0 to 100 with values closer to 100 indicating strong fidelity to a site. We used a Monte Carlo test to evaluate each indicator value using an α value of 0.05.

We used program DISTANCE (version 6.2) to estimate densities while accounting for imperfect detection for all grassland obligate or facultative bird species of interest that had ≥ 60 observations over the 4 yr of the study (Buckland et al., 2001; Thomas et al., 2010). For each

of the seven grassland species that had ≥ 60 observations, we fitted a model using a combination of key functions (half-normal and hazard-rate) and series expansions (cosine and Hermite polynomial) available in the program and recommended by previous studies (Thomas et al., 2010; Harms and Dinsmore, 2012). We designated the occupancy percentages of our four pastures as the strata (0%, 18%, 40%, and transitional) and fitted these to each species. For each individual species, we examined global detection function models using a variety of key functions and poststratified by prairie dog occupancy (i.e., landscape) to get species density estimates across each treatment (Buckland et al., 2001). We did not assess observer impact or the weather’s influence on detectability because preliminary models showed no impact of these nuisance variables on detection, and we used only two observers and had strict protocols in place for weather parameters to prevent it

Table 1

Average canopy cover estimates (%) along grassland breeding bird survey transects in mixed-grass prairie with varying levels of black-tailed prairie dog occupancy and by on – and off – prairie dog towns on the Standing Rock Sioux Reservation in South Dakota, USA, 2012 – 2015.

Species	Experimental landscape 1 ¹		Experimental landscape 2		Transitional		Experimental landscape 4	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<i>Amorpha canescens</i>	1.23	0.39	4.33	1.33	0.20	0.11	0.68	0.26
<i>Artemisia dracuncululus</i>	0.71	0.23	0.38	0.14	0.14	0.07	0.40	0.15
<i>Artemisia frigida</i>	0.27	0.06	0.44	0.10	0.16	0.05	0.41	0.08
Bare ground	21.78	3.96	27.07	3.87	41.68	4.20	16.74	1.64
<i>Bouteloua curtipendula</i>	1.12	0.33	0.44	0.16	0.75	0.46	2.42	0.49
<i>Bromus inermis</i>	0.49	0.11	0.85	0.32	0.03	0.02	0.28	0.08
<i>Carex spp.</i>	2.72	0.62	2.07	0.60	0.89	0.30	1.54	0.30
<i>Conyza canadensis</i>	0.12	0.04	0.22	0.07	0.28	0.09	0.02	0.01
<i>Dyssodia papposa</i>	0.67	0.20	1.02	0.23	1.38	0.28	0.12	0.07
<i>Echinacea angustifolia</i>	0.10	0.03	0.09	0.03	0.01	0.01	0.18	0.04
<i>Hesperostipa comata</i>	1.32	0.40	1.26	0.51	0.42	0.19	0.60	0.26
Litter	26.34	3.48	22.52	2.89	16.09	2.58	29.42	3.89
<i>Nassella viridula</i>	3.00	0.81	0.56	0.18	0.39	0.28	2.17	0.59
<i>Pascopyrum smithii</i>	4.43	0.83	8.93	1.76	10.52	2.34	8.35	1.49
<i>Poa pratensis</i>	8.95	1.62	7.20	1.98	2.19	0.90	9.79	1.62
<i>Psoralea argophylla</i>	0.62	0.19	0.14	0.05	0.23	0.13	0.57	0.14
<i>Ratibida columnifera</i>	0.20	0.08	0.20	0.11	0.11	0.03	0.11	0.04
<i>Schizachyrium scoparium</i>	0.20	0.10	0.48	0.15	0.08	0.05	0.28	0.10
<i>Solidago missouriensis</i>	0.08	0.02	0.29	0.07	0.43	0.13	0.09	0.02
<i>Sphaeralcea coccinea</i>	0.16	0.04	0.25	0.05	0.50	0.09	0.25	0.06
<i>Symphoricarpos occidentalis</i>	1.74	0.54	1.06	0.38	0.20	0.13	0.79	0.21

Species	On dog town		Off dog town	
	Mean	SE	Mean	SE
<i>Amorpha canescens</i>	0.12	0.04	3.10	0.71
<i>Artemisia dracuncululus</i>	0.10	0.03	0.71	0.14
<i>Artemisia frigida</i>	0.16	0.04	0.48	0.06
Bare ground	41.72	2.28	11.91	1.24
<i>Bouteloua curtipendula</i>	0.21	0.08	2.15	0.35
<i>Bromus inermis</i>	0.09	0.04	0.74	0.16
<i>Carex spp.</i>	0.69	0.16	2.92	0.41
<i>Conyza canadensis</i>	0.25	0.06	0.07	0.02
<i>Dyssodia papposa</i>	1.53	0.17	0.07	0.03
<i>Echinacea angustifolia</i>	0.02	0.01	0.17	0.03
<i>Hesperostipa comata</i>	0.11	0.06	1.70	0.33
Litter	17.49	1.86	29.69	2.52
<i>Nassella viridula</i>	0.37	0.14	2.68	0.50
<i>Pascopyrum smithii</i>	10.29	1.39	5.83	0.93
<i>Poa pratensis</i>	1.71	0.41	12.36	1.20
<i>Psoralea argophylla</i>	0.12	0.06	0.66	0.12
<i>Ratibida columnifera</i>	0.12	0.05	0.20	0.05
<i>Schizachyrium scoparium</i>	0.03	0.02	0.48	0.10
<i>Solidago missouriensis</i>	0.37	0.08	0.07	0.02
<i>Sphaeralcea coccinea</i>	0.43	0.05	0.15	0.03
<i>Symphoricarpos occidentalis</i>	0.12	0.04	1.77	0.32

¹ 18% of the area in Experimental landscape 1 was occupied by black-tailed prairie dogs, Experimental landscape 2 was 40% occupied by black-tailed prairie dogs, Transitional landscape was accidentally poisoned in yr 1 and went from 75% occupancy to 24%, and Experimental landscape 4 was not inhabited by black-tailed prairie dogs.

