South Dakota State University

Open PRAIRIE: Open Public Research Access Institutional Repository and Information Exchange

Electronic Theses and Dissertations

2019

Prairie Dogs and Livestock in Rangeland Systems: Balancing Biodiversity and Production in the Northern Mixed-Grass Prairie

Jameson Robert Brennan
South Dakota State University

Recommended Citation

Brennan, Jameson Robert, "Prairie Dogs and Livestock in Rangeland Systems: Balancing Biodiversity and Production in the Northern Mixed-Grass Prairie" (2019). *Electronic Theses and Dissertations*. 3670.
https://openprairie.sdstate.edu/etd/3670

PRAIRIE DOGS AND LIVESTOCK IN RANGELAND SYSTEMS: BALANCING BIODIVERSITY AND PRODUCTION IN THE NORTHERN MIXED-GRASS PRAIRIE

BY

JAMESON R. BRENNAN

A dissertation submitted in partial fulfillment of the requirement for the
Doctor of Philosophy
Major in Biological Sciences
South Dakota State University
2019

DISSERTATION ACCEPTANCE PAGE

Jameson Brennan

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Patricia S. Johnson
Advisor Date

Michele R. Dudash
Department Head Date

Dean, Graduate School Date

ACKNOWLEDGEMENTS

This project was supported by the South Dakota Agricultural Experiment Station and through funding provided by USDA AFRI NIFA (Grant Number 2011-68004-30052), through a grant awarded to North Dakota State University, with a sub-award to South Dakota State University. I would like to thank my wife, Prairey Walkling, for her patience and understanding in moving to an RV on the project site for two summers while pregnant or with an infant. I would like to thank all the field technicians that collected data and endured chigger bites on this project: Shauna Kopren, Joyce Basset, Kaitlyn Myers, Andrea Collins, Megan Jamison, and Tevan Jamison. I would also like to thank Janna Kincheloe for her efforts in collecting and storing rumen samples, Chris Schauer for providing livestock and labor for this project, and Wyatt Mack for his support managing the project site and spontaneously rounding up wayward cattle.

Lastly I would like to thank my committee members. I would like to thank Dr. Niall Hanan for his quick responses, thoughtful comments, and his outside perspective on the project. I would like to thank Dr. Lan Xu for her infectious passion about all things plants and ecology; she is truly one of the most dedicated educators I have had the pleasure of knowing. I would like to thank Dr. Kenneth Olson for his availability in listening to my wild ideas and answering my countless questions on all things livestock related. When I started in this position, I wasn’t entirely sure of the differences between a steer, a heifer, and a cow. You continually expected higher of me and pushed me to expand my knowledge and abilities, and for that I am grateful. Lastly, I would like to thank my major adviser Dr. Patricia Johnson. Your unwavering support and guidance

have allowed me to grow in confidence as a researcher and an individual over the past 5 years, and for that I will be eternally grateful. Without your belief in me, this dissertation would not be possible.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

PRAIRIE DOGS AND LIVESTOCK IN RANGELAND SYSTEMS: BALANCING BIODIVERSITY AND PRODUCTION IN THE NORTHERN MIXED-GRASS PRAIRIE

JAMESON BRENNAN

2019

A major constraint of beef production within the Standing Rock Reservation has been identified as a reduction in rangeland quality due in large part to wide-scale colonization by black-tailed prairie dogs (*Cynomys ludovicianus*). The desire exists within the community to design a holistic framework which incorporates livestock management with the goal of increasing production and rangeland health while still maintaining increased diversity associated with prairie dogs. Prairie dogs reduce the carrying capacity of cattle on rangelands by up to 50% on occupied hectares through direct consumption of vegetation and waste due to clipping to improve detection of predators. Livestock stocking rates that do not account for the level of prairie dog occupation can result in a reduction in animal performance and a further decrease in rangeland productivity due to overgrazing. Research is needed to understand season-long use of grazing cattle on and off prairie dog towns to better inform land manager decisions aimed at reducing over-utilization of grasslands and allowing higher production of livestock.

This dissertation study was part of a larger study that was conducted in northcentral South Dakota from 2012 to 2016. This dissertation sub-study was designed

to evaluate the impact of prairie dogs and cattle on plant community production and composition, and to determine impacts of colonization on livestock grazing behavior, diet quality, and forage intake. Three pastures with varying levels of prairie dog occupation (0%, 20%, and 40%) were studied. Pasture stocking rates were adjusted to account for the level of forage removed by prairie dogs (50%) on active colonies. Two study treatments were evaluated: Ecological Site (n=3) and grazing treatment (n=4). Ecological sites (ES) were Shallow Loam, Loamy, and Thin Claypan. Grazing treatments included two in off-town locations (non-graze (NG) and cattle only graze (CG)) and two in on-town locations (cattle and prairie dog graze (CPD), and prairie dog only graze (PD)). These treatments and their interactions were evaluated to determine their effects on vegetation (e.g. standing crop, diversity, species richness, etc.) and livestock (e.g. animal weight gains, diet quality and quantity, etc.) parameters.

Goals of the dissertation herein are to understand 1) the interactions of prairie dogs and livestock on plant communities and 2) the impact of prairie dog occupation on livestock production. Objectives of this dissertation are: 1) Evaluate plant community response to grazing on and off prairie dog towns to determine how livestock and prairie dogs alter plant community production and composition; 2) Develop strategies that enable identification of plant communities of interest on and off prairie dog towns using remote sensing techniques ; 3) Develop methods to utilize programming tools for efficient processing of GPS collar data ; 4) Evaluate relationships between plant communities and cattle grazing locations to identify patterns and trends in livestock grazing behavior throughout the growing season; 5) Evaluate diet nutrient composition and intake by cattle on plant communities on- and off-town over the grazing season; 6)

Develop a framework of cattle nutrient consumption in pastures with varying levels of prairie dog occupation; and 7) Synthesize existing research and results from this dissertation to explore potential synergism between prairie dogs and cattle on the landscape from a systems approach.

Vegetation analyses show a significant difference in standing crop biomass between grazing treatments, with sites grazed only by cattle having 36% more biomass than those grazed only by prairie dogs. Plant community data suggest that prairie dogs have a greater impact on production and species composition compared to cattle; percent composition of C3 grasses was greatest off-town, whereas percent composition of C4 grasses was greatest on-town. An invasive C3 species of concern in the Northern Great Plains, Kentucky bluegrass, was almost non-existent on-town, but increased substantially off-town over the 5 years of the study for all ES; the most dramatic increase occurred on the Thin Claypan ES. Species diversity was not different between grazing treatments, however species richness was generally greatest on-town. Additionally, for the entire duration of the study (2012-2016), 46 species were only observed on-town and 17 only observed off-town out of a total 113 species observed throughout the 5 years of the study.

The remote sensing analyses show that Random Forest (RF) models were highly effective at predicting different vegetation types associated with on and off prairie dog town locations (misclassification rates < 5% for each plant community). However, comparisons between the predicted plant community map using separate years indicate 6.7% of pixels on-town and 24.3% of pixels off-town changed class membership depending on the year. The results show that while RF models may predict with a high

degree of accuracy, transition zones between plant communities and inter-annual differences in rainfall may cause instability in fitted models.

An essential component of evaluating livestock behavior for this study was accomplished using GPG collars that record both location and activity. Traditional methods of hand-processing of GPS data require a large number of steps which are both time consuming and prone to errors. As part of this dissertation, methods were created to streamline the processing of livestock GPS collar data, resulting in a technical note publication. Due to the open source nature of Program R, custom functions can be created to merge GPS collar data, GIS data layers, and behavior algorithms to improve data processing efficiency.

Plant communities of interest for the livestock behavior and intake components of this study were identified as grass-dominated on-town sites (PDG), forb-dominated on-town sites (PDF), and grass dominated off-town sites (NPD). Livestock behavior analyses from this study show cattle slightly prefer grazing on prairie dog towns, with shifts occurring to off-town locations over the duration of the grazing season. Crude protein (CP) content from diet samples for PDF sites were significantly greater than for PDG and NPD sites. Little difference in many of the diet metrics existed, however, between grass dominated sites (PDG and NPD). Despite higher CP content on forb dominated sites on-town (PDF), intake levels were depressed on these communities due to high bare ground and low vegetation production. Individual livestock performance (average daily gains) averaged over the entire length of the study, were 0.74 kg. /day for the 0% occupied pasture, 0.86 kg. /day for the 20% occupied pasture, and 0.85 kg. /day for the 40% occupied pasture. Reduced stocking rate in prairie dog pastures may have contributed to greater individual animal performance. Higher livestock performance for the prairie dog pastures is potentially due to access to a more diverse diet. Reduced stocking rates in prairie dog pastures, however, resulted in a reduction in overall livestock production in terms of kg / ha. At low levels of colonization in pastures, livestock may potentially benefit from increased diet selection, however, reduction in plant biomass on town may negate any potential gains at higher levels of colonization.

The results from this study were combined to take a systems approach to understanding the impacts and interactions of prairie dogs and livestock on plant communities, and the impacts of prairie dog occupation on livestock production in northern mixed-grass prairie ecosystems. Our results indicate that having both on-town and off-town plant communities within a pasture can increase biodiversity and heterogeneity at broader landscape scales. Differences in plant community composition may increase diet diversity for grazing livestock, potentially benefitting individual animal gains, provided forage quantity is not limited. At low levels of colonization, livestock production may only be minimally impacted while still realizing benefits to biodiversity.

Introduction

The Standing Rock Reservation in north-central South Dakota has been identified as a food desert, meaning access to fresh nutritious food is often limited or difficult. This may seem contradictory in an area where the primary economic engine is agriculture, however, the majority of food produced on the reservation, specifically beef cattle fed on native rangelands, is exported away from the community to be finished and slaughtered only to return in limited availability at a premium price. Essential to the sustainability of this community is increased production of local beef which in turn can be made available to local communities on the reservation. A major constraint of beef production within the Standing Rock Reservation has been identified as a reduction in rangeland quality due in large part to wide-scale colonization of black tailed prairie dogs (*Cynomys ludovicianus*). Corson County, SD, which lies entirely within the Standing Rock Reservation, had an estimated 10,608 ha (26,213 acres) of prairie dog colonies, and of that 6,065 ha (14,989 acres) were on tribal land (Cooper and Gabriel 2005). Reduction in rangeland productivity due to prairie dog occupation is complicated by the fact that there is a desire within the Native American community to maintain prairie dogs on the land. Although seen as a nuisance by many ranchers, prairie dogs hold an ecological and cultural value for Native Americans, and are still considered a medicinal source for many native people (Hendrickson et al. 2016). The desire exists to design a holistic framework which incorporates livestock management with the goal of increasing production and rangeland health while still maintaining the increased diversity associated with prairie dogs.

Black-tailed prairie dogs are a controversial species in rangeland management. Prairie dogs have been identified as a keystone species and ecosystem engineers providing habitat to a number of other plant and wildlife species (Davidson et al. 2010, Kotliar et al. 1999). They are known to increase biotic diversity and community structure while playing an important role in ecosystem function (Hopson et al. 2015). In semi-arid grasslands of the southwest, prairie dogs were shown to increase essential ecosystem services of water infiltration rates, carbon storage rates, and soil stabilization (Martinez-Estevez et al. 2013). Despite the potential benefits of increased biodiversity and ecosystem services, prairie dog colonies are often seen as a detriment to beef production systems by limiting carrying capacity of rangelands.

Throughout most of the 20th century, prairie dog colonies were subject to control measures to reduce their numbers and eliminate purported competition with cattle for grazing resources (Sierra-Corona et al. 2015). Estimates of prairie dog town extent prior to European arrival vary widely from 40 million ha to 100 million ha, however there is little evidence to support these numbers (Vermeire et al. 2004). Although disagreements occur on extent of rangeland occupation, control efforts have no doubt limited their expanse over the past century, as wide-spread eradication efforts have sought to reduce occupation to increase rangeland productivity for cattle (Weltzin et al. 1997). Competition between prairie dogs and livestock is a major concern for land managers looking to optimize beef production while still conserving wildlife species (Augustine and Springer 2013).

Cattle and prairie dogs exhibit up to a 60% dietary overlap in a mixed-grass prairie, which is a cause of concern for livestock producers (Miller et al. 2007). Prairie dogs can limit forage quantity available to grazing livestock directly through consuming or clipping vegetation, or indirectly by shifting plant communities to a lower seral state through repeated and persistent defoliation. A study conducted by Gabrielson (2009) on a mixed-grass prairie in South Dakota, found that prairie dogs removed over four times more biomass on-town than cattle on-town. Stoltenberg (2004) attributed up to 90% of forage disappearance due to prairie dogs as the result of non-consumptive activities such as clipping. As colonies age, older core areas of prairie dog towns are often characterized by high percentage bare ground, low vegetation production, and dominance by annual forb and dwarf shrub species; areas more recently colonized typically remain grass dominated (Guenther and Detling 2003, Coppock et al., 1983). Plant communities on-town shift from mid-grass to shortgrass species dominance (Agnew et al. 1986; Koford 1958), probably attributable to the high grazing resistance of blue grama (*Bouteloua gracilis* Willd. Ex Kunth) and buffalograss (*Bouteloua dactyloides* Nutt.) (Derner et al. 2006). The replacement of mid-grasses with grazing tolerant shortgrasses, and increases in bare ground has the potential to significantly reduce forage quantity available to grazing livestock.

Numerous studies have shown prairie dogs significantly reduce herbaceous biomass compared with off-colony sites, with some estimates as high as a 60% decrease in standing crop biomass on-town (Augustine and Springer 2013; Gabrielson 2009; Johnson-Nistler et al. 2004; Stoltenberg 2004); however, it has been argued that this decrease in forage quantity can somewhat be offset by an increase in forage quality that has been observed on-town (Augustine and Springer 2013; Connell et al. 2019; Coppock et al. 1983). Johnson-Nistler et al. (2004) measured forage quantity and quality on a northern mixed-grass prairie of Montana, and found that plants on sites occupied by prairie dog towns were characterized by an increase in percentage crude protein, however they also showed a decrease in standing crop biomass and total standing crop crude protein when compared to off-town sites. Vermeire et al. (2004) noted that for livestock grazing prairie dog colonies, realizing the benefits of increased forage quality still depends on the amount of forage available, and forage quantity becomes more limited as colonies age and occupy greater portions of an area, potentially impacting livestock production.

While there are many issues and concerns associated with prairie dogs and livestock production, very little research has really focused on livestock-prairie dog interactions and management systems to accommodate both. In one of the few studies on the consequences to livestock production associated with prairie dog colonization, Derner et al. (2006) demonstrated that an increase of prairie dog towns within pastures led to a decrease in cattle weight gains; the decrease was not, however, proportional to the increase in colony size. Other studies have attempted to understand cattle grazing behavior in pastures colonized by prairie dogs by evaluating the preference of cattle for on- and off-town sites. For example, in visual roadside observations, Guenther and Detling (2003) concluded cattle selection of prairie dog sites differed little from random use; the largest percentage of pasture colonized in their study was, however, only 10.7%. Within the Chihuahua desert grasslands, researchers reported that cattle preferentially grazed on prairie dog colonies in the fall and winter grass dormancy season and spent most of their time foraging on off colony sites in the summer (Sierra-Corona et al. 2015). Specific studies on livestock grazing behavior on prairie dog towns, however, are limited and further research is needed to understand how changes in forage quantity and quality may be driving changes in grazing behavior across multiple growing seasons.

Additionally, research studies measuring livestock forage intake on- and off-town are non-existent, yet essential for understanding the value of prairie dog towns to contribute to overall livestock diets within prairie dog managed pastures.