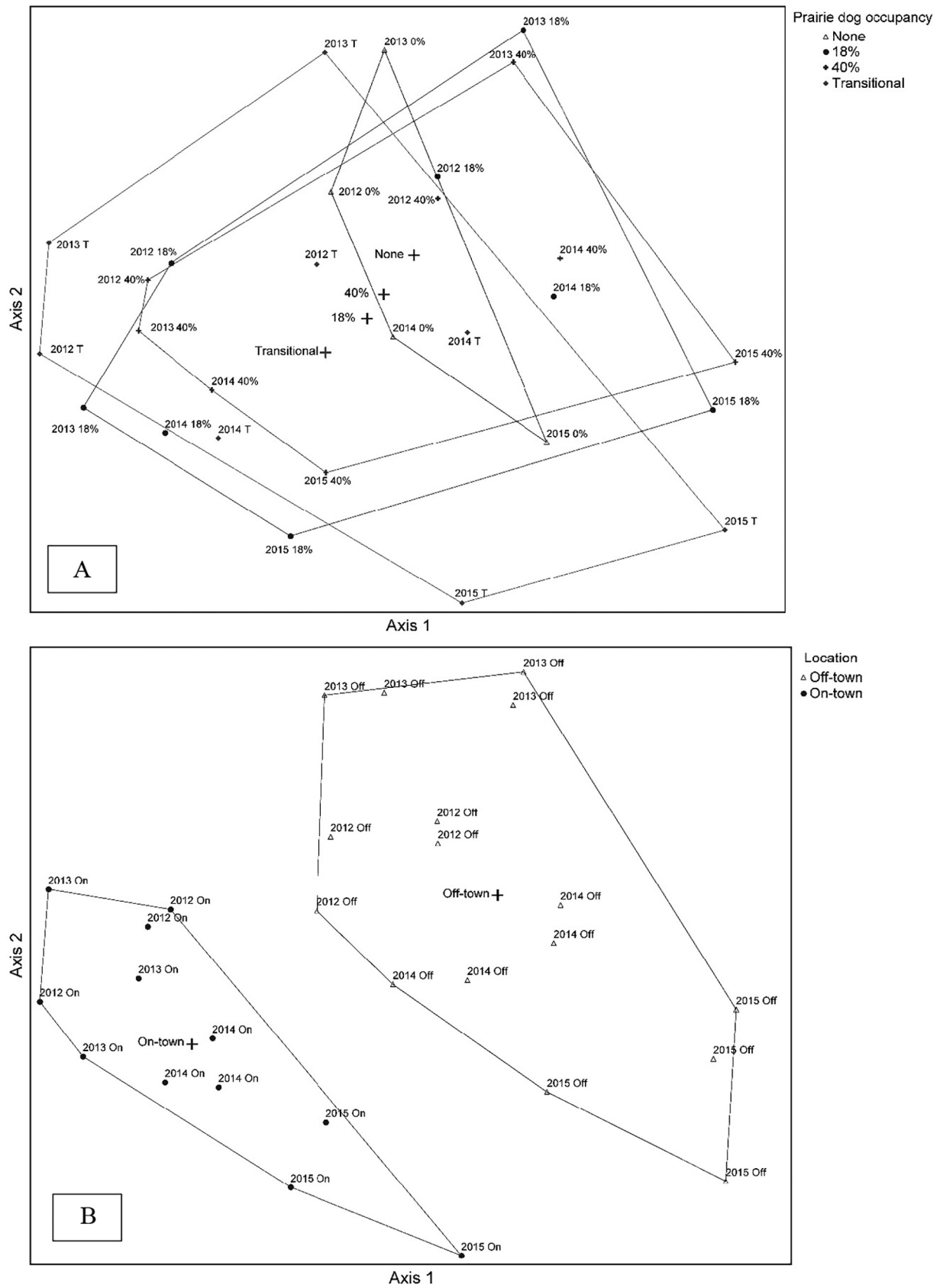


Figure 2. Nonmetric multidimensional scaling ordination examining differences in bird and plant communities on (a) experimental landscapes with 1) 18% 2) 40% 3) transitional and 4) 0% of pasture area colonized by prairie dogs and (b) on and off prairie dog colonies at the Standing Rock Reservation, ND, 2012–2015. Each shape represents a transect and background points are individual variables.

from affecting detection. We selected models for each species based on Akaike's Information Criterion (AIC) adjusted for small sample sizes (AICc) and chi-square (χ^2) goodness-of-fit test scores (Buckland et al., 2001; Burnham and Anderson 2002). The best model for each species was used to calculate species densities, standard errors, and 95% confidence interval across pastures.

Results

Community Associations

We recorded 144 plant and 21 grassland bird species (Appendices B and C). Grass and shrub cover averaged 37% (SE = 0.45) and 4% (SE = 0.20), respectively, of the canopy cover at off-town locations while grass cover averaged 18% (SE = 0.39) and shrubs 1% (SE = 0.15) of on-town canopy cover across all landscapes (Table 1). Forbs were the dominant functional group averaging 19% (SE = 0.09) of the canopy cover on town. Conversely, grass cover dominated off-town locations where forbs on average comprised only 14% (SE = 0.06) of the plant canopy cover off town.

The plant and bird communities were not strongly grouped relative to differences in the ecological gradient of prairie dog occurrence (pasture, MRPP test: $T = 0.39, P = 0.61$) but instead showed stronger grouping in ordination space according to on versus off town (MRPP test: $T = -12.39, P < 0.001, Fig. 2$). The NMS ordination produced a good fit in two dimensions (stress = 9.1) and accounted for 93% of

the variance across grazed landscapes. The primary axis accounted for 58% of the variation observed in data, characterized on — and off — prairie dog colony locations, and was negatively correlated with bare ground ($r = -0.92$) and positively correlated with measures of vegetation structure including VOR ($r = 0.76$), litter depth ($r = 0.60$), and live ($r = 0.75$) and dead ($r = 0.60$) vegetation height (see Fig. 2). Strong correlations existed between axis 1 and many native and non-native plants (Table 2). Needle-and-thread ($r = 0.87$), green-needle grass ($r = 0.61$), scarlet beeblossom (*Gara coccinea*; $r = 0.58$), and purple coneflower ($r = 0.72$) were highly, positively correlated native plants. Kentucky bluegrass ($r = 0.57$) and cheatgrass (*Bromus tectorum*; $r = 0.52$) were non-native plants strongly correlated with axis 1. Fetid marigold, a common forb on prairie dog colonies, was negatively correlated with axis 1 ($r = -0.55$).

Individual species within the bird community responded differently to the presence of prairie dogs with only grasshopper sparrow abundance (*Ammodramus savannarum*) positively correlated ($r = 0.84$) to axis 1 (off-town sites) and horned lark bird species negatively correlated ($r = -0.79$) with axis 1 (i.e., favoring on-town sites). All other grassland birds showed no strong correlation to on- versus off-town sites based on ordinations.

Axis 2 of the NMS ordination accounted for 35% of the variation in the data and was associated with annual variability in precipitation patterns (see Fig. 2 and Appendix A). Axis 2 was strongly correlated with litter cover ($r = 0.9$) and negatively correlated with maximum dead vegetation height ($r = -0.60$). Several forb species were strongly, negatively correlated with axis 2 including annual forbs like small spotted sandmat (*Chamaesyce maculate*; $r = -0.55$) and Canadian horseweed (*Conyza Canadensis*; $r = -0.56$) and perennial forbs including western dock (*Rumex aquaticus*; $r = -0.59$) and scarlet globemallow (see Table 2; $r = -0.62$). Red-winged blackbird (*Agelaius phoeniceus*; $r = -0.52$) was the only bird species exhibiting a strong negative correlation with axis 2.

The species indicator analyses found that 28% of plants and 19% of bird species showed fidelity to either on or off towns (Table 3). In total, 21

Table 2
Plant species strongly correlated ($r \geq 0.5$) with the principal and secondary nonmetric multidimensional scaling ordination axes. Axis 1 driven by on — and off — prairie dog colony and Axis 2 driven by annual variation in weather.

Species	Axis 1	Axis 2
<i>Agropyron cristatum</i>	0.55	
<i>Amorpha canescens</i>	0.75	—
<i>Andropogon gerardii</i>	0.60	
<i>Aristida purpurea</i>	0.59	
<i>Artemisia dracunculus</i>	0.56	
<i>Artemisia frigida</i>	0.64	—
<i>Artemisia ludoviciana</i>	0.70	
<i>Asclepia speciose</i>	—	-0.53
<i>Bouteloua curtipendula</i>	0.61	—
<i>Bromus inermis</i>	0.70	—
<i>Bromus tectorum</i>	0.52	—
<i>Carex spp.</i>	0.83	—
<i>Chamaesyce maculate</i>	—	-0.55
<i>Conyza canadensis</i>	0.57	-0.56
<i>Dalea purpurea</i>	0.58	—
<i>Dyssodia papposa</i>	-0.55	—
<i>Echinacea angustifolia</i>	0.72	—
<i>Gaura coccinea</i>	0.58	—
<i>Hesperostipa comata</i>	0.87	—
<i>Hordeum pusillum</i>	—	-0.60
<i>Koeleria macrantha</i>	0.62	—
<i>Lactuca tatarica</i>	0.54	—
<i>Liatris punctate</i>	0.70	—
<i>Lygodesmia juncea</i>	0.55	—
<i>Melilotus officinalis</i>	0.51	—
<i>Nassella viridula</i>	0.61	—
<i>Oxalis stricta</i>	—	-0.62
<i>Poa pratensis</i>	0.57	—
<i>Prunus americana</i>	0.53	—
<i>Psoralea esculenta</i>	0.59	—
<i>Ratibida columnifera</i>	0.61	-0.51
<i>Rosa arkansana</i>	0.59	—
<i>Schedonnardus paniculatus</i>	—	-0.61
<i>Solanum triflorum</i>	—	-0.53
<i>Solidago missouriensis</i>	—	-0.51
<i>Sphaeralcea coccinea</i>	—	-0.62
<i>Schizachyrium scoparium</i>	0.61	—
<i>Symphoricarpos occidentalis</i>	0.65	—
<i>Tragopogon dubius</i>	0.5	—
<i>Verbena bracteata</i>	—	-0.50

Table 3
Plant and bird species revealed to have strong association with either on — or off — prairie dog towns ($P \leq 0.05$) during indicator analysis. Indicator values are provided in parentheses and range from 0 to 100 with greater values suggesting increased fidelity.