Dissertation Objectives

Prairie dogs and cattle are often portrayed as being in direct competition for achieving conservation and production goals. Yet rangelands occupied by prairie dogs are frequently used for livestock grazing, and the two species are inextricably linked together within an agro-ecological system. In 2012 a large, multi-state, multi-institution, collaborative project (USDA NIFA AFRI CAP grant # 2011-68004-30052) was initiated with the overall goal of increasing food security for the people on the Standing Rock Sioux Reservation by improving livestock production on rangelands with extensive prairie dog occupation. While the debate over prairie dogs on rangelands has primarily been framed as on- versus off-town, and livestock versus prairie dogs, the objective of this study was understand prairie dog-cattle systems and potential impacts and interactions between them as they relate to wildlife habitat, plant communities, and agricultural production. A major component of that effort was to study livestock use of on- and off-town plant communities to determine their preferences and to evaluate the quality and quantity of forages that cattle obtain from the different plant communities on the pastures. Goals of the dissertation herein are to understand 1) the interactions of prairie dogs and livestock on plant communities and 2) the impact of prairie dog occupation on livestock production.

There are 7 objectives addressed within this dissertation, around which the dissertation is organized. Those objectives, and the chapters in which they are addressed are: 1) Evaluate plant community response to grazing on and off prairie dog towns to determine how livestock and prairie dogs alter plant community production and composition (Chapter 1); 2) Develop strategies that enable identification of plant communities of interest on and off prairie dog towns using remote sensing techniques (Chapter 2); 3) Describe methods to utilize programming tools for efficient processing of GPS collar data (Chapter 3); 4) Evaluate relationships between plant communities and cattle grazing locations to identify patterns and trends in livestock grazing behavior throughout the growing season (Chapter 4); 5) Evaluate diet nutrient composition and intake by cattle on plant communities on- and off-town over the grazing season (Chapter 4); 6) Develop a framework of cattle nutrient consumption in pastures with varying level of prairie dog occupation (Chapter 4); and 7) Synthesize existing research and results from this dissertation to explore potential synergism between prairie dogs and cattle on the landscape from a systems approach (Chapter 5). We hypothesize 1) prairie dogs will be the primary driver of changes in biomass and community composition; 2) high resolution satellite imagery converted to NDVI will give a relatively accurate and precise identification of on-town and off-town plant communities with stability in the model across years; 3) cattle will preferentially graze on prairie dog towns early in the growing season as they will be attracted to the higher quality/greener vegetation; however, grazing behavior will shift to off-town locations as the season progresses and forage becomes more limited at on-colony sites; and 4) livestock nutrient consumption will be disproportionately made up of off town locations due to the reduction in standing crop biomass on prairie dog sites.

We expect the results from this study will aid land managers in making decisions on how to better manage prairie dog occupied pastures for increased livestock production and improved rangeland health.

Literature Cited

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

Augustine, D.J., & Springer, T.L. (2013). Competition and facilitation between a native and a domestic herbivore: trade-offs between forage quantity and quality. *Ecological Applications, 23*, 850-863

Connell, L.C., Porensky, L.M., & Scasta, J.D. (2019). Prairie Dog (Cynomys ludovicianus) Influence on Forage Quantity and Quality in a Grazed Grassland-Shrubland Ecotone. *Rangeland Ecology & Management, 72*, 360-373

Cooper, J., & Gabriel, L. (2005). South Dakota Black-Tailed Prairie Dog Conservation and Management Plan. In. https://gfp.sd.gov/UserDocs/nav/prairiedog-management-plan.pdf: South Dakota Game, Fish, and Parks

Coppock, D.L., Detling, J.K., Ellis, J.E., & Dyer, M.I. (1983). Plant-herbivore interactions in a North American mixed-grass prairie. *Oecologia, 56*, 1-9

Davidson, A.D., Ponce, E., Lightfoot, D.C., Fredrickson, E.L., Brown, J.H., Cruzado, J., Brantley, S.L., Sierra-Corona, R., List, R., Toledo, D., & Ceballos, G. (2010). Rapid response of a grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock. *Ecology, 91*, 3189-3200

Derner, J.D., Detling, J.K., & Antolin, M.F. (2006). Are livestock weight gains affected by black-tailed prairie dogs? *Frontiers in Ecology and the Environment, 4*, 459-464

Gabrielson, M.L. (2009). Effects of Black-tailed Prairie Dogs (Cynomys ludovicianus) and Cattle on Vegetation Composition and Disappearance in the Mixed-Grass Prairie (M.S. Thesis). South Dakota State University

Guenther, D.A., & Detling, J.K. (2003). Observations of cattle use of prairie dog towns. *Journal of Range Management, 56*, 410-417

Hendrickson, J.R., Black Elk, L., & Faller, T. (2016). Development of the Renewal on the Standing Rock Sioux Reservation Project. *Rangelands, 38*, 1-2

Hopson, R., Meiman, P., & Shannon, G. (2015). Rangeland dynamics: investigating vegetation composition and structure of urban and exurban prairie dog habitat. *Peerj, 3*

Johnson-Nistler, C.M., Sowell, B.F., Sherwood, H.W., & Wambolt, C.L. (2004). Black-tailed prairie dog effects on Montana's mixed-grass prairie. *Journal of Range Management, 57*, 641-648

Koford, C.B. (1958). *Prairie dogs, whitefaces, and blue grama*. Wildlife Society

Kotliar, N.B., Baker, B.W., Whicker, A.D., & Plumb, G. (1999). A Critical Review of Assumptions About the Prairie Dog as a Keystone Species. *Environmental Management, 24*, 177-192

Martinez-Estevez, L., Balvanera, P., Pacheco, J., & Ceballos, G. (2013). Prairie Dog Decline Reduces the Supply of Ecosystem Services and Leads to Desertification of Semiarid Grasslands. *Plos One, 8*

Miller, B.J., Reading, R.P., Biggins, D.E., Detling, J.K., Forrest, S.C., Hoogland, J.L., Javersak, J., Miller, S.D., Proctor, J., Truett, J., & Uresk, D.W. (2007). Prairie dogs: An ecological review and current biopolitics. *Journal of Wildlife Management, 71*, 2801-2810

Sierra-Corona, R., Davidson, A., Fredrickson, E.L., Luna-Soria, H., Suzan-Azpiri, H., Ponce-Guevara, E., & Ceballos, G. (2015). Black-Tailed Prairie Dogs, Cattle, and the Conservation of North America's Arid Grasslands. *Plos One, 10*

Stoltenberg, M. (2004). Effects of prairie dogs on plant community composition and vegetation disappearance in Mixed-Grass Prairie (M.S. Thesis). South Dakota State University

Vermeire, L.T., Heitschmidt, R.K., Johnson, P., & Sowell, B. (2004). The Prairie Dog Story: Do We Have It Right?. *Bioscience, 54*, 689-695

Weltzin, J.F., Dowhower, S.L., & Heitschmidt, R.K. (1997). Prairie dog effects on plant community structure in southern mixed-grass prairie. *Southwestern Naturalist, 42*, 251-258

Chapter 1: Livestock and Prairie Dog Impact on Plant Community Production, Composition, and Dynamics

Abstract

Prairie dog occupation of rangelands is often seen as a detriment to beef production because of altered plant communities and reduced quantity of forage. Within northern mixed-grass prairie, prairie dog colonies are often converted to low growing perennial grasses intermixed with patches dominated by annual forbs. Despite the potential conflict over prairie dog colonization on livestock production, many studies have focused on plant community differences between on-colony and off-colony sites, ignoring the impact of livestock within these systems. A study was conducted in 2012-2016 near McLaughlin, South Dakota in a northern mixed-grass prairie ecosystem to determine the combined and separate impacts of cattle and prairie dogs on plant community production, composition, and dynamics across three Ecological Sites (ES; Thin Claypan, Loamy, and Shallow Loam). Twenty-five paired sample sites on- and off-colony were established and randomly assigned to be fenced to exclude livestock or remain open to livestock grazing, creating four grazing treatments: two in off-town locations (non-graze (NG) and cattle only graze (CG)) and two in on-town locations (cattle and prairie dog graze (CPD), and prairie dog only graze (PD)). Within each sample site three 0.25m^2 permanent plots were randomly located. Plots were sampled in early August of each year to estimate biomass for every species in each plot. A mixed model ANOVA was used to test for differences in standing crop biomass and percent biomass for C3 grasses, C4 grasses, and forbs between treatments and ES. For biomass, there were no significant interactions between ES and grazing treatment; results suggest plant communities follow somewhat predictable responses across ES. There was a significant difference ($P < 0.05$) in total biomass between all grazing treatments. On-town sites tended to be characterized by a reduction in C3 graminoid biomass and an increase in C4 graminoid and forb biomass compared on off-town. The PD treatment had 37% less biomass than the CG treatment, potentially due to increased level of herbivory and replacement of C3 mid-grasses with C4 shortgrasses. Plant community composition differed primarily along on-town and off-town sites. For on-town plant communities, dominant species were relatively stable through time, with re-ordering occurring only of sub-dominants. For off-town plant communities, there was less re-ordering of sub-dominants, but there was a major shift in dominant species associated with Kentucky bluegrass production. Results of this study indicate that herbivory, specifically presence or absence of prairie dogs, is a primary driver in plant community production and composition.

Introduction

Colonization by prairie dogs and subsequent increases in grazing pressure can result in a shift of plant communities to those characterized by higher cover of perennial shortgrasses and annual forbs (Winter et al. 2002). Wetzlin et al., (1997) showed that warm and cool season mid-grasses dominated uncolonized sites, whereas the shortgrass *Schedonnardus paniculatus* was an on-colony dominant. As colonies age, older areas may become dominated by forbs and dwarf shrubs with extensive areas of bare ground and low vegetation production, while areas more recently colonized remain grass dominated (Guenther and Detling 2003, Coppock et al., 1983). Archer et al. (1987) reported that, following prairie dog habitation, biodiversity increased at the site, most likely the result of decreasing the competitive capacity of mid-grasses to exclude other species (e.g. forbs). Because graminoids are extensively and repeatedly defoliated by prairie dogs, they eventually lose their competitive advantage over other functional groups (Detling 1998).

Competition between prairie dogs and livestock is a major concern for land managers looking to optimize beef production while still conserving wildlife species (Augustine and Springer 2013). The shift in plant species on the Northern Great Plains from a midgrass to a shortgrass dominated plant community associated with prairie dogs has a large potential impact on livestock production, but may conversely carry benefits in terms of increases in biodiversity. Prairie dogs have been identified as a keystone species, often seen as ecosystem engineers providing habitat to a number of other plant and wildlife species (Davidson et al. 2010, Kotliar et al. 1999). They are known to increase biotic diversity and community structure while playing an important role in ecosystem function, and have been shown to significantly increase plant species richness and diversity, mostly reflected in an increase in forb species and a more uniform distribution of biomass among species on-town versus off-town (Fahnestock and Detling 2002).

Throughout most of the 20th century prairie dog colonies have been subject to control measures to reduce their numbers and eliminate purported competition with cattle for grazing resources (Sierra-Corona et al. 2015). Estimates of prairie dog town extent prior to European arrival vary widely from 40 million ha to 100 million ha; these estimates are based on early 20th century data with no evidence to support population numbers prior to European settlement (Vermeire et al. 2004). Although there are disagreements about the extent to which prairie dogs occupied rangelands, control efforts have no doubt limited their expanse over the past century as wide-spread eradication efforts have sought to reduce occupation to increase rangeland productivity for cattle (Weltzin et al. 1997).

Cattle and prairie dogs exhibit a dietary overlap of up to 60% in Northern Great Plains mixed-grass prairie (Miller et al. 2007). Prairie dogs can reduce availability of forage for livestock by directly reducing the quantity of forage available (through direct consumption, clipping plants to increase predator detection, and building soil mounds), and by changing species composition (Derner et al. 2006). A study conducted by Gabrielson (2009) on a mixed-grass prairie in South Dakota, noted that prairie dogs removed over four times more biomass on-town than cattle on-town. Similar results were observed by Stoltenberg (2004), who showed that prairie dogs removed 2-3 times more forage on-town than cattle on-town. He also attributed up to 90% of forage disappearance due to prairie dogs as the result of non-consumptive activities such as clipping. Stoltenberg (2004) also determined that cattle removed 2 times more forage off-town compared to on-town when comparing similar ecological sites, a result mirrored by Gabrielson (2009). On northern mixed-grass prairie in Montana, Johnson-Nistler et al. (2004) observed a significant standing crop biomass reduction on colonized sites versus uncolonized sites (233.2 vs 585.7 kg/ha), and a 65% reduction in C3 grass biomass on prairie dog colonies.

Although these studies demonstrate the potential impact of prairie dog colonization on forage available for livestock grazing, relatively little research exists studying the separate and combined impacts of livestock and prairie dogs on plant communities occupying the same pastures. Furthermore, much of the past research on the impacts of prairie dog colonization on vegetation has focused on differences between on-colony and off-colony sites, ignoring the impact of cattle or other large herbivores within these systems. Research is needed to compare how cattle and prairie dogs drive differences in plant community responses over time, as well as the combined impact of prairie dog and cattle grazing. The objectives of this study are to evaluate plant community response to grazing on and off prairie dog towns to determine how livestock and prairie dogs alter plant community production and composition. We hypothesize that prairie dogs will be the primary driver of changes in biomass and community composition on the landscape.

Materials and Methods

Study Area

The study area (45.74N, 100.65W) is located near McLaughlin, South Dakota on a northern mixed-grass prairie ecosystem. Predominant soils at the site are clays and loams. Ecological Sites (ES), and the plant communities they support, vary widely; Loamy and Clayey are the predominant ES at the study area (Barth et al. 2014). Other common ES include Shallow Loam, Dense Clay, Shallow Clay, Clayey and Thin Claypan. Ecological Sites associated with prairie dog towns were predominantly Thin Claypan, Loamy, and Shallow Loam.

Vegetation on the site is largely native, including western wheatgrass (*Pascopyrum smithii* Rydb.), green needlegrass (*Nassella viridula* Trin.), and needleandthread (*Hesperostipa comata* Trin.. & Rupr.), intermixed with shortgrasses (blue grama (*Bouteloua gracilis* Willd. Ex Kunth) and buffalograss (*Bouteloua* *dactyloides* Nutt.) and sedges (*Carex* spp.). Kentucky bluegrass (*Poa pratensis* Boivin & Love) is an invasive exotic of concern at the site. Plant communities on areas occupied by prairie dog towns on the study site are largely dominated by western wheatgrass and shortgrasses intermixed with patches of bare ground and annual forb dominated areas. Common forbs on prairie dog towns include annuals such as prostrate knotweed (*Polygonum aviculare* L.), fetid marigold (*Dyssodia papposa* Vent.), and dwarf horseweed (*Conyza ramosissima* Cronquist) as well as perennials such as scarlet globemallow (*Sphaeralcea coccinea* Nutt.).

A weather station has been maintained on site from May 2013 operated by South Dakota Mesonet (South Dakota Climate and Weather, 2017). Climate data for the site for 2012 through April 2013 was acquired from a nearby weather station in Mobridge, SD (40 km east, www.usclimatedata.com). Precipitation totals were compared between the Mobridge weather station and the onsite weather station for similarity in 2014-2016; average yearly difference between the sites was 71 mm, with the Mobridge site consistently having higher estimates. Historical (1981-2010) mean annual precipitation at the Mobridge weather station was 414 mm (U.S. Climate Data, 2017). Total annual precipitation (Jan.-Dec.) and total growing season precipitation (April-September) are presented in Table 1.1.

Four pastures at the study site, each approximately 200 ha in size, were fenced to include varying levels of prairie dog occupation (0%, 20%, 40%, 70%), with a total of 283 ha of pasture occupied by prairie dog colonies. Pastures were continuously grazed by yearling steers from June until the beginning of October. Stocking rates were calculated to achieve approximately 50% utilization in each pasture based on research by

Stoltenberg (2004) that showed that cattle removed only half as much forage on-town compared to off-town when comparing similar ES. Thus, stocking rates for pastures with 0%, 20%, 40% and 70% prairie dog occupation were 0.8, 1.03, 1.36, and 3.58 ha/AUM, respectively.

Treatments

This study evaluated 2 treatments, ES and grazing. The 3 ES treatments were those often associated with prairie dog colonies on the study area: Thin Claypan, Loamy, and Shallow Loam. Topographic positions of these ES were toe slope (Thin Claypan), backslope (Loamy), and summit (Shallow Loam). Four grazing treatments were established. Two were located in off-town locations: non-graze (NG) and cattle only graze (CG). Two were located on established prairie dog towns: cattle and prairie dog graze (CPD), and prairie dog only graze (PD).

Sample Sites

Twenty-five sample sites were established on the study area (Table 1.2). Nine sample sites were established off-town, with 3 sites on each of the ES treatments. Sixteen samples sites were established on-town. Of those, there were 6 sample sites each on Thin Claypan and Loamy ES. Due to limited availability of the prairie dog town occupation of the Shallow Loam ES sites, we were able to establish only 4 sample sites on that ES.

At each sample site, two 30 x 30 m areas of similar vegetation composition were identified. One was randomly assigned to be fenced to exclude livestock (exclosures) and the other was left unfenced and open to livestock grazing (non-exclosures). Exclosures were fenced with barbed wire; on-town exclosures provided the PD treatment and off-town exclosures provided the NG treatment. The corners of non-exclosures were marked unobtrusively with disk plates fixed in place with a long bolt driven through the center into the ground. On-town non-exclosures provided the CPD treatment and off-town non-exclosures provided the CG treatment.

Vegetation Sampling

Within each exclosure and non-exclosure, three 0.25m^2 permanent plots were randomly located for a total of 150 plots (75 within exclosures and 75 within non-exclosures). Plots were sampled in early August of each year from 2012-2016 to correspond to peak standing crop biomass during the summer. For every species in each plot, observers ocularly estimated cover, measured average plant height, and estimated current year biomass using a reference unit double sampling technique similar to that described by Boyda et al. (2015). For each year, ten additional plots on-town and ten off-town were established for individual observer calibrations for dominant species at the site. For off-town calibration plots, western wheatgrass, green needlegrass, and shortgrass (*Bouteloua* and *Carex* spp.) were sampled; for on-town calibration plots, shortgrass, tumble grass, and western wheatgrass were sampled. Once sampling was complete, the dominant species in each calibration plot were clipped and separated into bags by species. Reference units for each species for each observer were bagged separately. All vegetation samples were dried for at least 72 hours at 60º Celsius and weighed. Biomass estimates, species richness, and diversity measurements for individual plots were treated as subsamples and averaged for each exclosure/non-exclosure, with exclosure/non-exclosure being treated as the experimental unit.

Statistical Analysis

Biomass, height, species richness, and diversity data were analyzed in Program R using a linear mixed effects model ANOVA with year and exclosure/non-exclosure as random factors, and exclosure/non-exclosure nested within year to account for repeated measures across years. Fixed effects in the models included grazing treatment and ES treatment and any interaction between the two. Response variables were total current year standing crop biomass (TCYSC); percent of biomass composed of forb species, C3 grasses, and C4 grasses; species richness; and species diversity. TCYSC biomass was the sum of the current year standing crop biomass of all species in a plot (g/0.25m^2) and converted to kg/ha. Species richness was the total number of species per 0.25m^2 plot, and species diversity was calculated using the Shannon-Wiener diversity index. Exclosure/non-exclosure was the experimental unit. For all analyses, least square means were calculated and pairwise comparisons computed using Tukey's HSD. For all models, residuals were checked for normality to meet the assumptions of the ANOVA model.

Plant community composition differences between grazing treatments were determined using a Multi-Response Permutation Procedure (MRPP) with the Sorensen Bray-Curtis distance method. MRPP is a nonparametric procedure used for testing hypotheses between two or more groups (Mitchell et al. 2015). MRPP analysis was performed using PC-ORD 6 software (McCune and Mefford 2002). To evaluate plant community change through time, species rank abundance was calculated as the TCYSC biomass estimate (g/0.25m^2) summed across all plots for each species in each year and treatment combined across ecological sites. The mean rank shift metric was used to quantify changes in species rank abundance to indicate shifts in relative abundance through time (Collins et al. 2008). Additionally, species turnover across all ES by grazing treatment from one year to the next was calculated as: (the number of species gained + the number of species lost)/ total number of species (Cleland et al. 2013). To visualize temporal changes in species dominance, rank clocks were constructed based on the four dominant species on-town and off-town (Batty 2006). Plant community dynamic metrics were computed using the ‘codyn’ package in Program R (Hallett et al. 2016).

To understand the plant community changes that occurred as a result of Kentucky bluegrass invasion between the beginning (2012) and end (2016) of the study, percent biomass comprised of Kentucky bluegrass was analyzed in Program R using ANOVA. Year (n=2), grazing treatment, and ES were treated as fixed effects in the model. Due to the minimal presence of Kentucky bluegrass on-town, a second model was created using only off-town grazing treatments (CG and NG). For all models, least square means were computed, and pairwise comparisons analyzed using Tukey’s honest significant difference test. Model residuals were checked for normality to meet the assumptions of the ANOVA model.

Results and Discussion

Total Current Year Standing Crop (TCYSC) Biomass

There was a significant ES effect (P=0.0006) and a grazing treatment effect (P <0.0001) for TCYSC biomass, but no interaction (P =0.5173). Both Shallow Loam and the Loamy ES had significantly higher TCYSC biomass compared to Thin Claypan (P =0.037 and P =0.0023, respectively) (Table 1.3). Ode et al. (1980) demonstrated that sites occupying lowland areas may be more productive compared with upland sites in a South Dakota mixed-grass prairie, likely the result of greater water availability. The low-lying sites in our study area are, however, Thin Claypans, which have a restricted layer at shallow depths (5-15 cm; (NRCS 2003)). Barth et al. (2014) reported longer infiltration times associated with thin claypan sites, which could negate any of the potential increase in productivity of these sites due to down slope location.

TCYSC biomass was different ($P<0.05$) between all grazing treatments (Table 1.4). It was greatest for NG as might be expected since there were no major grazers (i.e. cattle or prairie dogs) grazing these sites in any year. TCYSC biomass was lower for the CG treatment compared to NG with just cattle utilization, and lower still on sites where only prairie dogs had access (PD). The lowest TCYSC biomass was on the CPD treatment which was grazed by both cattle and prairie dogs. Given the moderate cattle stocking rates applied to the pastures and only 5 years protection from grazing in the NG treatment, the 17% reduction in standing biomass from NG to CG is likely a result of utilization rather than a major shift in plant community to lower production species. The nearly 50% reduction in TCYSC from NG to PD, however, is likely driven by both utilization and the plant community change that had occurred over the many years the site had been occupied by prairie dogs.

The PD treatment had 37% less TCYSC biomass than the CG treatment; likely factors include the moderate livestock stocking rate and heavy use (consumption and clipping) by prairie dogs, as well as the vegetation changes associated with long-term prairie dog occupation. It has been reported that prairie dogs have a dramatic impact on vegetation relative to other large native ungulate grazers (Detling 1998). Johnson-Nistler et al. (2004) reported a 60% reduction in standing crop biomass between colonized and uncolonized sites, although most of their sites were chosen to avoid areas grazed by cattle prior to sampling. The CPD treatment had the lowest TCYSC of the four treatments; the addition of cattle grazing on prairie dog towns reduced (P =0.0265) TCYSC by 19% from PD to CPD. Within the Chihuahua desert grasslands, Davidson et al. (2010) reported that plots accessible to both prairie dogs and cattle consistently had the lowest biomass compared to plots accessible to either species alone; differences, however, were not significant. Gabrielson (2009) observed that, of the total forage disappearance on-town, cattle removed 17.4%, with the other 82.6% attributed to prairie dogs. These results are similar to ours, where an 18.8% reduction in biomass between the PD and CPD sites was observed. Interestingly, the impact of cattle grazing on TCYSC is similar whether on off-town sites (17% reduction on CG compared to NG) or on-town (19% reduction on CPD compared to PD). The lack of interaction between the main effects of ES and grazing treatment for TCYSC suggests that grazing is occurring similarly across an ecological gradient, and the main driver of differences in TCYSC is the effect of grazing treatment.

Main effects of ES and grazing treatment were significant for percent of TCYSC made up by forb species, C3 grasses, and C4 grasses (Tables 1.2 and 1.3); there was, however, no interaction (forb: P =0.27, C3: P =0.15, C4: P =0.35). Shallow Loam ES, located on summit position, had a higher percent of biomass comprised of forb and C4 grass species and lower percent biomass of C3 grass species compared with the Loamy (backslope) and Thin Claypan (toe slope) ES (Table 1.3). This is very characteristic of ES in our study area in which plant communities typically increase in forbs and C4 grasses as you shift upslope. This is also consistent with Ode et al. (1980), who observed that upland plant communities had a higher percentage of biomass comprised of C4 species compared to lowland sites. The C4 photosynthetic pathway provides an adaptive advantage in habitats characterized by high levels of irradiance, high daytime temperatures, and low levels of water availability (Teeri and G. Stowe 1976), all of which are expected on higher slope positions. The results from our TCYSC biomass analysis suggest plant differences follow somewhat predictable responses across ES.

Grazing treatment had a significant effect on percent of TCYSC biomass of forb species, C3 grasses, and C4 grasses (Table 1.4). Percent forb biomass in the CPD treatment was greater than the other three treatments. Percent forb biomass was lowest for CG and NG, followed by PD (CG vs PD P =0.067, NG vs PD P =0.082). Within the same site, Geaumont et al. (2019) reported forbs were a dominant functional group on-town averaging 19% of cover. Percent of biomass in cool season C3 grass species was significantly different between on-town and off-town treatments, with lower percentages occurring on-town. Conversely, percent biomass in C4 grasses was generally higher on-town versus off-town (P ≤0.05 except P = 0.06 for CPD vs. CG). In general, then, on-town plant communities are characterized by a higher percentage of biomass comprised of forbs and C4 grasses and lower percentage of C3 grasses compared with off-town sites.

Irisarri et al. (2016) observed in both the shortgrass prairie and northern mixed-grass prairie that C3 grass biomass decreased and C4 grass biomass increased along an increasing gradient of grazing intensity. Though their study focused solely on livestock grazing, the increased grazing pressure associated with prairie dogs is likely driving similar results on our study. In most areas of mixed-grass prairies, needleandthread and western wheatgrass (C3 grasses) are considered decreasers while blue grama and buffalograss (C4 grasses) are considered increasers; thus buffalograss and blue grama should be expected to increase and western wheatgrass to decrease in response to prairie dog colonization (Koford 1958). Agnew et al. (1986) reported that buffalograss provided 34% cover and was the dominant plant on-town, providing significantly greater cover on-compared to off-colony sites.

Species Richness and Diversity

There was a significant (P = 0.0082) grazing treatment by ES interaction for species richness (Table 1.5). Within each grazing treatment, Shallow Loam had the highest species richness followed by Loamy and Thin Claypan ES. Treatment comparisons within ES indicate that species richness was significantly higher in on-town locations versus off-town locations for the Shallow Loam and Loamy ES, but not for Thin Claypan. On the same study area, Field (2017) also reported that ES influenced species richness, with Thin Claypan having lower species richness than Loamy and Shallow Loam. He suggested that this is likely related to the dense argillic horizon of claypan soils, which may inhibit the growth of many species.

There was no significant grazing treatment effect (Table 1.4) or interaction for species diversity (Shannon-Wiener index). There was, however, a significant ES effect (P <0.001), with all pairwise comparisons between ecological sites significant (Table 1.3). Shallow loam sites had the highest diversity index and Thin Claypan sites had the lowest. The increase in diversity from the bottom of the slope to the top is likely related to the shifts in composition (% forb, C3 grass, and C4 grass biomass) as discussed above, where percent forb biomass and percent C4 biomass increase as ES changes moving upslope. Yearly rank abundance curves (Figure 1.1) also reflect the lower log abundance of Thin Claypan sites compared to the other two ecological sites.

An interesting outcome from the species diversity analyses is that there was no significant difference between the four grazing treatments (Table 1.4). This is consistent with Archer et al. (1987), who reported that, while diversity increased in the first 3 years following colonization, after 4-6 years diversity values dropped to those comparable with off-town sites. Thus, age (>20 years) of colonies on the study site may explain the lack of differences in species diversity. Additionally, the Shannon-Wiener diversity index accounts for both richness and evenness of species present. Low diversity index across treatments is likely due to a few graminoids (shortgrasses, western wheatgrass, and Kentucky bluegrass) accounting for the vast majority of biomass at both on-town or off-town sites. Though a larger percentage of biomass at on-colony sites is made up of C4 grasses, this is often a replacement of C3 grass species not prevalent on prairie dog towns, such as green needlegrass and Kentucky bluegrass.

Plant Communities Analysis

As expected, there are significant differences ($P < 0.05$) between on-town and off-town plant community composition (i.e. CG vs PD; CG vs CPD; NG vs PD; NG vs CPD) for every year of the study (Table 1.6). This suggests that the presence/absence of prairie dogs is a major factor determining plant community composition. Comparisons within on-town communities (PD vs. CPD) and within off-town communities (CG vs NG) vary between year. Only in 2013 was there a significant difference ($P = 0.03$) between PD and CPD. This is likely related to the high species turnover (Figure 1.2) observed in 2012-2013 for the PD treatment, potentially due to differences in precipitation, as 2012 was the only year with below average moisture (Table 1.2). The CG vs NG treatment comparison p-values were very large at the beginning of the study, but declined over the years, with a significant difference occurring in 2016 (Table 1.6). This may indicate that plant community composition has diverged within 4 years between areas that are protected from cattle grazing (NG) and those that are not (CG). Additional years of data beyond the scope of this project would be needed to confirm whether divergence in NG and CG plant communities occurred or if the 2016 result was due to statistical noise. Field (2017) also observed significant differences between on- and off-town plant community composition at the study site, but found no difference between sites based on presence/exclusion of cattle.

As indicated above, species richness (# species/0.25 m^2) is generally higher for on-town compared to off-town sites (Table 1.5). Total number of species encountered on-town was also greater than off-town (Table 1.7). Of particular interest is the number of species unique to on- or off-town treatments in each year. Between 51.5 and 59.2 % of the species found in on-town plant communities were unique to on-town locations; species unique to off-town communities ranged from 25.6 to 42.9 %, depending on year. Also of note was the higher proportion of annual unique species on-town compared to a low number of annual species off-town. Archer et al. (1987) suggested the high level of herbivory on prairie dog towns may decrease the competitive capacity of mid-grasses to exclude other species (e.g. forbs). Overlap of species between on- and off-town communities was low, with 60.9 – 68.1% of total plant species found within a year located either on-town or off-town but not on both. It is important to note that a greater number of plots were sampled on-town compared to off-town, which may have increased total number of species encountered on-town to some extent. The number of unique species which occur on-town and off-town agree with the results from the MRPP analysis above which shows a separation of plant communities along on-town and off-town sites; this is documented in other studies. Archer et al. (1987) showed in a detrended correspondence analysis of plant communities ranging from uncolonized, 2 years post colonization, and 4-6 years post colonization, that uncolonized sites were clustered at one extreme and the 4-6 year sites at the other extreme; and suggested that 69% of the floristic variation was attributable to time since colonization. Within the study site, Geaumont et al. (2019) reported that plant community showed a stronger grouping in ordination space according to on-town versus off-town location, with scarlet globemallow and fetid marigold correlated with on-town sites, and green needlegrass, Kentucky bluegrass, and needleandthread correlated with off-town sites.