On town	Off town
Plant species	
<i>Amaranthus alba</i> (49)	<i>Amorpha canescens</i> (80)
<i>Asclepias pumila</i> (69)	<i>Antennaria neglecta</i> (44)
<i>Bouteloua dactyloides</i> (53)	<i>Aristida purpurea</i> (66)
<i>Carduus nutans</i> (33)	<i>Artemisia canescens</i> (74)
<i>Chamaesyce maculate</i> (65)	<i>Artemisia dracunculus</i> (66)
<i>Cirsium arvense</i> (69)	<i>Artemisia frigida</i> (73)
<i>Conyza ramosissima</i> (49)	<i>Bouteloua curtipendula</i> (75)
<i>Dalea candida</i> (62)	<i>Bromus inermis</i> (76)
<i>Dyssodia papposa</i> (92)	<i>Carex sp.</i> (72)
<i>Hedeoma hispida</i> (44)	<i>Dalea purpurea</i> (70)
<i>Hordeum jubatum</i> (79)	<i>Echinacea angustifolia</i> (82)
<i>Plantago patagonica</i> (91)	<i>Helianthus pauciflorus</i> (44)
<i>Rumex aquaticus</i> (56)	<i>Hesperostipa comate</i> (83)
<i>Schedonnardus paniculatus</i> (85)	<i>Koeleria macrantha</i> (71)
<i>Solanum rostratum</i> (42)	<i>Liatris punctata</i> (73)
<i>Solanum triflorum</i> (58)	<i>Nassella viridula</i> (71)
<i>Solidago missouriensis</i> (68)	<i>Opuntia fragilis</i> (44)
<i>Sphaeralcea coccinea</i> (65)	<i>Poa pratensis</i> (64)
<i>Urtica dioica</i> (40)	<i>Psoralea argophylla</i> (74)
<i>Verbena bracteata</i> (50)	<i>Schizachyrium scoparium</i> (89)
	<i>Symphoricarpos occidentalis</i> (71)
Bird species	
<i>Eremophila alpestris</i> (94)	<i>Ammodramus savannarum</i> (91)
<i>Charadrius vociferous</i> (58)	
<i>Chondestes grammacus</i> (70)	
<i>Zenaida macroura</i> (69)	
<i>Agelaius phoeniceus</i> (67)	
<i>Barrtramia longicauda</i> (67)	

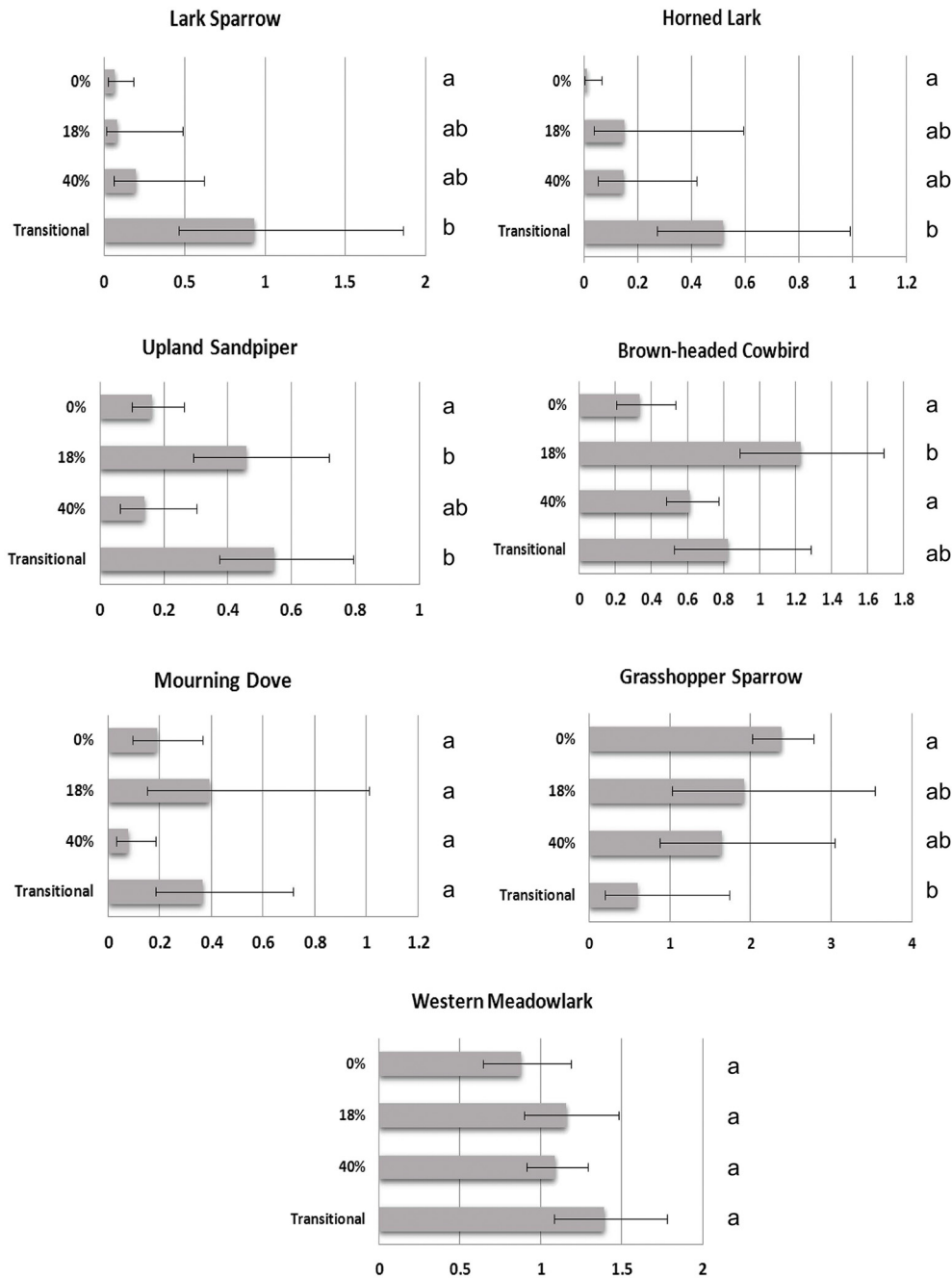


Figure 3. Density estimates for grassland bird species across a range of experimental landscape colonized by prairie dogs. The y-axis represents each experimental landscape and the x-axis is equal to the density of birds per hectare (error bars, 95% CI; letters indicate differences in bird density among landscapes at the 95% confidence level) at the Standing Rock Reservation, ND, 2012–2015. Individual densities varied greatly across experimental landscapes with many species reaching their highest density in the landscape that originally had the greatest prairie dog occupancy but was accidentally poisoned and allowed to recolonize (transitional). Variable responses in species densities across landscapes illuminates the need for variation in disturbance across space and time for maximum diversity.