The 5-year timeframe of this study provided a unique opportunity to compare community dynamics between on-town and off-town plant communities through time. An evaluation of mean species rank abundance (biomass) shifts indicates sites located on prairie dog towns (PD and CPD) underwent a large re-ordering of abundance of species, especially from 2014 to 2016 (Figure 1.3). Conversely, mean rank species abundance of off-town sites (NG and CG) declined and then stabilized over the 5 years of the study. This may suggest that there is greater community stability off-town versus on-town, as fewer species are shifting in abundance. The rank clock of dominant species diagrams (Figures 1.4 and 1.5), however, suggest a somewhat different interpretation. Rank clocks allow a temporal visualization of rank order abundance (biomass in g) over time in a circle starting with a vertical axis at 12 o'clock (Collins et al. 2008). It is clear from the rank clock diagrams for on-town sites (Figure 1.4) that there is no re-ordering of species abundance through time among the four most dominant species on-town, with only yearly fluctuations occurring, likely due to differences in amount and timing of precipitation. This can be contrasted with rank shift clocks for off-town treatments (Figure 1.5), where there is a major shift occurring in species dominance off-town. In these sites, Kentucky bluegrass became the dominant species after 2015, largely replacing western wheatgrass. It appears that, over time, on-town plant communities had a relatively stable group of dominant species, with re-ordering occurring within the group of sub-dominant species, likely in response to yearly fluctuations in climatic variables. Off-town communities had less re-ordering of species, but a major shift in community composition as Kentucky bluegrass became the off-town dominant.

The shift to dominance by Kentucky bluegrass has significant implications for the native northern mixed-grass prairie plant communities. For example, in a synthesis by Toledo et al. (2014), it is clear that plant communities dominated by Kentucky bluegrass have significantly less cover and diversity of native grass and forb species, and that once dominant, Kentucky bluegrass can influence available niches that other subdominant plants occupy. Bluegrass canopy cover has also been significantly correlated with a decline in flowering forb species richness (Kral-O'Brien et al. 2019). Thus the decline of mean species rank shift (Figure 1.3) in off-town species in 2014-2016 corresponds to the increase in dominance of Kentucky bluegrass during that period, and is likely the result of sub-dominant species, primarily forbs, being suppressed due to invasion.

There was a significant (P =0.005) 3-way interaction between grazing treatment, ES, and year (2012 vs 2016) for the percentage that Kentucky bluegrass represented of TCYSC biomass for the model, including all on- and off-town grazing treatments (Table 1.8). Kentucky bluegrass was absent from most (67%) on-town sites in both years. The greatest Kentucky bluegrass biomass composition on-town was 2.0% for CPD on Shallow Loamy ES in 2012; percent composition was 0% for those same sites in 2016. By contrast, Kentucky bluegrass composition off-town ranged from 1.8% to 37.0% in 2012 and 25.6 to 54.6% in 2016. Similar results for Kentucky bluegrass on-town were observed by Archer et al. (1987), who reported Kentucky bluegrass was locally extinct two years after prairie dog habitation. This they suggest could be due to either a reduced tolerance to the heavy grazing on-town or to increased grazing pressure if Kentucky bluegrass were more preferred.

Because Kentucky bluegrass was largely missing on-town, a reduced data model was run using only off-town grazing treatment sites (CG & NG) to test again for fixed effects of grazing treatment, ES, and year. Results indicate a significant ES x year interaction ($P = 0.009$), suggesting change in the invasive grass species occurred differently across ES between 2012 and 2016 (Figure 1.6). In 2012, percent composition of Kentucky bluegrass on the Thin Claypan ES was lower ($P = 0.0044$) than on the Loamy ES (4.4% vs. 36.1%, respectively). Percent composition on Shallow Loam (13.26%) was not different ($P > 0.05$) from the other two ES. Although Kentucky bluegrass appeared to increase in all three ES off-town, the change on the Thin Claypan ES was the most dramatic and the only increase that was significant ($P < 0.0001$). It went from 4.4% Kentucky bluegrass composition in 2012 to 52.4% in 2016, an almost 11-fold increase. By contrast, increases for off-town Loamy and Shallow Loam ES from 2012 to 2016 were much smaller (1.38- and 2.37-fold increases, respectively) and not significant ($P = 0.6003$ and 0.3436, respectively). Kentucky bluegrass composition was not different in 2016 between any of the ES off-town. Increases in Kentucky bluegrass colonization were observed in North Dakota during the 1990’s, where Kentucky bluegrass had increased from near 0% foliar cover in 1984 to over 60% in the 2000’s, (Sanderson et al. 2015). It was hypothesized that higher than average precipitation during those years may have provided a competitive advantage to Kentucky bluegrass. Four consecutive years of our study, 2013-2016, had above average annual precipitation and 2014-2016 had high growing season precipitation (Table 1.2), which may have contributed to the large expansion of Kentucky bluegrass on the off-town Thin Claypan ES.

DeKeyser et al. (2013) observed in a natural area on the northern mixed-grass prairie, where sites were not grazed for a 23-year period, species composition shifted from a high percentage of native graminoids and forbs to a high percentage of invasive species, mainly smooth brome and Kentucky bluegrass. In our study however, livestock presence or absence did not have an impact on colonization of Kentucky bluegrass; there was no difference between CG and NG within any ES for either 2012 or 2016 (Table 1.8). This is in stark contrast to the impact of prairie dogs during that same time period, where Kentucky bluegrass composition was < 2.1% on all ES. Kentucky bluegrass composition was lower on-town compared to off-town for all ES in both years except for Thin Claypan in 2012. These results strongly suggest that heavy grazing on-town by prairie dogs is very effective at controlling the spread of Kentucky bluegrass in these ecosystems, whereas lighter grazing by cattle was ineffective.

The rapid shift in Kentucky bluegrass dominance (3-5 years) at our study site (Figures 1.5 and 1.6) in off-town locations is one of the more surprising findings of our study. Another is that, while cattle grazing may have delayed Kentucky bluegrass dominance (Figure 1.5), it was not ultimately effective in preventing it. Cattle stocking rates in our study pastures were, at most, moderate; they were established to prevent overgrazing by taking into consideration the utilization levels on-town by prairie dogs. Our cattle stocking rates were likely not high enough to limit Kentucky bluegrass dominance as was observed by Sanderson et al. (2015), where Kentucky bluegrass was slower to establish and become dominant on high stocking rate pastures compared to lower stocking rate pastures. These results off-town and the virtual absence of Kentucky bluegrass on-town in our study, suggest that the use of intensive grazing to combat invasive cool season grasses warrants further investigation.

Summary

Overall these results provide information to land managers on expected plant community responses across ecological sites for pastures managed with both prairie dogs and cattle. The lack of interaction between ecological site and treatment for total biomass suggests that plant production changes occur somewhat predictably across ecological sites, but the primary driver is grazing pressure from either cattle, prairie dogs, or both species. Over the course of the study, there were two major drivers of change for plant community composition. The first is herbivory, specifically the presence or absence of prairie dogs. The extensive differences between sites with prairie dogs (PD and CPD) and those without prairie dogs (NG and CG) as well as the lack of differences in community composition between CPD and PD and between NG and CG suggest the presence or absence of prairie dogs, and not cattle, on the landscape is a major driver of change in species composition. The second major driver of change is invasion, specifically the shift towards a Kentucky bluegrass dominant system. Presence or absence of cattle grazing had no effect of the rate of invasion, likely due to the low to moderate stocking rates;

however, the absence of Kentucky bluegrass on-town suggests that the high severity grazing by prairie dogs may act as a barrier to plant community invasion. Though invasion is driving plant community change in off-town sites, the level of herbivory is also driving the susceptibility of a plant community to resist establishment of a non-native.

Literature Cited

Agnew, W.D., W. Uresk, D., & M. Hansen, R. (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

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

Augustine, D.J., & Springer, T.L. (2013). Competition and facilitation between a native and a domestic herbivore: trade-offs between forage quantity and quality. *Ecological Applications, 23,* 850-863

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, 78,* 2054-2060

Batty, M. (2006). Rank clocks. *Nature, 444,* 592

Boyda, E.D., Butler, J.L., & L., X. (2015). Estimating herbaceous biomass of grassland vegetation using the reference unit method. *The Prairie Naturalist,* 73-83

Cleland, E.E., Collins, S.L., Dickson, T.L., Farrer, E.C., Gross, K.L., Gherardi, L.A., Hallett, L.M., Hobbs, R.J., Hsu, J.S., Turnbull, L., & Suding, K.N. (2013). Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology, 94,* 1687-1696

Collins, S.L., Suding, K.N., Cleland, E.E., Batty, M., Pennings, S.C., Gross, K.L., Grace, J.B., Gough, L., Fargione, J.E., & Clark, C.M. (2008). Rank clocks and plant community dynamics. *Ecology, 89,* 3534-3541

Coppock, D.L., Detling, J.K., Ellis, J.E., & Dyer, M.I. (1983b). Plant-herbivore interactions in a North American mixed-grass prairie : I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia, 56,* 1-9

Davidson, A.D., Ponce, E., Lightfoot, D.C., Fredrickson, E.L., Brown, J.H., Cruzado, J., Brantley, S.L., Sierra-Corona, R., List, R., Toledo, D., & Ceballos, G. (2010). Rapid response of a grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock. *Ecology, 91*, 3189-3200

DeKeyser, E.S., Meehan, M., Clambey, G., & Krabbenhoft, K. (2013). Cool Season Invasive Grasses in Northern Great Plains Natural Areas. *Natural Areas Journal, 33*, 81-90

Derner, J.D., Detling, J.K., & Antolin, M.F. (2006). Are livestock weight gains affected by black-tailed prairie dogs? *Frontiers in Ecology and the Environment*, *4*, 459-464

Detling, J.K. (1998). Mammalian herbivores: ecosystem-level effects in two grassland national parks. *Wildlife Society Bulletin*, *26*, 438-448

Fahnestock, J.T., & Detling, J.K. (2002). Bison-prairie dog-plant interactions in a North American mixed-grass prairie. *Oecologia, 132*, 86-95

Field, A. (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 (PhD Dissertation). In, *Agriculture and Applied Science*: North Dakota State University

Gabrielson, M.L. (2009). Effects of Black-tailed Prairie Dogs (Cynomys ludovicianus) and Cattle on Vegetation Composition and Disappearance in the Mixed-Grass Prairie (M.S. thesis). South Dakota State University

Geaumont, B.A., Hovick, T.J., Limb, R.F., Mack, W.M., Lipinski, A.R., & Sedivec, K.K. (2019). Plant and Bird Community Dynamics in Mixed-Grass Prairie Grazed by Native and Domestic Herbivores. *Rangeland Ecology & Management, 72*, 374-384

Guenther, D.A., & Detling, J.K. (2003). Observations of cattle use of prairie dog towns. *Journal of Range Management, 56*, 410-417

Hallett, L.M., Jones, S.K., MacDonald, A.A.M., Jones, M.B., Flynn, D.F.B., Ripplinger, J., Slaughter, P., Gries, C., & Collins, S.L. (2016). codyn: An r package of community dynamics metrics. *Methods in Ecology and Evolution, 7*, 1146-1151

Irisarri, J.G.N., Derner, J.D., Porensky, L.M., Augustine, D.J., Reeves, J.L., & Mueller, K.E. (2016). Grazing intensity differentially regulates ANPP response to precipitation in North American semiarid grasslands. *Ecological Applications, 26*, 1370-1380

Johnson-Nistler, C.M., Sowell, B.F., Sherwood, H.W., & Wambolt, C.L. (2004). Black-tailed prairie dog effects on Montana's mixed-grass prairie. *Journal of Range Management, 57*, 641-648

Koford, C.B. (1958). *Prairie dogs, whitefaces, and blue grama*. Wildlife Society

Kotliar, N.B., Baker, B.W., Whicker, A.D., & Plumb, G. (1999). A Critical Review of Assumptions About the Prairie Dog as a Keystone Species. *Environmental Management, 24*, 177-192

Kral-O'Brien, K.C., Limb, R.F., Hovick, T.J., & Harmon, J.P. (2019). Compositional Shifts in Forb and Butterfly Communities Associated with Kentucky Bluegrass Invasions. *Rangeland Ecology & Management, 72*, 301-309

McCune, B., & Mefford, M. (2002). PC-ORD for windows. *Multivariate analysis of ecological data. Version, 6*

Miller, B.J., Reading, R.P., Biggins, D.E., Detling, J.K., Forrest, S.C., Hoogland, J.L., Javersak, J., Miller, S.D., Proctor, J., Truett, J., & Uresk, D.W. (2007). Prairie dogs: An ecological review and current biopolitics. *Journal of Wildlife Management, 71*, 2801-2810

Mitchell, S., Palmquist, K., Cohen, S., & Christensen, N.L. (2015). Patterns of vegetation composition and diversity in pine-dominated ecosystems of the Outer Coastal Plain of North Carolina: Implications for ecosystem restoration. *Forest Ecology and Management, 356*, 64-73

NRCS. (2003). Ecological site description for: Thin Claypan R054XY033ND. In. https://efotg.sc.egov.usda.gov/references/public/SD/R054XY033NDthinclaypan.pdf

Ode, D.J., Tieszen, L.L., & Lerman, J.C. (1980). The Seasonal Contribution of C"3 and C"4 Plant Species to Primary Production in a Mixed Prairie. *Ecology, 61*, 1304-1311

Sanderson, M.A., Liebig, M.A., Hendrickson, J.R., Kronberg, S.L., Toledo, D., Derner, J.D., & Reeves, J.L. (2015). Long-term agroecosystem research on northern Great Plains mixed-grass prairie near Mandan, North Dakota. *Canadian Journal of Plant Science, 95*, 1101-1116

Sierra-Corona, R., Davidson, A., Fredrickson, E.L., Luna-Soria, H., Suzan-Azpiri, H., Ponce-Guevara, E., & Ceballos, G. (2015). Black-Tailed Prairie Dogs, Cattle, and the Conservation of North America's Arid Grasslands. *Plos One, 10*

South Dakota Climate and Weather, 2017 *South Dakota Climate and Weather Mesonet at SDSTATE* Available at: https://climate.sdstate.edu/archive/ (2017), Accessed 1st Dec 2017

Stoltenberg, M. (2004). Effects of prairie dogs on plant community composition and vegetation disappearance in Mixed-Grass Prairie (M.S. thesis). South Dakota State University

Teeri, J.A., & G. Stowe, L. (1976). Climatic patterns and the distribution of C4 grasses in North America. *Oecologia*, *2*, 1-2.

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

US Climate Data, 2017. Climate Mobridge - South Dakota and Weather Averages Mobridge. Available at: www.usclimatedata.com/climate/mobridge/south-dakota/united-states/ussd0227. Accessed 1st Dec 2017.

Vermeire, L.T., Heitschmidt, R.K., Johnson, P.S., & Sowell, B.F. (2004). The prairie dog story: Do we have it right? *Bioscience, 54*, 689-695

Weltzin, J.F., Dowhower, S.L., & Heitschmidt, R.K. (1997). Prairie dog effects on plant community structure in southern mixed-grass prairie. *Southwestern Naturalist, 42*, 251-258

Winter, S.L., Cully, J.F., & Pontius, J.S. (2002). Vegetation of prairie dog colonies and non-colonized short-grass prairie. *Journal of Range Management, 55*, 502-508

Table 1.1: Total cumulative yearly precipitation (ppt) and growing season ppt (April-September) from weather stations located in Mobridge, SD and on the study site near McLaughlin, SD (May 2013 through 2016) for 2012 – 2016. Long term (LT) averages are from the Mobridge weather station.

Year	Yearly Mobridge ppt (mm)	Yearly McLaughlin ppt (mm)	Growing Season Mobridge ppt (mm)	Growing Season McLaughlin ppt (mm)
2012	350.3	-	328.4	-
2013	554.5	-	393.5	335.3[A]
2014	512.3	460.5	466.1	439.2
2015	567.2	427.2	514.9	385.8
2016	481.8	456.7	369.1	397.8
LT	414.0	-	320.0	-

[A] Growing season data only includes May-September.

Table 1.2: The number of sample sites by ecological site and treatment on the study site near McLaughlin, South Dakota. Twenty-five samples sites were established, and at each sample site, two 30 x 30 m areas of similar vegetation composition were identified. One was randomly assigned to be fenced to exclude livestock (exclosures) and the other was left unfenced and open to livestock grazing (non-exclosures). Sites were established across three ecological sites: Thin Claypan, Loamy, and Shallow Loam and four treatments: CPD (cattle and prairie dog grazing), PD (prairie dog only grazing), CG (cattle only grazing), and NG (neither cattle nor prairie dog grazing).

	Thin Claypan	Loamy	Shallow Loam
CPD	6	6	4
PD	6	6	4
CG	3	3	3
NG	3	3	3

Table 1.3: (TCYSC) Total current year standing crop biomass; percent of biomass made up by forbs, C3 species, and C4 species; and Shannon Wiener Index least square means followed by standard errors for 3 ecological sites studied on the study site near McLaughlin, South Dakota. Means within columns followed by a different letter are significantly different ($P<0.05$)

Ecological site	TCYSC Biomass (kg/ha)	Percent Forb Biomass (%)	Percent C3 Biomass (%)	Percent C4 Biomass (%)	Shannon Wiener Index
Shallow Loam	1755.4^{A} (283)	19.5^{A} (2.5)	51.7^{A} (3.8)	27.8^{A} (2.8)	1.23^{A} (0.07)
Loamy	1819.7^{A} (281)	12.4^{B} (2.3)	69.5^{B} (3.6)	17^{B} (2.7)	1.03^{B} (0.07)
Thin Claypan	1534.5^{B} (281)	11.9^{B} (2.3)	73.2^{B} (3.6)	14.7^{B} (2.7)	0.83^{C} (0.07)

Table 1.4: (TCYSC) Total current year standing crop biomass; percent of biomass made up by forbs, C3 species, and C4 species; and Shannon Wiener Index least square means followed by standard errors for the 4 grazing treatments evaluated on the study site near McLaughlin, South Dakota. Means within columns followed by a different letter are significantly different ($P<0.05$). Grazing treatments are CPD (cattle and prairie dog grazing), PD (prairie dog only grazing), CG (cattle only grazing), and NG (neither cattle nor prairie dog grazing).

Grazing Treatment	TCYSC Biomass (kg/ha)	Percent Forb Biomass (%)	Percent C3 Biomass (%)	Percent C4 Biomass (%)	Shannon Wiener Index
NG	2447^{A} (285)	9.3^{A} (2.7)	74.4^{A} (4.0)	14.3^{A} (3.0)	0.97^{A} (0.07)
CG	2036^{B} (288)	8.5^{A} (2.9)	75.8^{A} (4.2)	15.1^{AB} (3.2)	1.07^{A} (0.08)
PD	1285^{C} (282)	15.9^{A} (2.4)	56.9^{B} (3.6)	27.1^{C} (2.7)	1.03^{A} (0.07)
CPD	1043^{D} (282)	24.6^{B} (2.4)	52.3^{B} (3.6)	22.9^{BC} (2.7)	1.04^{A} (0.07)

Table 1.5: Species richness (# species/0.25 m^2) for grazing treatments within ecological sites on the study site near McLaughlin, South Dakota. Grazing treatments are CPD (cattle and prairie dog grazing), PD (prairie dog only grazing), CG (cattle only grazing), and NG (neither cattle nor prairie dog grazing). Means followed by a different letter are significantly different ($P<0.05$).

Ecological Site	Grazing Treatment	Species Richness (#/0.25 m^2)
Shallow Loam	NG	6.4^{BCD} (0.4)
	CG	7.04^{ABC} (0.56)
	PD	8.47^{A} (0.4)
	CPD	8.17^{AB} (0.4)
Loamy	NG	5.6^{CD} (0.46)
	CG	5.16^{CD} (0.46)
	PD	7.58^{AB} (0.32)
	CPD	7.74^{AB} (0.32)
Thin Claypan	NG	4.78^{D} (0.46)
	CG	5.13^{D} (0.46)
	PD	$5.22^{D\,(}$0.32)
	CPD	5.5^{CD} (0.32)

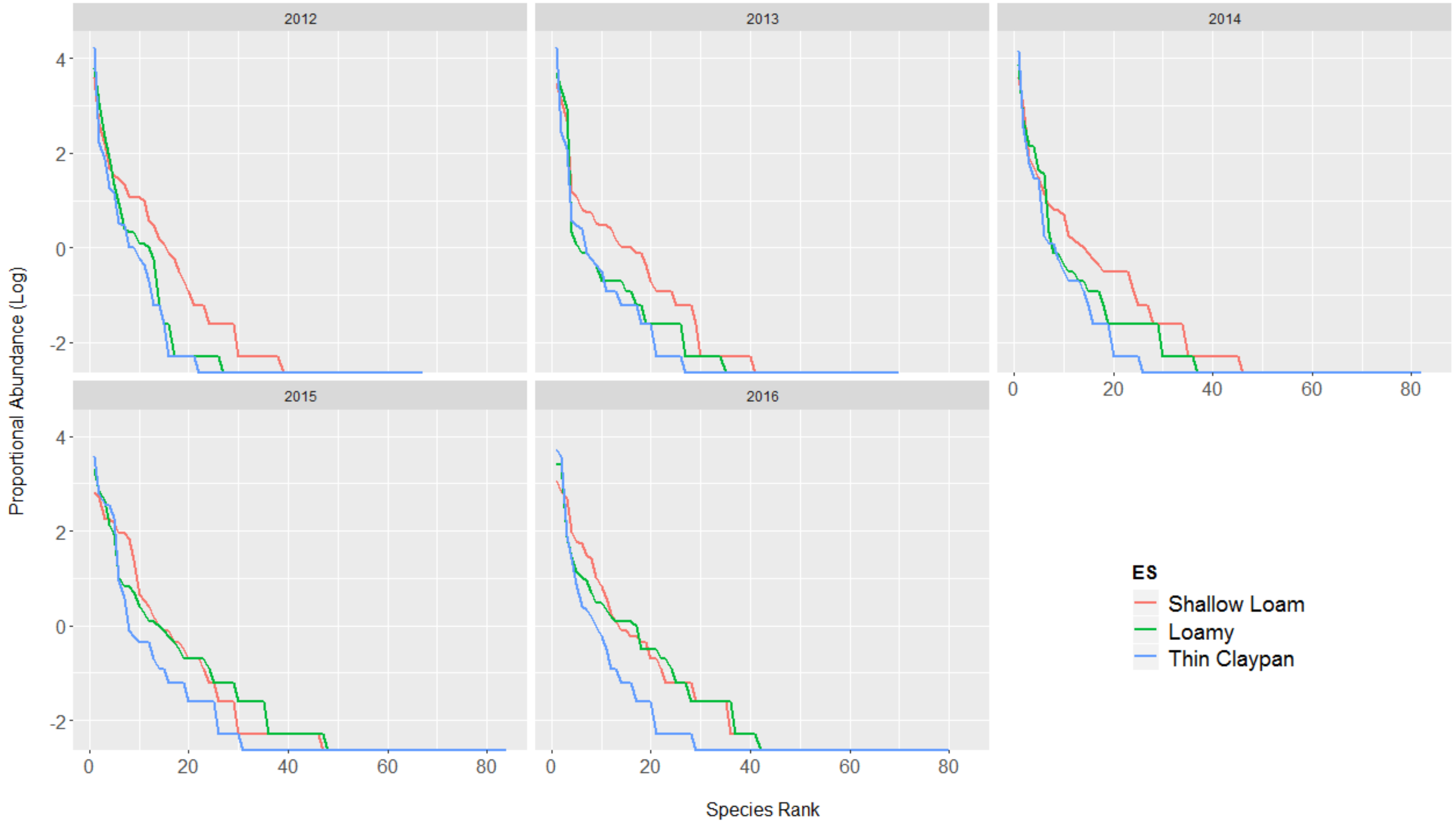

Figure 1.1: Rank proportional abundance curves for each ecological site (ES) in each year on the study site near McLaughlin, South Dakota. The y-axis is the log proportional abundance of the total standing crop biomass of each species plotted against their species rank. Sites with a more gradual curve have a greater distribution of species biomass and longer slope of line has greater richness.

Table 1.6: Pairwise comparisons between plant community composition each year on the study site near McLaughlin, South Dakota using the Multi-Response Permutation Procedure. Values are estimated p-values for grazing treatment comparisons for each year. Grazing treatments are CPD (cattle and prairie dog grazing), PD (prairie dog only grazing), CG (cattle only grazing), and NG (neither cattle nor prairie dog grazing).

Year	CG vs PD	CG vs CPD	NG vs PD	NG vs CPD	CG vs NG	PD vs CPD
2012	0.001	0.001	0.001	0.001	0.91	0.78
2013	0.001	0.001	0.001	0.001	0.37	0.03
2014	0.001	0.001	0.001	0.001	0.36	0.4
2015	0.001	0.001	0.001	0.001	0.059	0.11
2016	0.001	0.001	0.001	0.001	0.004	0.07

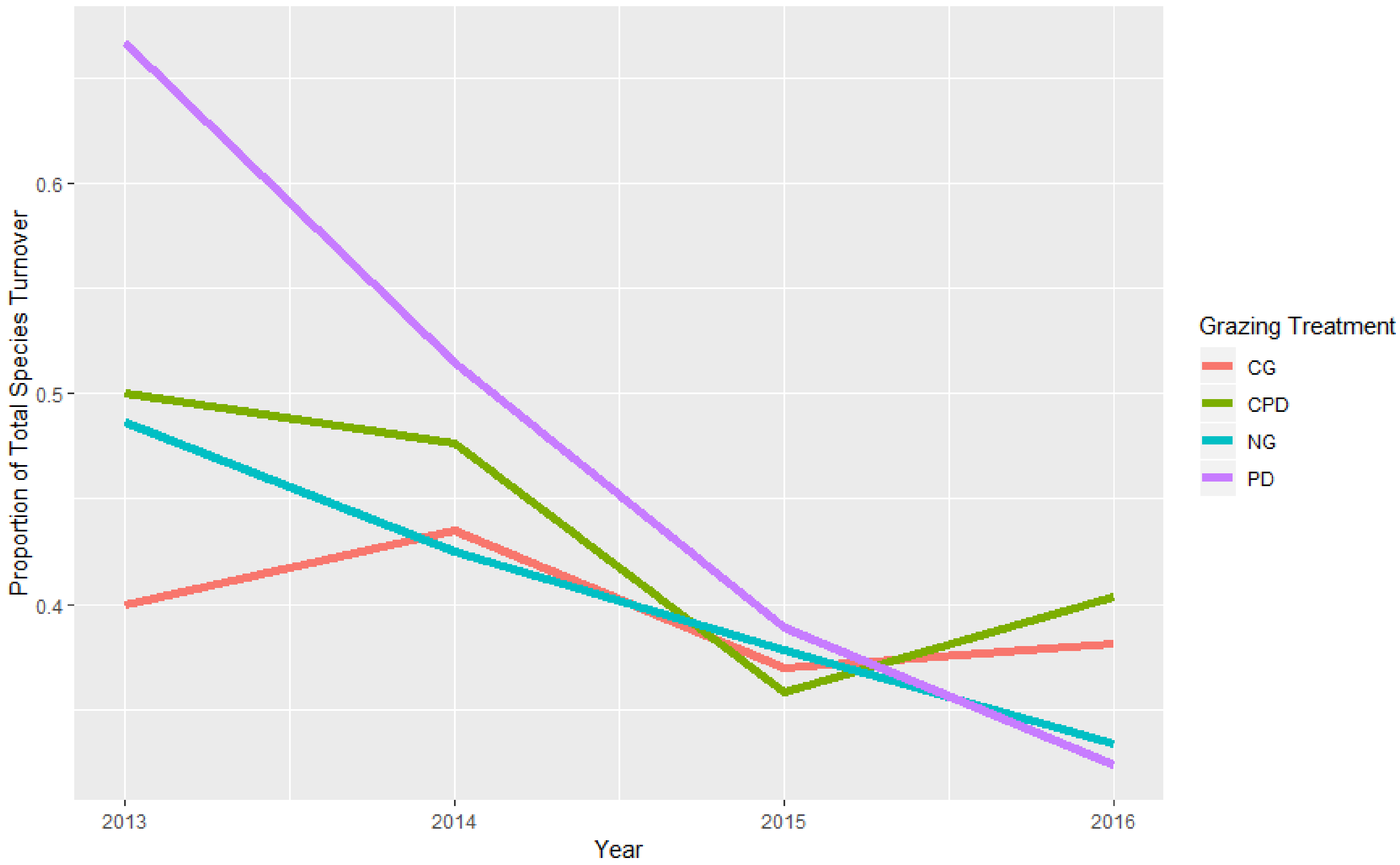

Figure 1.2: Percentage of total species turnover (appearances + disappearance) for each grazing treatment on the study site near McLaughlin, South Dakota. Grazing treatments are CPD (cattle and prairie dog grazing), PD (prairie dog only grazing), CG (cattle only grazing), and NG (neither cattle nor prairie dog grazing).   Turnover is calculated as the percent of species either present or absent from one current year to previous year, e.g. difference between 2012-2013.

Table 1.7: For each year, 2012-2016, on the study site near McLaughlin, South Dakota, number of plant species present (Total #), number of unique species (occurring only on that type of site; # Unique, number in parenthesis are # of annuals), and percent that unique species represent of all species (% Unique) occurring on-town and off-town; and total number of species occurring on- and off-town combined, sum of on- and off-town unique species, and percent unique species represent of all on- and off-town species.

Year	On-Town Species			Off-Town Species			On- and Off-Town Combined		
	Total #	# Unique	% Unique	Total #	# Unique	% Unique	Total #	# Unique	% Unique
2012	49 (9)	29 (9)	59.2	35 (1)	15 (1)	42.9	64 (10)	44 (10)	68.1
2013	52 (14)	28 (12)	53.8	41 (4)	17 (2)	41.5	69 (16)	45 (14)	65.2
2014	66 (15)	34 (13)	51.5	48 (3)	16 (1)	33.3	82 (16)	50 (14)	60.9
2015	72 (17)	40 (14)	55.6	43 (4)	11 (1)	25.6	83 (18)	51 (15)	61.4
2016	64 (10)	35 (9)	54.7	42 (2)	13 (1)	31.0	77 (11)	48 (10)	62.4

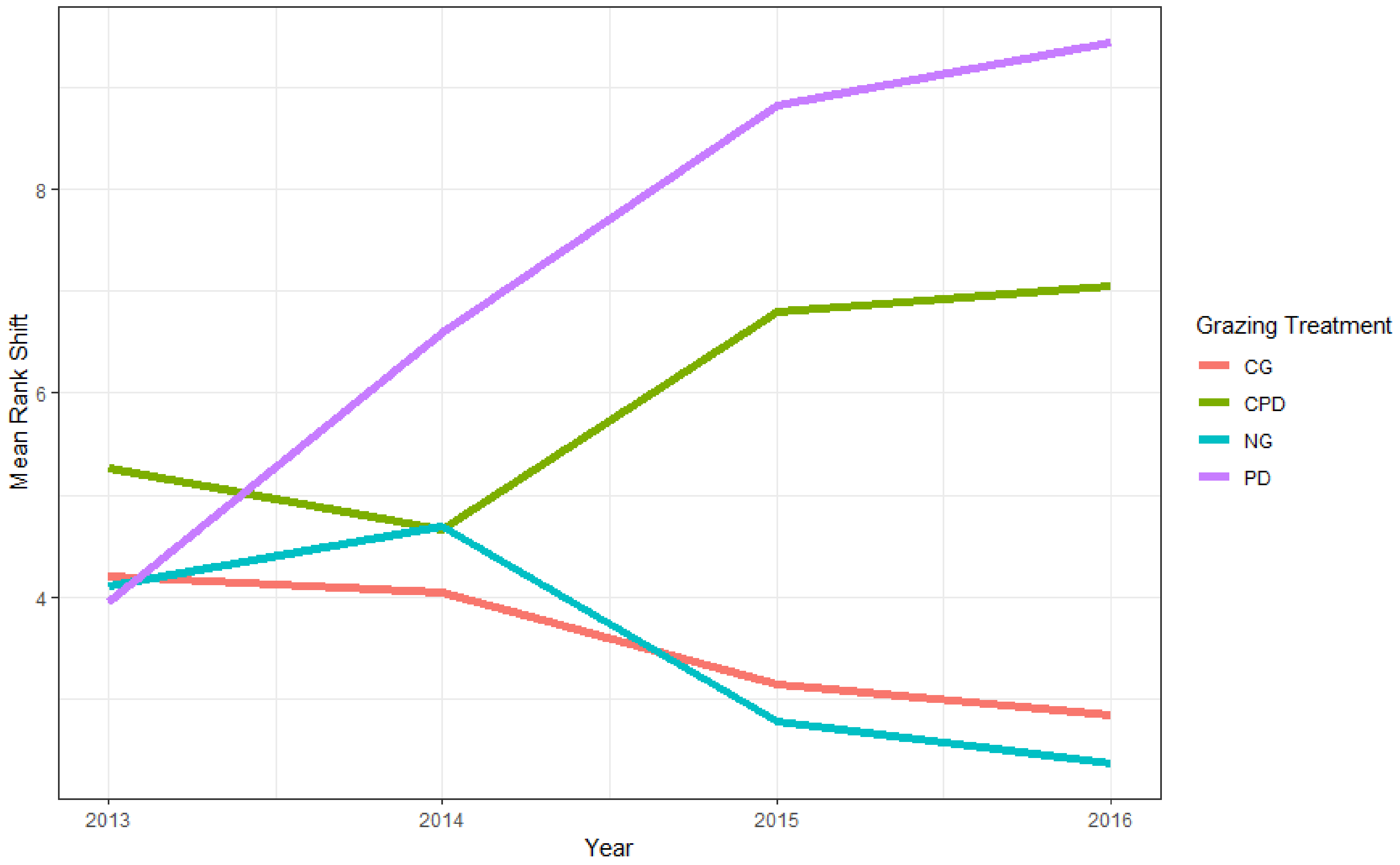

Figure 1.3: Plot of the mean species rank shift (MRS) through time by grazing treatment on the study site near McLaughlin, South Dakota. MRS quantifies changes in species rank abundance of current year standing crop biomass and indicates re-ordering of relative abundance through time. Grazing treatments are CPD (cattle and prairie dog grazing), PD (prairie dog only grazing), CG (cattle only grazing), and NG (neither cattle nor prairie dog grazing).