plant species showed fidelity to off-town locations and 20 plant species expressed strong site association toward on-town locations. The grasshopper sparrow showed fidelity to off-town locations ($IV = 91$), while six other bird species showed affinity for prairie dog towns (see Table 3).

Bird Density

The half-normal key and standard cosine expansion model performed the best for all species. Western meadowlark was the most frequently detected species and had similar densities across all four experimental pastures ranging from 0.8 birds·ha⁻¹ in the unoccupied landscape to 1.3 birds·ha⁻¹ in the transitional pasture (Fig. 3; 95% confidence intervals overlapped). Similarly, we found that mourning

dove densities did not differ across experimental pastures (see Fig. 3). Brown-headed cowbird (*Molothrus ater*) was the third most observed species (691 detections) and had an average density of 0.75 (SE = 0.19) birds·ha⁻¹, but it also showed no clear pattern across the ecological gradient of prairie dog occurrence (see Fig. 3). Horned lark and lark sparrow (*Chondestes grammacus*) reached their greatest densities in the transitional pasture (0.5 and 0.9 birds·ha⁻¹, respectively) and had relatively low densities in the unoccupied pasture (0.05 and 0.1, respectively). Conversely, grasshopper sparrow densities decreased as prairie dog occupancy increased (range = 0.6–2.4 birds·ha⁻¹) and they had densities four times greater in the pasture void of prairie dogs when compared with the transitional pasture (see Fig. 3). Finally, upland sandpipers had the greatest densities in the transitional pasture (0.55

birds·ha⁻¹) and the lowest density in the pasture 40% occupied by prairie dogs (0.15 birds·ha⁻¹).

Discussion

We found that the presence of prairie dogs in pastures grazed by cattle is more influential on plant and bird communities than the specific level of prairie dog occupancy. Despite the common negative perception of prairie dogs in working rangeland landscapes (O'Meilia et al., 1982; Lybecker et al., 2002; Delibes-Mateos et al., 2011), they can provide multiple benefits including improved digestibility and protein concentrations of forage for cattle (Detling, 2006) and vegetation structural attributes necessary for specialized wildlife as our results indicate. In our study, areas used by cattle and void of prairie dogs generally had little bare ground, greater litter accumulation, and relatively tall vegetation, which contrasted vegetation characteristics located on prairie dog colonies. The resulting structural variation allowed for a diverse bird community at broad scales. As a result, management and conservation that focus on prairie dog colonies in landscapes managed with domestic cattle stocked at moderate rates may simultaneously promote conservation of pattern and process that is critical for biodiversity while maintaining private cattle production if consideration are made for spatial and temporal scales (Knopf, 1996; Fuhlendorf et al., 2012).

Prairie dog colonies are critical to grassland species assemblages and community structure, creating ecological interactions important in working landscapes throughout much of the Great Plains (Agnew et al., 1986; Archer et al., 1987; Smith and Lomolino, 2004). Community analysis showed a lack of contrast in vegetation and bird communities across all pastures but did reveal a definitive contrast in vegetation and bird communities between on- and off-town locations. Similarly, prairie dog and domestic herbivory in the shortgrass prairie of the Oklahoma panhandle increased landscape heterogeneity, manipulated plant communities, and provided habitat for a diverse avian community (Barko et al., 1999). In line with our predictions, we found that prairie dogs altered vegetation dynamics through greater forb abundance primarily driven by fetid marigold on colony and consistently greater graminoid abundance off colony. These findings are consistent with other research assessing vegetation composition on mixed-grass prairie and the effects ungulates and prairie dogs have on vegetation communities (Fahnestock et al., 2003). In addition, we observed that Kentucky bluegrass, an invasive species expanding throughout northern Great Plains (Toledo et al., 2014), was nearly absent from areas grazed by prairie dogs but relatively abundant in off-town areas. Despite this not being a major focus of our research, it demonstrates the importance of natural disturbances in rangelands for maintaining resistance of native plant communities to invasion.

Prairie dog activities can create an extreme disturbance that can shape a plant community through tolerance to repeated defoliation and alterations to soil properties (Barth, 2012). Indicator analyses revealed fetid marigold and woolly plantain are most tolerant of prairie dog clipping and were commonly associated with on-town sites while leadplant (*Amorpha canescens*) and other shrublike plants were not. The indicator analyses support previous studies that have demonstrated the contribution to diversity provided by maintaining disturbances associated with prairie dogs on the landscape, as many species demonstrated site affinity to on-town locations (Agnew et al., 1986). Similarly, a multitude of birds showed various levels of site fidelity to on-town sites, further implicating prairie dogs as an important mechanism to improve grassland bird diversity in the region.