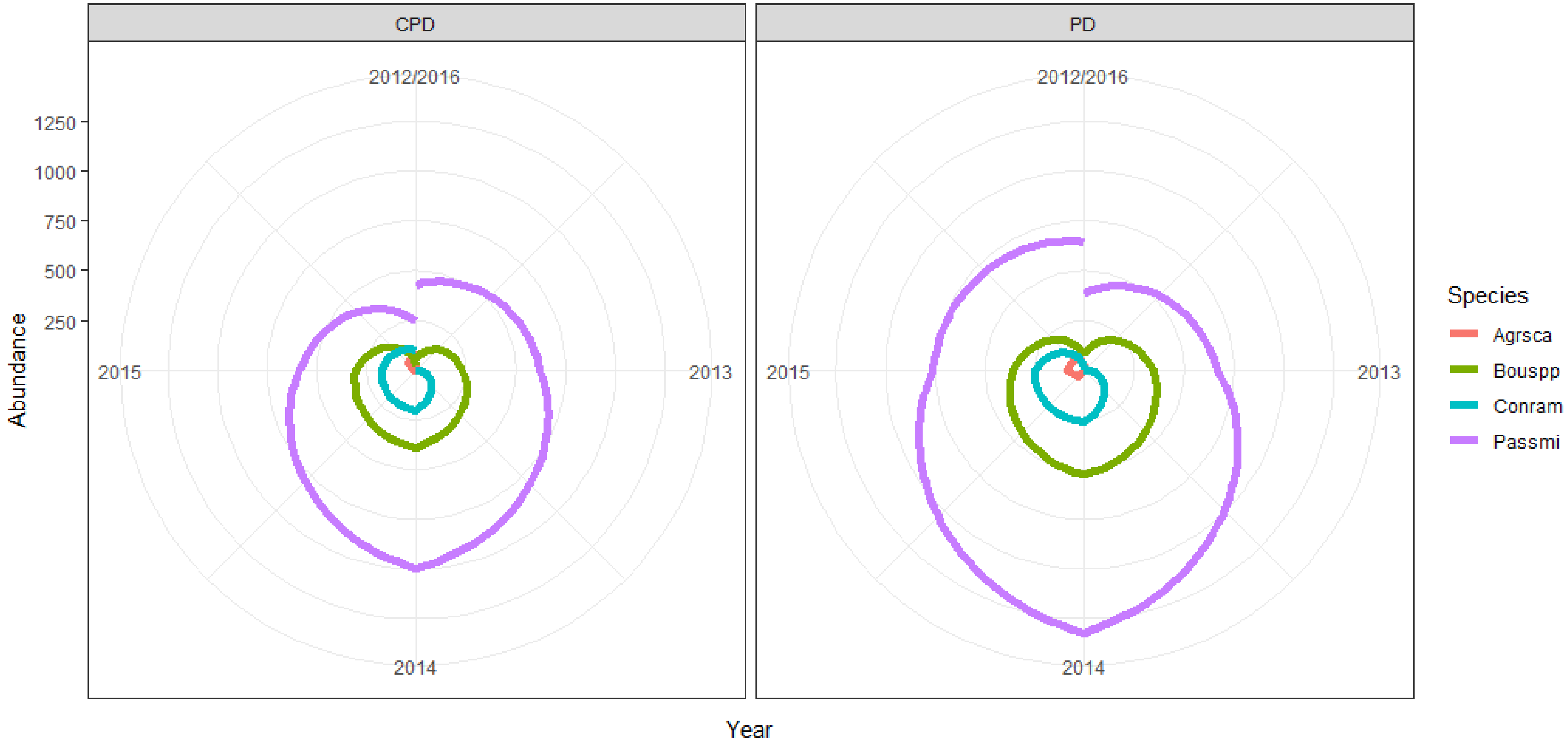

Figure 1.4: Rank clock of the four most dominant species standing crop biomass abundance for on-town grazing treatments on the study site near McLaughlin, South Dakota. Abundance is measured as the total standing crop biomass abundance (g/0.25m^2) summed across all plots for each of the four species. Species are ticklegrass (Agrsca), short grasses (Bouspp), dwarf horseweed (Conram), and western wheatgrass (Passmi). Grazing treatments are CPD (cattle and prairie dog grazing) and PD (prairie dog only grazing).

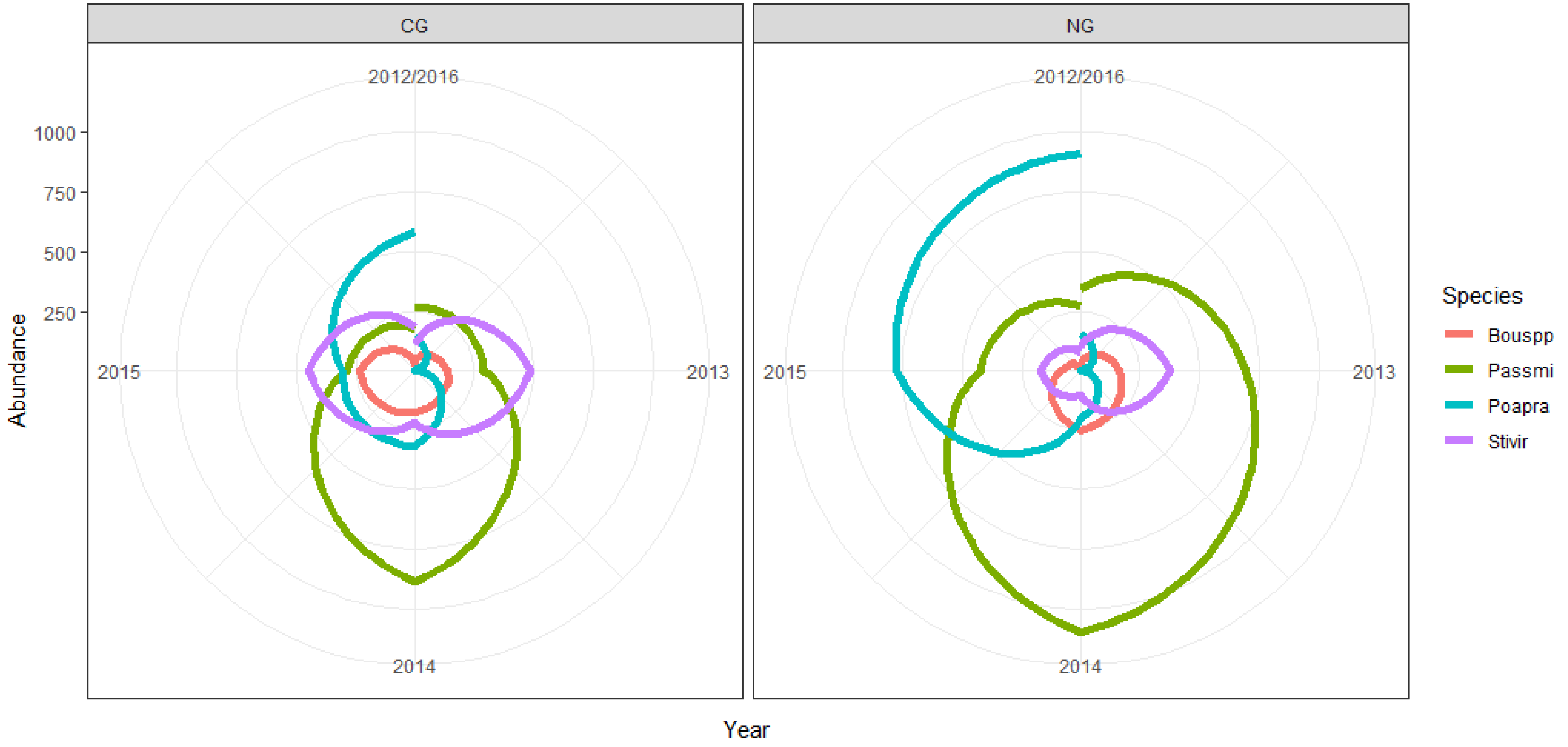

Figure 1.5: Rank clock of the four most dominant species standing crop biomass abundance for off-town grazing treatments. Abundance is measured as the total standing crop biomass abundance (g/0.25m^2) summed across all plots for each of the four species. Species are shortgrasses (Bouspp), western wheatgrass (Passmi), Kentucky bluegrass (Poapra), and green needle grass (Stivir). Grazing treatments are CG (cattle only grazing), and NG (neither cattle nor prairie dog).

Table 1.8. Percentage (%) of total current year standing crop biomass composed of Kentucky Bluegrass by ecological sites on the study site near McLaughlin, South Dakota. Treatments are CPD (cattle and prairie dog grazing), PD (prairie dog only grazing), CG (cattle only grazing), and NG (neither cattle nor prairie dog grazing). Results had a significant three-way interaction between treatment, ecological site, and year (P =0.005). Means followed by a different letter across rows and columns are significantly different (P<0.05).

	2012			2016		
	Thin Claypan	Loamy	Shallow Loam	Thin Claypan	Loamy	Shallow Loam
NG	1.8 ^{ef}	35.0 ^{bc}	11.0 ^{ef}	52.3 ^{a}	45.0 ^{ab}	25.6 ^{cd}
CG	7.0 ^{ef}	37.0 ^{bc}	15.6 ^{de}	52.6 ^{a}	54.6 ^{a}	37.4 ^{bc}
PD	0.0 ^{f}	0.0 ^{f}	0.0 ^{f}	0.0 ^{f}	0.39 ^{f}	0.0 ^{f}
CPD	0.0 ^{f}	0.58 ^{f}	2.0 ^{ef}	0.0 ^{f}	1.14 ^{f}	0.0 ^{f}

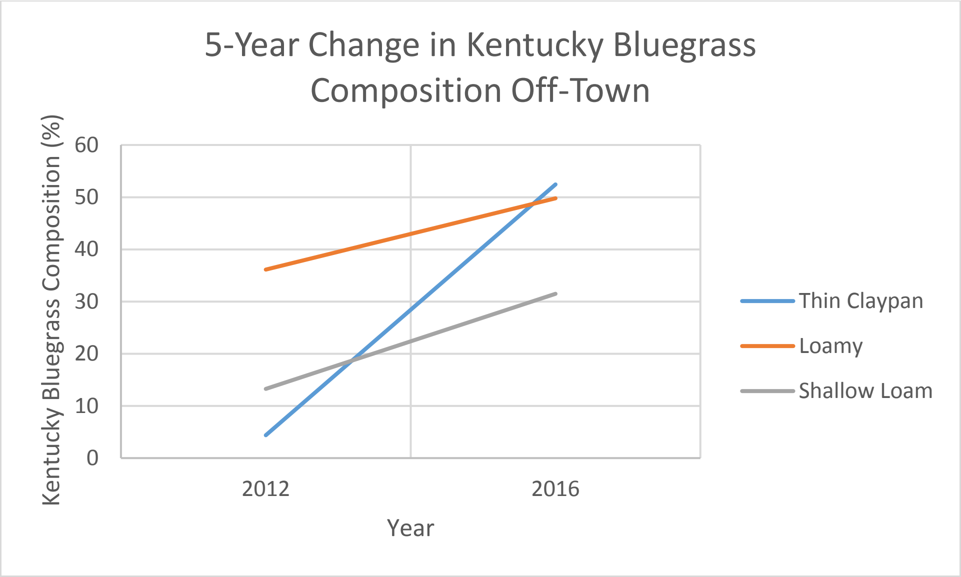

Figure 1.6. Graph of Kentucky bluegrass percent composition from 2012 to 2015 for 3 Ecological Sites on off-town locations in pastures on the Standing Rock study site in northcentral South Dakota.

Chapter 2: Comparing Random Forest Models to Map Northern Great Plains Plant Communities Using 2015 and 2016 Pleiades Imagery

This paper in its current form (as reproduced, below) has been accepted into *Biogeosciences Discuss* under the citation:

Brennan, J., Johnson, P., and Hanan, N. (2019) Comparing Stability in Random Forest Models to Map Northern Great Plains Plant Communities Using 2015 and 2016 Pleiades Imagery. *Biogeosciences Discuss*., https://doi.org/10.5194/bg-2019-194, in review

Abstract

The use of high resolution imagery in remote sensing has the potential to improve understanding of patch level variability in plant structure and community composition that may be lost at coarser scales. Random forest (RF) is a machine learning technique that has gained considerable traction in remote sensing applications due to its ability to produce accurate classifications with highly dimensional data and relatively efficient computing times. The aim of this study was to test the ability of RF to classify five plant communities located both on and off prairie dog towns in mixed grass prairie landscapes of north central South Dakota, and assess the stability of RF models among different years. During 2015 and 2016, Pleiades satellites were tasked to image the study site for a total of five monthly collections each summer (June-October). Training polygons were mapped in 2016 for the five plant communities and used to train separate 2015 and 2016 RF models. The RF models for 2015 and 2016 were highly effective at predicting different vegetation types associated with, and remote from, prairie dog towns (misclassification rates < 5% for each plant community). However, comparisons between the predicted plant community map using the 2015 imagery and one created with the 2016 imagery indicate 6.7% of pixels on-town and 24.3% of pixels off-town changed class membership depending on the year used. Given the low model

misclassification error rates, one would assume that low changes in class belonging between years. The results show that while RF models may predict with a high degree of accuracy, overlap of plant communities and inter-annual differences in rainfall may cause instability in fitted models. Researchers should be aware of similarities between target plant communities as well as issues that may arise with using single season or single year images to produce vegetation classification maps.

Introduction

Remote sensing of rangelands greatly improves our ability to study and understand complex ecological interactions across the landscape. One of the main advantages of remote sensing data is its capacity to cover wide areas, allowing assessment of plant communities at landscape level scales as compared to traditional point-based assessments (Ramoelo et al. 2015; Yu et al. 2018). Numerous studies have demonstrated the utility of remote sensing applications in monitoring rangeland condition, including mapping of vegetation communities, plant species composition, biomass estimation, and impact of grazing intensity on the landscape (Blanco et al. 2008; Franke et al. 2012). Successive images throughout a growing season may potentially help explain patterns of cattle distribution and landscape utilization across temporal scales, or capture phenological changes within the landscape to distinguish differences in warm- and cool-season grass life history, or changes associated with early brown-down in forb- versus grass-dominated communities on prairie dog towns.

Within the Northern Great Plains, black tailed prairie dog colonization is an issue of concern for livestock producers (Miller et al. 2007). Competition between prairie dogs and livestock is a major concern for land managers looking to optimize beef production while still conserving wildlife species (Augustine and Springer 2013). Prairie dogs can reduce availability of forage for livestock by directly reducing the quantity of forage available (through direct consumption, clipping plants to increase predator detection, and building soil mounds), and by changing species composition (Derner et al. 2006). Older core areas of prairie dog towns often become characterized by extensive areas of bare ground and low vegetation production, which is generally limited to annual forb and dwarf shrub species. Pastures containing extensive areas of bare ground due to prairie dog colonization may potentially depress livestock forage intake rates and ultimately beef production. Understanding the impact of prairie dogs on plant communities, and use patterns of livestock within rangelands occupied by prairie dogs requires the ability to map plant communities at landscape scales.

Advances in remote sensing technology have facilitated the mapping and assessment of a broad range of habitats at different scales (Corbane et al. 2015). For example, Schmidtlein et al. (2007) used hyperspectral imagery at 2m resolution in combination with ordination techniques to map functional plant group gradients in a Bavarian pasture. Within the Delaware Gap National Recreation Area, multiple Landsat 7 scenes were used (30m resolution) with classification tree algorithms to map forest and plant communities for the National Park Service Vegetation Mapping Program (de Colstoun et al. 2003). In Majella National Park, Italy, 4m resolution imagery was used with NDVI to map and predict grass and herbaceous biomass variability over a 200 km^2 area (Cho et al. 2007). While the focus of many of these remote sensing studies is on mapping plant communities at landscape scales to study land use changes and address conservation related issues, the utility of using thematic maps derived from high resolution satellite imagery to study plant and animal interactions has been less explored.

Several methods for accurately classifying plant communities using remote sensing techniques have been used in numerous ecological and natural resource studies. One method, random forest classification (RF), has gained considerable traction in the remote sensing community for its ability to produce accurate classifications, handle highly dimensional data, and provide efficient computing times (Belgiu and Drăguţ 2016). RF is seen as an improvement over simple classification tree analysis by reducing noise and misclassification of outliers (Laliberte et al. 2007; Nitze et al. 2015). RF is an ensemble decision tree classifier which combines bootstrap sampling to construct several individual decision trees from which a class probability is assigned (Mellor et al. 2013). RF builds each tree using a deterministic algorithm selecting a random set of variables and a random sample from the calibration data set (Ramoelo et al. 2015).

The utility of random forest algorithms has been proven in remote sensing applications. Lowe and Kulkarni (2015) showed that RF outperformed maximum likelihood, support vector machine, and neural network classification models using two Landsat scenes. Ramoelo et al. (2015) successfully used RF modeling to predict leaf nitrogen content using World-View 2 satellite images in grassland and forest communities. Similarly, Mutanga et al. (2012) concluded that RF regression modelling provided an effective methodology for variable selection and predicting biomass in wetland environments. The greatest limitation of the general use of RF has been, and continues to be, due to the lack of off-the-shelf tools for RF implementation within the most common GIS and remote sensing software packages (Hamiton 2013).

Considerable research has focused on the application of RF classification across different plant communities at various scales, however, concerns exist over the transferability of these models to different sites or between seasons. Previous research has shown that RF models have a high degree of classification accuracy at local scales, but model accuracy decreases significantly when applied to spatially separated sites, showing a lack of stability in the model (Juel et al. 2015). Other research has focused on the use of seasonality of image acquisition on improvement of RF models due to spectral differences in plant communities as a result of phenological change during a growing season. Corcoran et al. (2013) showed an improvement of RF model accuracy in classifying wetlands in northern Minnesota with the inclusion of spring Landsat 5 images across two years over a full season versus summer only, and fall only models.

Many of the plant community classification studies in remote sensing tend to focus on acquiring a single image or multiple images across a single growing season, reducing the influence of inter-annual precipitation on NDVI values (Adjorlolo et al. 2014; Beeri et al. 2007; Guo et al. 2000). Furthermore, most research studies focus solely on spectral differences in plant communities and fail to analyze community differences on the ground at the species level (de Colstoun et al. 2003; Geerken et al. 2005). While classification rates are often reported in studies, the potential overlap in plant community species is rarely explored as a potential source of error within the models. Additionally, very little research has examined how yearly differences in NDVI values across plant communities can alter classification models, especially in high resolution satellite imagery.

We conducted a large, collaborative study from 2012-2016 designed to evaluate livestock production on mixed-grass prairie pastures with varying levels of prairie dog occupation. A major goal of that study was to determine which plant communities on the pastures cattle preferred to graze, and how those preferences shifted within and between years. Plant communities on the site were categorized based on location (on- or off-town) and visually apparent dominant plant functional groups. We expected the plant communities to remain relatively stable during the study, however their signatures on satellite imagery could change within and between years as a result of the timing and magnitude of rainfall and dry periods, timing of green up, phenological progression, and other factors. The overall goal, then, was to develop maps that accurately classify plant communities based on satellite imagery collected between seasons and years. Specific objectives of this study were to 1) determine differences in the five identified plant communities based on species composition, 2) assess the utility of using a RF model with high resolution satellite imagery to classify plant communities of interest within the Northern Great Plains, and 3) determine the stability of the RF model when using subsequent years of satellite imagery with identical training data. Our ability to map and understand these plant dynamics and patterns at large scales will give researchers insight into applying RF models across years. Research from this study will allow us to better assess how plant communities drive cattle foraging behavior, and evaluate how changes throughout a growing season can cause cattle to shift behavior in response to new resources becoming available.

METHODS

Study site

The study area (45.74N, 100.65W) was located near McLaughlin, South Dakota on a northern mixed-grass prairie ecosystem. Native prairie pastures (810 ha total area) were leased from 2012-2016; pastures were continuously stocked with yearling steers from June-October of each year to achieve 50% utilization. Of the 810 ha, approximately 186 ha were occupied by black-tailed prairie dogs (*Cynomys ludovicianus*). Predominant soils at the site were clays and loams. Ecological sites, and the plant communities they support vary widely; Loamy and Clayey were the predominant Ecological Sites at the site with inclusions of Dense Clay, Shallow Clay, and Thin Claypan (Barth et al. 2014). Plant species dominating the site were largely native, including western wheatgrass (*Pascopyrum smithii* Rydb.), green needlegrass (*Nassella viridula* Trin.), and needle-and-thread (*Hesperostipa comata* Trin. & Rupr), intermixed with blue grama (*Bouteloua gracilis* Willd. Ex Kunth), buffalograss (*Bouteloua dactyloides* Nutt.), and sedges (*Carex* spp.). The most common non-native species on the site was Kentucky bluegrass (*Poa gracilis* Boivin & Love). Woody draws occupied moist drainage areas; vegetation consists primarily of bur oak (*Quercus macrocarpa* Nutt.), American plum (*Prunus americana* Marshall), and chokecherry (*Prunus virginiana* L.). These draws were frequently flanked by snowberry-dominated patches (*Symphoricarpos occidentalis* Hook.). Plant communities on areas occupied by prairie dog towns on the site were largely dominated by western wheatgrass and shortgrasses (buffalograss, blue grama, and sedges) intermixed with patches of bare ground and annual forb dominated areas. Common annual forbs on prairie dog towns included prostrate knotweed (*Polygonum aviculare* L.), fetid marigold (*Dyssodia papposa* Vent.), and dwarf horseweed (*Conyza ramosissima* Cronquist) as well as perennials such as scarlet globemallow (*Sphaeralcea* *coccinea* Nutt.). Mean annual precipitation at the site in 2015 and 2016 was 427.2 and 456.7 mm, respectively (South Dakota Climate and Weather 2017).

Five plant communities of interest for our study site were identified: 1) Forb-dominated sites on prairie dog towns (PDF), 2) Grass-dominated sites on prairie dog towns (PDG), 3) Snowberry-dominated sites off-town (SNOW), 4) Cool season grass-dominated sites off-town (COOL), and 5) Warm season-dominated sites off-town (WARM).

Training sites

To facilitate classification, training site polygons were mapped for PDF, PDG, COOL, WARM, and SNOW plant communities using ArcPad for Trimble GPS units in the summer of 2016. Twenty training sites were mapped for each of the plant communities except WARM, for which only 8 sites were mapped due to the difficulty of finding homogenous stands of warm season grasses. Plant species in the Northern Great Plains are dominated by cool season species; warm season species, where they occur, are typically intermixed into stands of cool season species. Training sites for each plant community were selected from across the entire study area to capture potential site differences across research pastures. Sites were mapped in the field by walking the perimeter of the plant community patch with a Trimble GPS unit. Training polygon perimeter boundaries were always at least 3 meters interior of patch edge to minimize error introduced to the training data as a result of GPS signal noise. Identified patches were then converted into a polygon shapefile within ArcGIS to be used as training polygons for the RF classification algorithm. Within each training site polygon, three

$0.25\ m^2$ plots were randomly located. Within each plot, percent cover by species was recorded in the summer of 2016 at the time of polygon mapping.

Plant Community Analysis

Plant community analysis was performed on vegetation data collected from the three $0.25m^2$ plots measured in each training polygon. Differences between plant community compositions were determined using a Multi-Response Permutation Procedure (MRPP) with the Sorensen Bray-Curtis distance method. MRPP is a nonparametric procedure used for testing hypotheses between two or more groups (Mitchell et al. 2015). Differences in community compositions were analyzed separately between on-town groups (PD = PDF and PDG) and off-town groups (NPD = COOL, WARM, and SNOW). Although differences between all 5 plant communities are likely to occur, comparisons between on-town and off-town were not made. On-town and off-town sites were mutually exclusive from each other; for example, PDG cannot occur off-town. To analyze trends in species composition between plant community plots, Non-metric Multidimensional Scaling (NMS) ordination was used (Kruskal 1964). Only species that occurred in 3 or more plots were included in the ordination analysis. NMS analysis was conducted using the Sorensen Bray-Curtis distance method with 250 iterations and a stability criterion of 0.00001. Analysis was repeated five times to confirm ordination pattern in the data. Similarity index matrices were generated to compare plot differences between off-town plant communities and between on-town plant communities and averaged by plant community. All ordination analyses (MRPP and NMS) were performed using PC-ORD 6 software (McCune and Mefford 2002).

Imagery

During the summers of 2015 and 2016, Pleiades satellites were tasked to image the study site. Pleiades satellites, which are members of the SPOT family of satellites, are operated by AIRBUS Defense and Space. This platform was chosen due to its high spatial resolution (0.5 m pan chromatic, 2 m multispectral) and four band spectral resolution: pan chromatic (480-830 nm), red (600-720nm), green (490-610 nm), blue (430-550 nm), and near infrared (750-950 nm). Pleiades satellites were designed for commercial tasking and monitoring, allowing multiple revisits to a project site. A total of ten image collections were acquired in the summer of 2015 and 2016 (five each year) from June through October during the 1st-15th of each month (Table 2.1). Image collection times were chosen to correspond to the time periods when cattle were actively grazing on the site. Multispectral images were pan-sharpened and orthorectified by the image provider (Apollo Imaging Corp). Boundaries of the prairie dog town were mapped in the fall of 2015 using a handheld Trimble GPS unit. Post collection processing of the images included extracting off-town and on-town locations using the “Extract By Mask” tool in ArcGIS. Separate RF models were developed for on-town and off-town plant communities because such plant communities are mutually exclusive on the site (e.g. PDG cannot exist at off-town locations). Each monthly image collection was converted into an NDVI image using the formula:

$$NDVI = \frac{NIR - Red}{NIR + Red}$$

Random Forest Model

For the RF model, the Random Forest package of the Comprehensive R Archive Network (CRAN) implemented by Liaw and Wiener (2002) was utilized. Training data were constructed by stacking all satellite imagery spectral bands (Red, Blue, Green, and

NIR) and NDVI bands for each month of each year (25 total dimensions per year) to create a raster stack for each year's imagery (2015 and 2016). To train the model, pixel values were extracted from the satellite imagery raster stack for each training polygon mapped in the field. The random forest models were built using 100 decision trees and default number of nodes at each split, with plant community data as the response category (WARM, COOL, SNOW, PDF, PDG) and spectral band values as the predictor. Models built for comparison include 2015 off-town, 2015 on-town, 2016 off-town, and 2016 on-town. A combined years model was also constructed using all available spectral data from 2015 and 2016 (50 dimensions).

Within the random forest package, Out of Bag (OOB) error rates were calculated by reserving one-third of the training data to test the accuracy of the predictions. Models were then used to predict class belonging for 2015 and 2016 raster stacks and the combined 2015 and 2016 stack. To assess the stability of the RF models from year to year, the "Combinatorial And" tool in ArcGIS was used to create a new raster combining plant community prediction data from 2015 and 2016. The output was used to calculate percent of pixels that were unchanged between the 2015 and 2016 model predictions and percent of change that occurred between years for plant community predictions.

Results and Discussion

MRPP pairwise comparisons were made within on-town communities (PDF vs. PDG) and within off-town communities (COOL vs. WARM vs. SNOW), but not between on- and off-town communities (Table 2.2). Each plant community was significantly different from all other communities within its on-town or off-town area ($P < 0.001$). Substantial differences are evident between off-town plant communities in the 2-D plot of the NMS ordination (final stress = 15.465, instability < 0.00001 after 98 iterations), with some overlap occurring between communities (Figure 2.1). The On-Town 2-D NMS ordination plot (final stress = 15.591, instability = 0.0005 after 50 iterations) also indicates substantial differences between communities, but with fairly minimal overlap (Figure 2.1). While there is some overlap between plant communities, in general similarities between plant communities are low, with a similarity index generated from a Sorensen (Bray-Curtis) distance matrix of 21.5 – 27.9% when comparing off-town plant communities and 15.6% when comparing PDF and PDG (Table 2.2).

Variable importance factor graphs indicate that NDVI training values by month tend to contribute the most to each model for both years, both on- and off-town (Figure 2.2). Similar results were observed by (Mishra and Crews 2014), where spectral classification features (mean NDVI or ratio NDVI) were the most significant for classifying vegetation morphology in a savanna grassland. Differences between importance of months between years within site is likely the result of interannual precipitation timing between the years, with plant communities greening up or browning down earlier or later depending on seasonal rainfall. Results from the RF model show low OOB misclassification error rates (Table 2.3) indicating a high degree of accuracy in the model. The lower similarity index (Table 2.2) for on-town communities compared to off-town communities may help explain the lower OOB classification error rates (Table 2.3) as well as the lower frequency of pixels changing class in the on-town communities (Table 2.4). OOB error rate was below 5% for all models. OOB accuracy is an unbiased estimate of the overall classification accuracy eliminating the need for cross-validation (Breiman 2001). Lawrence et al. (2006) showed OOB error rates to be reliable estimates of class accuracy for identifying invasive species. Similarly, OOB error rates have been reported to be reliable in mapping corn and soybean fields across multiple years (Zhong et al. 2014). Belgiu and Drăguţ (2016) acknowledge that the reliability of OOB error measurements needs to be further tested using a variety of datasets in different scenarios

Consistency in error rates for plant communities appears to indicate stability in the 2015 and 2016 RF models which used identical training sites on consecutive yearly satellite imagery. However, when comparing yearly predicted plant community maps, differences between community classifications are slightly more pronounced, indicating the models may not be as stable as predicted based solely on the OOB error rates. The pixels that were classified as representing one plant community in 2015 and a different one in 2016 were 24.3% of the total off-town pixels and 6.7% of total on-town pixels (Table 2.4). The pixels changing from COOL to SNOW and SNOW to COOL represented the highest percentage of pixels that changed plant community in off-town areas. COOL and SNOW plant communities, however, occupied the largest area on the site, and represented 70.3 and 21.0% of total pixels in 2015 and 68.5 and 25.1 % of total off-town pixels in 2016, respectively.