The addition of prairie dogs to grazed landscapes creates structural heterogeneity that increased grassland bird diversity. We found horned larks and lark sparrows on pastures consisting of short vegetation with ample bare ground typically occupied by prairie dogs. Conversely, species such as mourning doves, western meadowlarks, upland sandpipers, and cowbirds showed minimal association with a specific landscape location but instead used areas on and off prairie dog colonies. Presumably, these species use the entire suite of vegetation that occurs

on and off colony for nesting, foraging, and loafing (Knopf, 1996; Fuhlendorf et al., 2006; Augustine and Baker, 2013). Furthermore, species such as upland sandpipers benefit from grassland heterogeneity as they use less disturbed sites for nesting but forage in heavily disturbed areas (Sandercock et al., 2015). In general, we found that most species abundances were the greatest in the transitional pasture, which originally had high prairie dog occupancy but was then accidentally poisoned and allowed to recolonize in the final 2 yr of the study. This suggests that both spatial and temporal variation in vegetation structure resulting from prairie dogs can influence native birds and provides interesting implications for prairie dog colonies that are poisoned or die from plague and are later recolonized.

Population densities for the seven 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 habitat use (Agnew et al., 1986). The western meadowlark had the greatest density of the seven most detected species, but we found no significant difference in densities across the pastures. Numerous studies report western meadowlarks are commonly 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). In addition, our results show that grasshopper sparrows require greater vegetation structure and were often found on transects farther away from areas occupied by prairie dogs. Although lower in numbers, grasshopper sparrows were detected on prairie dog colonies, possibly using these areas for foraging. Results from population studies show that upland sandpipers and grasshopper sparrows require tracts of undisturbed grassland where vegetation structure was greater (Weins, 1969; Herkert, 1998; Dechant et al., 2003).

Implications

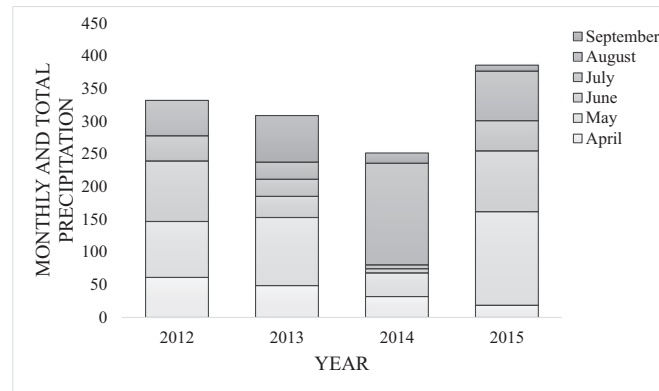
Our findings provide strong support that native fossorial herbivores and domestic cattle can create dynamic vegetation communities that benefit grassland-dependent organisms. Although our study does not provide a single level of prairie dog occupancy that benefits all species, it is clear that the presence of prairie dogs on the landscape increases both plant and avian diversity at broader scales. This research adds to a growing body of literature that demonstrates the value of promoting heterogeneity for rangeland landscapes (Fuhlendorf et al., 2012; Hovick et al., 2015). Moreover, this research demonstrates how prairie dog colonies can provide a unique disturbance that is necessary to western landscapes, yet they continue to disappear when not properly protected (Hoogland, 1996; Augustine and Baker, 2013). Conservation of prairie dogs should look past the single species and instead focus on conserving many communities of plants and animals that are dependent on the natural disturbance they provide.

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Appendix A. Monthly and total growing season precipitation for McLaughlin, 2012, and Mahto, 2013–2015, South Dakota.



Appendix B. Alphabetical list of plant species detected during the investigation of domestic cattle (*Bos taurus*) and native black-tailed prairie dog (*Cynomys ludovicianus*) influence on native plant and bird communities at the Standing Rock Reservation, South Dakota, 2012–2015.

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

Appendix C. Four-letter alpha codes and common names of 36 bird species and their detection totals from bird surveys in pastures grazed by prairie dogs and cattle on the Standing Rock Sioux Reservation, South Dakota, 2012 – 2015.

4-letter code	Common name	Total observations	4-letter code	Common name	Total observations
AMGO	American goldfinch	75	GRCA	Gray catbird	34
BAEA	Bald eagle	3	GRSP	Grasshopper sparrow ^{1,2}	932
BANS	Bank swallow	10	HOLA	Horned lark ^{1,2}	196
BARS	Barn swallow	77	KILL	Killdeer ^{1,2}	39
BBMA	Black-billed magpie	50	LASP	Lark sparrow ^{1,2}	164
BHCO	Brown-headed cowbird ^{1,2}	691	MODO	Mourning dove ^{1,2}	206
BLGR	Blue grosbeak	26	NOFL	Northern flicker	37
BOBO	Bobolink ¹	40	RHWO	Red-headed woodpecker	9
BRBL	Brewer's blackbird	33	RNEP	Ring-necked pheasant ¹	20
BRTH	Brown thrasher	88	RWBL	Red-winged blackbird ^{1,2}	161
CHSP	Chipping sparrow	9	SPTO	Spotted towhee	65
CCSP	Clay-colored sparrow ¹	20	STGR	Sharp-tailed grouse ¹	20
CLSW	Cliff swallow	74	TUVU	Turkey vulture	11
COGR	Common grackle	16	UPSA	Upland sandpiper ^{1,2}	280
DICK	Dickcissel ¹	24	VESP	Vespers sparrow ¹	16
EAKI	Eastern kingbird ^{1,2}	153	WEKI	Western kingbird ¹	24
FISP	Field sparrow ¹	14	WEME	Western meadowlark ^{1,2}	995
GOEA	Golden eagle	5	YEWA	Yellow warbler	94

¹ Indicates inclusion in community analysis.

² Indicates density estimates were calculated.

References

- Acevedo, M.A., Restrepo, C., 2008. Land-cover and land-use change and its contribution to the large-scale organization of Puerto Rico's bird assemblages. *Diversity and Distributions* 14, 114–122.
- Agnew, W., Uresk, D.W., Hansen, R.M., 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. *Journal of Range Management* 39, 135–139.
- Allred, B.W., Fuhlendorf, S.D., Hovick, T.J., Elmore, R.D., Engle, D.M., Joern, A., 2013. Conservation implications of native and introduced ungulates in a changing climate. *Global Change Biology* 19, 1875–1883.
- Anderson, R.C., 2006. Evolution and origin of the central grassland of North America: climate, fire, and mammalian grazers. *Journal of the Torrey Botanical Society* 133, 626–647.
- Archer, S., Garrett, M.G., Detling, J.K., 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. *Vegetatio* 72, 159–166.
- Askins, R.A., 1999. History of grassland birds in eastern North America. *Studies in Avian Biology* 19, 60–71.
- Askins, R.A., 2000. Restoring North America's birds: lessons from landscape ecology. Yale University Press, New Haven, CT, USA, 349pp.
- Augustine, D.J., Baker, B.W., 2013. Associations of grassland bird communities with black-tailed prairie dogs in the North American Great Plains. *Conservation Biology* 27, 324–334.
- Baker, B.W., Augustine, D.J., Sedgwick, J.A., Lubow, B.C., 2013. Ecosystem engineering varies spatially: a test of the vegetation modification paradigm for prairie dogs. *Ecography* 36, 230–239.
- Barko, V.A., Shaw, J.H., Leslie Jr., M., 1999. Birds associated with black-tailed prairie dog colonies in southern short grass prairie. *Southwest Nature* 44, 484–489.
- Barth, C.J., 2012. Prairie dog (*Cynomys ludovicianus*) contributions to soil change on grazed mixed-grass prairie [doctoral dissertation]. North Dakota State University, Fargo, ND, 100pp.
- Barth, C.J., Liebig, M.A., Hendrickson, J.R., Sedivec, K.K., Halvorson, G., 2014. Soil change induced by prairie dogs across three ecological sites. *Soil Science Society of America Journal* 48, 2054–2060.
- Bibby, C.J., Burgess, N.D., Hill, D.A., Mustoe, S., 2000. Bird census techniques. 2nd ed. Academic Press, Cambridge, MA, USA.
- Brennan, L.A., Kuvlesky Jr., W.P., 2005. North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* 69, 1–13.
- Briggs, J.M., Hoch, G.A., Johnson, L.C., 2002. Assessing the rate, mechanism, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* 5, 578–586.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press Inc., New York, NY, USA 432 pp.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, NY, USA 515pp.
- Daubenmire, R., 1959. A canopy-coverage method of vegetation analysis. *Northwest Science* 33, 43–64.
- Davidson, A.D., Detling, J.K., Brown, J.H., 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment* 9, 477–486.
- Dechant, J.A., Dinkins, M.F., Johnson, D.H., Igl, L.D., Goldade, C.M., Parkin, B.D., Euliss, B.R., 2003. Effects of management practices on grassland birds: upland sandpiper. Northern Prairie Wildlife Research Center, Jamestown, ND, USA, 38pp.
- Delibes-Mateos, M., Smith, A.T., Slobodchikoff, C.N., Swenson, J.E., 2011. The paradox of keystone species persecuted as pests: a call for the conservation of abundant small mammals in their native range. *Biology Conservation* 144, 1335–1346.
- Derner, J., Detling, J., Antolin, M., 2006. Are livestock weight gains affected by black-tailed prairie dogs? *Frontiers in Ecology and the Environment* 4, 459–464.
- Detling, J.K., 2006. Do prairie dogs compete with livestock? In: Hoogland, J.L. (Ed.), Conservation of the black-tailed prairie dog. Island Press, Washington, DC, USA, pp. 65–88.
- Fahnestock, J.T., Larson, D.L., Plumb, G.E., Detling, J.K., 2003. Effects of ungulates and prairie dogs on seed banks and vegetation in a North American mixed-grass prairie. *Plant Ecology* 167, 255–268.
- Field, A.L., 2017. An exploration of the effects of cattle grazing, prairie dog activity, and ecological site on plant community composition and western wheatgrass vegetative reproduction in northern mixed grass prairie [doctoral dissertation]. North Dakota State University, Fargo, ND, USA, 120pp.
- Field, A., Sedivec, K., Hendrickson, J., Johnson, P., Geumont, B., Xu, L., Gates, R., Limb, R., 2016. Effects of short-term cattle exclusion on plant community composition: prairie dog and ecological site influences. *Rangelands* 38, 34–37.
- Fleischner, T.L., 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8, 629–644.
- Fuhlendorf, S.D., Engle, D.M., Elmore, R.D., Limb, R.F., Bidwell, T.G., 2012. Conservation of pattern and process: developing an alternative paradigm of rangeland management. *Rangeland Ecology & Management* 65, 579–589.
- Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C.A., Leslie Jr., D.M., 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecology Applications* 16, 1706–1716.
- Geumont, B.A., Sedivec, K.K., Mack, W., 2016. History of occurrence and present home territory sizes for black-tailed prairie dogs on the Standing Rock Sioux Reservation. *Rangelands* 38, 38–42.
- Goguen, C.B., 2012. Comparison of bird and mammal communities on black-tailed prairie dog (*Cynomys ludovicianus*) colonies and uncolonized shortgrass prairie in New Mexico. *Journal of Arid Environments* 80, 27–34.
- Harms, T.M., Dinsmore, S.J., 2012. Density and abundance of secretive marsh birds in Iowa. *Waterbirds* 35, 208–216.
- Henwood, W.D., 1998. An overview of protected areas in the temperate grasslands biome. *Parks* 8, 3–8.
- Herkert, J.R., 1998. The influence of the CRP on grasshopper sparrow population trends in the mid-continental United States. *Wildlife Society Bulletin* 26, 227–231.
- Hill, D.A., Fasham, M., Tucker, G., Shewry, M., Shaw, P., 2005. Handbook of biodiversity methods: survey, evaluation and monitoring. Cambridge University Press, Cambridge, UK, pp. 219–222.
- Hoogland, J.L., 1996. Mammalian species: *Cynomys ludovicianus*. *American Society of Mammalogists* 535, 1–10.
- Hovick, T.J., Elmore, R.D., Fuhlendorf, S.D., Engle, D.M., Hamilton, R.G., 2015. Spatial heterogeneity increases diversity and stability in grassland bird communities. *Ecological Applications* 25, 662–672.
- Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C., Towne, E.G., 1999. The keystone role of bison in North American tallgrass prairie bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience* 49, 39–50.
- Knopf, F.L., 1996. Preserving North America's most endangered ecosystem. *Prairie Conservation* 10, 135–148.
- Knowles, C.J., Proctor, J.D., Forrest, S.C., 2002. Black-tailed prairie dog abundance and distribution in the Great Plains based on historic and contemporary information. *Great Plains Research* 12, 219–254.

- Kotliar, N.B., 2000. Application of the new keystone-species concept to prairie dogs: how well does it work? *Conservation Biology* 14, 1715–1721.
- Lamb, B.L., Reading, R.P., Andelt, W.F., 2006. Attitudes and perceptions about prairie dogs. In: Hoogland, J.L. (Ed.), *Conservation of the black-tailed prairie dog*. Island Press, Washington, DC, USA, pp. 108–114.
- Limb, R.F., Engle, D.M., Bidwell, T.G., Althoff, D.P., Anderson, A.B., Gipson, P.S., Howard, H.R., 2010. Restoring biopedturbation in grasslands with anthropogenic focal disturbance. *Plant Ecology* 210, 331–342.
- Lipinski, A.R., 2014. *Rangeland vegetation, black-tailed prairie dogs, and grassland birds: community dynamics and nest habitat selection on grazed mixed-grass prairie* [thesis]. North Dakota State University, Fargo, ND, USA, 109pp.
- Lybecker, D., Lamb, B.L., Ponds, P.D., 2002. Public attitudes and knowledge of the black-tailed prairie dog: a common and controversial species. *BioScience* 52, 607–613.
- Mabry, C.M., Brudvig, L.A., Atwell, R.C., 2010. The confluence of landscape context and site-level management in determining Midwestern savanna and woodland breeding bird communities. *Forest Ecology and Management* 260, 42–51.
- McCune, B., Grace, J.B., 2002. *Analysis of ecological communities*. MjM Software Design, Geneden Beach, OR, USA.
- McCune, B., Mefford, M.J., 2011. *PC-ORD. Multivariate analysis of ecological data*. Version 6. MjM Software, Geneden Beach, OR, USA.
- National Agricultural Statistics Service, 2012. *Meat animals production, disposition, and income 2011 summary*. NASS, USDA, Washington, DC, USA.
- Olson, K.C., Schauer, C.S., Engal, C., Kinchloe, J.J., Brennan, J.R., Hauptman, B.L., 2016. Effect of grazing prairie dog colonized rangeland on cattle nutrition and performance: a progress report. *Rangelands* 38, 29–33.
- O'Meilia, M.E., Knopf, F.L., Lewis, J.C., 1982. Some consequences of competition between prairie dogs and beef cattle. *Journal of Range Management* 35, 580–585.
- Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P., Starfield, A., 2005. Conserving species in a working landscape: land use with biological and economical objectives. *Ecological Applications* 15, 1387–1401.
- Proctor, J., Haskins, B., Forrest, S.C., Hoogland, J.L., 2006. Focal areas for conservation of prairie dogs and the grassland ecosystem. *Conservation of the black-tailed prairie dog: Saving North America's western grasslands* Island Press, Washington, DC, USA, pp. 232–247.
- Robel, R.J., Briggs, J.N., Dayton, A.D., Hulbert, L.C., 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23, 295–297.
- Sandercock, B.K., Alfaro-Barrios, M., Casey, A.E., Johnson, T.N., Mong, T.W., Odom, K.J., Strum, K.M., Winder, V.L., 2015. Effects of grazing and prescribed fire on resource selection and nest survival of upland sandpipers in an experimental landscape. *Landscape Ecology* 30, 325–337.
- Sharps, J.C., Uresk, D.W., 1990. Ecological review of black-tailed prairie dogs and associated species in western South Dakota. *Great Basin Naturalist* 50, 339–345.
- Smith, G.A., Lomolino, M.V., 2004. Black-tailed prairie dogs and the structure of avian communities on the shortgrass plains. *Oecologia* 138, 592–602.
- Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture, 2018. *Web Soil Survey*. Available at: <https://websoilsurvey.sc.egov.usda.gov/>, Accessed date: 18 September 2018.
- South Dakota Climate and Weather, 2015. *Mesonet at SDSTATE*. Available at: <https://climate.sdstate.edu/archive/>, Accessed date: 1 December 2015.
- Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R., Marques, T.A., Burnham, K.P., 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *The Journal of Applied Ecology* 47, 5–14.
- Toledo, D., Sanderson, M., Spaeth, K., Hendrickson, J., Printz, J., 2014. Extent of Kentucky bluegrass and its effect on native plant species diversity and ecosystem services in the northern Great Plains of the United States. *Invasive Plant Science and Management* 7, 543–552.
- United States Department of Agriculture-NRCS, 2017. *The PLANTS Database*. Available at: <http://plants.usda.gov>, Accessed date: 19 June 2017.
- Weins, J.A., 1969. *An approach to the study of ecological relationships among grassland birds*. Ornithology Monographs No.8.
- Whicker, A., Detling, J., 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38, 778–785.