It is unlikely in this northern mixed-grass prairie ecosystem that all the changes in plant communities indicated by classification of pixels were real changes from one plant community type to another over one year. Such major shifts in species composition typically occur much more slowly. The results from the plant community analysis indicate training sites were chosen appropriately to account for differences in species composition on the ground, therefore apparent changes are much more likely due to factors that affect the spectral signature of the vegetation. One explanation for the difference in year to year classification could be attributed to the interannual variability of rainfall between 2015 and 2016 (Figure 2.3). While overall total rainfall between years was similar, differences in timing of precipitation that occurred likely affected timing of green up and dormancy for many of the cool and warm season species on the site. This, then, would create different NDVI patterns between years (Figure 2.4). Wehlage et al. (2016) for example, found that yearly rainfall differences resulted in large differences in NDVI and biomass measurements across two years in a dry mixed-grass prairie. Goward and Prince (1995) suggested that the relationship between NDVI and annual rainfall in any given year also depends on the previous year history of rainfall at the site, and Oesterheld et al. (2001) showed that annual above ground primary production of shortgrass communities is related to current as well as previous two years precipitation. The above average rainfall at the study site in 2015 could have added to the increase in average NDVI in 2016 when compared to 2015 through an increase in cumulative biomass or production at the site. Another possible cause for changes in plant community classifications between years is overlap of plant community species where two plant communities share a boundary. The edges of plant communities in the NGP are seldom sharp; more often there is a transition zone, where species from each community intermingle. This, along with variability in phenological development of different plants (e.g. cool season vs. warm season) associated with precipitation, as mentioned above, could result in pixels appearing to be associated with one plant community in one year and its neighboring plant community the next. It should also be noted that plant communities in the region, which are predominantly comprised of cool season grasses, often include varying levels of warm season species; and snowberry thickets often have an understory of grasses, especially near the perimeter. Thus one should expect some level of spectral mixing within each community, and the possibility that climatic factors could result in changes in NDVI values that, at least initially, might suggest apparent changes between plant communities.

As noted above, one issue with using categorically classified vegetation maps is that plant communities in space are rarely mutually exclusive, and tend to change along a continuum with environmental gradients (Equihua 1990). Thus, within both on-town and off-town plant communities, transition zones are likely to account for a portion of the classification change between plant communities between years (Figure 2.5). Alternative approaches to mapping plant communities can be the recognition of fuzzy properties enabling a single point in space to exhibit characteristics of a number of plant communities (Duff et al. 2014; Fisher 2010). For example, Schmidtlein et al. (2007) used NMS of species data in combination with imaging spectroscopy to produce ordination maps of community structure. While fuzzy classification maps are more likely to give a better picture of plant community composition on a per pixel basis, they are also more difficult to use to draw inferences of species dominance and livestock use across landscapes.

A final RF model combining all available bands and NDVI values for 2015 and 2016 reduced error rates for all plant communities below 1% (Table 2.3). While we have shown that error rates may not result in more stable predictions, using all available data for a model will likely improve accuracy and result in a more accurate thematic map (Figure 2.6). Zhou et al. (2018) using RF models showed that using a combination of four seasons of Sentinel-1 images and a GaoFen-1 satellite winter image produced the highest classification rate of urban land cover scenes over individual seasonal images. Likewise, several other studies have reported increases in classification accuracy in RF models with the addition of combined seasonal images, hyperspectral data, LiDAR images, radar (SAR) images, and ancillary geographical data such as elevation and soil types (Corcoran et al. 2013; Pu et al. 2018; Shi et al. 2018; Xia et al. 2018; Yu et al. 2018). RF models have the ability to handle highly dimensional correlated data, and data combined from multiple different data sources across different temporal scales. The internal information provided by the model, such as variable importance, can be a useful tool for researchers to select features of greatest importance to reduce computation times in the instance of large datasets. At the size of our study area (810 ha) and a maximum of 50 variables, the combined 2015-16 data model only slightly added to computation time, but not enough to warrant feature trimming from the dataset. Variable importance plots from the combined data model also indicate that different months between years contribute highly to the classification accuracy between models. For example June 2016 NDVI and October 2015 NDVI were the most important for classification of the data based on the variable importance plot from the combined years' model.

Implications

Stability of models is important when applying similar techniques across different sites, plant communities, and in this case years. Differences in year-to-year NDVI values may alter classification results; those differences may be even more pronounced if only one or two satellite imagery scenes are used from a single year. One of the main benefits to RF classification in remote sensing is the relatively fast computing time (Belgiu and Drăguţ 2016), and, given the availability of free satellite imagery, researchers would be prudent to include multiple images across years and seasons in their model to improve accuracy. Furthermore, while the desired outcome is often to produce thematic maps, recognizing that plant communities rarely exist in discrete communities is important when trying to interpret remotely sensed classification maps. This is likely to be magnified as pixel size increases, resulting in less "pure" vegetation structure in the classified pixel. Further work should examine the reliability of OOB error rates across different scenarios, and the influence of year and timing of image acquisition on classification results.

LITERATURE CITED

Adjorlolo, C., Mutanga, O., & Cho, M.A. (2014). Estimation of Canopy Nitrogen Concentration Across C3 and C4 Grasslands Using WorldView-2 Multispectral Data. *Ieee Journal of Selected Topics in Applied Earth Observations and Remote Sensing, 7*, 4385-4392

Augustine, D.J., & Springer, T.L. (2013). Competition and facilitation between a native and a domestic herbivore: trade-offs between forage quantity and quality, *Ecological Applications, 23*, 850-863

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, 78*, 2054-2060

Beeri, O., Phillips, R., Hendrickson, J., Frank, A.B., & Kronberg, S. (2007). Estimating forage quantity and quality using aerial hyperspectral imagery for northern mixed-grass prairie. *Remote Sensing of Environment, 110*, 216-225

Belgiu, M., & Drăguţ, L. (2016). Random forest in remote sensing: A review of applications and future directions. *Isprs Journal of Photogrammetry and Remote Sensing, 114*, 24-31

Blanco, L.J., Aguilera, M.O., Paruelo, J.M., & Biurrun, F.N. (2008). Grazing effect on NDVI across an aridity gradient in Argentina. *Journal of Arid Environments, 72*, 764-776

Breiman, L. (2001). Random Forest. *Machine Learning, 45*, 5-32

Cho, M.A., Skidmore, A., Corsi, F., van Wieren, S.E., & Sobhan, I. (2007). Estimation of green grass/herb biomass from airborne hyperspectral imagery using spectral indices and partial least squares regression. *International Journal of Applied Earth Observation and Geoinformation, 9*, 414-424

Corbane, C., Lang, S., Pipkins, K., Alleaume, S., Deshayes, M., Milian, V.E.G., Strasser, T., Vanden Borre, J., Spanhove, T., & Foerster, M. (2015). Remote sensing for mapping natural habitats and their conservation status - New opportunities and challenges. *International Journal of Applied Earth Observation and Geoinformation, 37*, 7-16

Corcoran, J., Knight, J., & Gallant, A. (2013). Influence of Multi-Source and Multi-Temporal Remotely Sensed and Ancillary Data on the Accuracy of Random Forest Classification of Wetlands in Northern Minnesota. *Remote Sensing, 5*, 3212

de Colstoun, E.C.B., Story, M.H., Thompson, C., Commisso, K., Smith, T.G., & Irons, J.R. (2003). National Park vegetation mapping using multitemporal Landsat 7 data and a decision tree classifier. *Remote Sensing of Environment, 85*, 316-327

Derner, J.D., Detling, J.K., & Antolin, M.F. (2006) Are livestock weight gains affected by black-tailed prairie dogs?. *Frontiers in Ecology and the Environment, 4*, 459-464

Duff, T.J., Bell, T.L., & York, A. (2014). Recognising fuzzy vegetation pattern: the spatial prediction of floristically defined fuzzy communities using species distribution modelling methods. *Journal of Vegetation Science, 25*, 323-337

Equihua, M. (1990). Fuzzy Clustering of Ecological Data. *Journal of Ecology, 78*, 519-534

Fisher, P.F. (2010). Remote sensing of land cover classes as type 2 fuzzy sets. *Remote Sensing of Environment, 114*, 309-321

Franke, J., Keuck, V., & Siegert, F. (2012). Assessment of grassland use intensity by remote sensing to support conservation schemes. *Journal for Nature Conservation, 20*, 125-134

Geerken, R., Zaitchik, B., & Evans, J.P. (2005). Classifying rangeland vegetation type and coverage from NDVI time series using Fourier Filtered Cycle Similarity. *International Journal of Remote Sensing, 26*, 5535-5554

Goward, S.N., & Prince, S.D. (1995). Transient Effects of Climate on Vegetation Dynamics: Satellite Observations. *Journal of Biogeography, 22*, 549-564

Guo, X., Price, K.P., & Stiles, J.M. (2000). Modeling Biophysical Factors for Grasslands in Eastern Kansas Using Landsat TM Data. *Transactions of the Kansas Academy of Science (1903-), 103*, 122-138

Hamilton, G. (2013). Random Forest: The Landscape Toolbox. Jornada Experimental Range. In: https://wiki.landscapetoolbox.org/doku.php/remote_sensing_methods:random_forests

Juel, A., Groom, G.B., Svenning, J.-C., & Ejrnæs, R. (2015). Spatial application of Random Forest models for fine-scale coastal vegetation classification using object based analysis of aerial orthophoto and DEM data. *International Journal of Applied Earth Observation and Geoinformation, 42,* 106-114

Kruskal, J.B. (1964). Nonmetric multidimensional scaling: A numerical method. *Psychometrika, 29*, 115-129

Laliberte, A.S., Fredrickson, E.L., & Rango, A. (2007). Combining decision trees with hierarchical object-oriented image analysis for mapping arid rangelands. *Photogrammetric Engineering and Remote Sensing, 73*, 197-207

Lawrence, R.L., Wood, S.D., & Sheley, R.L. (2006). Mapping invasive plants using hyperspectral imagery and Breiman Cutler classifications (randomForest). *Remote Sensing of Environment, 100,* 356-362

Liaw, A., & Wiener, M. (2002). Classification and Regression by Random Forest. *R News, 2*, 18-22

Lowe, B., & Kulkarni, A. (2015). Multispectral Image Analysis Using Random Forest. *International Journal on Soft Computing, 6*, 1-14

McCune, B., & Mefford, M. (2002). PC-ORD for windows. *Multivariate analysis of ecological data. Version, 6*

Mellor, A., Haywood, A., Stone, C., & Jones, S. (2013). The Performance of Random Forests in an Operational Setting for Large Area Sclerophyll Forest Classification. *Remote Sensing, 5*, 2838-2856

Miller, B.J., Reading, R.P., Biggins, D.E., Detling, J.K., Forrest, S.C., Hoogland, J.L., Javersak, J., Miller, S.D., Proctor, J., Truett, J., & Uresk, D.W. (2007). Prairie dogs: An ecological review and current biopolitics, *Journal of Wildlife Management, 71,* 2801-2810

Mishra, N.B., & Crews, K.A. (2014). Mapping vegetation morphology types in a dry savanna ecosystem: integrating hierarchical object-based image analysis with Random Forest. *International Journal of Remote Sensing, 35,* 1175-1198

Mitchell, S., Palmquist, K., Cohen, S., & Christensen, N.L. (2015). Patterns of vegetation composition and diversity in pine-dominated ecosystems of the Outer Coastal Plain of North Carolina: Implications for ecosystem restoration. *Forest Ecology and Management, 356,* 64-73

Mutanga, O., Adam, E., & Cho, M.A. (2012). High density biomass estimation for wetland vegetation using WorldView-2 imagery and random forest regression algorithm. *International Journal of Applied Earth Observation and Geoinformation, 18,* 399-406

Nitze, I., Barrett, B., & Cawkwell, F. (2015). Temporal optimisation of image acquisition for land cover classification with Random Forest and MODIS time-series. *International Journal of Applied Earth Observation and Geoinformation, 34*, 136-146

Oesterheld, M., Loreti, J., Semmartin, M., & Sala, O.E. (2001). Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *Journal of Vegetation Science, 12*, 137-142

Pu, R.L., Landry, S., & Yu, Q.Y. (2018). Assessing the potential of multi-seasonal high resolution Pleiades satellite imagery for mapping urban tree species. *International Journal of Applied Earth Observation and Geoinformation, 71*, 144-158

Ramoelo, A., Cho, M.A., Mathieu, R., Madonsela, S., van de Kerchove, R., Kaszta, Z., & Wolff, E. (2015). Monitoring grass nutrients and biomass as indicators of rangeland quality and quantity using random forest modelling and World View-2 data. *International Journal of Applied Earth Observation and Geoinformation, 43*, 43-54

Schmidtlein, S., Zimmermann, P., Schüpferling, R., & Weiß, C. (2007). Mapping the floristic continuum: Ordination space position estimated from imaging spectroscopy. *Journal of Vegetation Science*, *18*, 131-140

Shi, Y.F., Wang, T.J., Skidmore, A.K., & Heurich, M. (2018). Important LiDAR metrics for discriminating forest tree species in Central Europe. *Isprs Journal of Photogrammetry and Remote Sensing, 137,* 163-174

South Dakota Climate and Weather, 2017 *South Dakota Climate and Weather Mesonet at SDSTATE* Available at: https://climate.sdstate.edu/archive/ (2017), Accessed 1st Dec 2017

Wehlage, D.C., Gamon, J.A., Thayer, D., & Hildebrand, D.V. (2016). Interannual Variability in Dry Mixed-Grass Prairie Yield: A Comparison of MODIS, SPOT, and Field Measurements. *Remote Sensing, 8,* 19

Xia, J.S., Yokoya, N., & Iwasaki, A. (2018). Fusion of Hyperspectral and LiDAR Data with a Novel Ensemble Classifier. *Ieee Geoscience and Remote Sensing Letters, 15*, 957-961

Yu, Y., Li, M.Z., & Fu, Y. (2018). Forest type identification by random forest classification combined with SPOT and multitemporal SAR data. *Journal of Forestry Research*, *29*, 1407-1414

Zhong, L., Gong, P., & Biging, G.S. (2014). Efficient corn and soybean mapping with temporal extendibility: A multi-year experiment using Landsat imagery. *Remote Sensing of Environment*, *140*, 1-13

Zhou, T., Zhao, M.F., Sun, C.L., & Pan, J.J. (2018). Exploring the Impact of Seasonality on Urban Land-Cover Mapping Using Multi-Season Sentinel-1A and GF-1 WFV Images in a Subtropical Monsoon-Climate Region. *Isprs International Journal of Geo-Information, 7*

Table 2.1. Acquisition dates of Pleiades satellite imagery tasked for each month (June – October) in 2015 and 2016.

2015 Dates of Acquisition	2016 Dates of Acquisition
6/1/2015	6/5/2016
7/9/2015	7/2/2016
8/4/2015	8/2/2016
9/1/2015	9/11/2016
10/8/2015	10/1/2016

Table 2.2: Similarity index (Sorensen (Bray-Curtis) distance method) values averaged by plot across plant communities.

Community[1]	Similarity Index (%)
COOL vs. SNOW	27.9
COOL vs. WARM	27.6
SNOW vs. WARM	21.5
PDG vs. PDF	15.6

[1] Plant communities on prairie dog towns are grass-dominated (PDG) and forb-dominated (PDF); plant communities in off-town areas are cool season grass-dominated (COOL), warm season grass-dominated (WARM), and snowberry-dominated (SNOW).

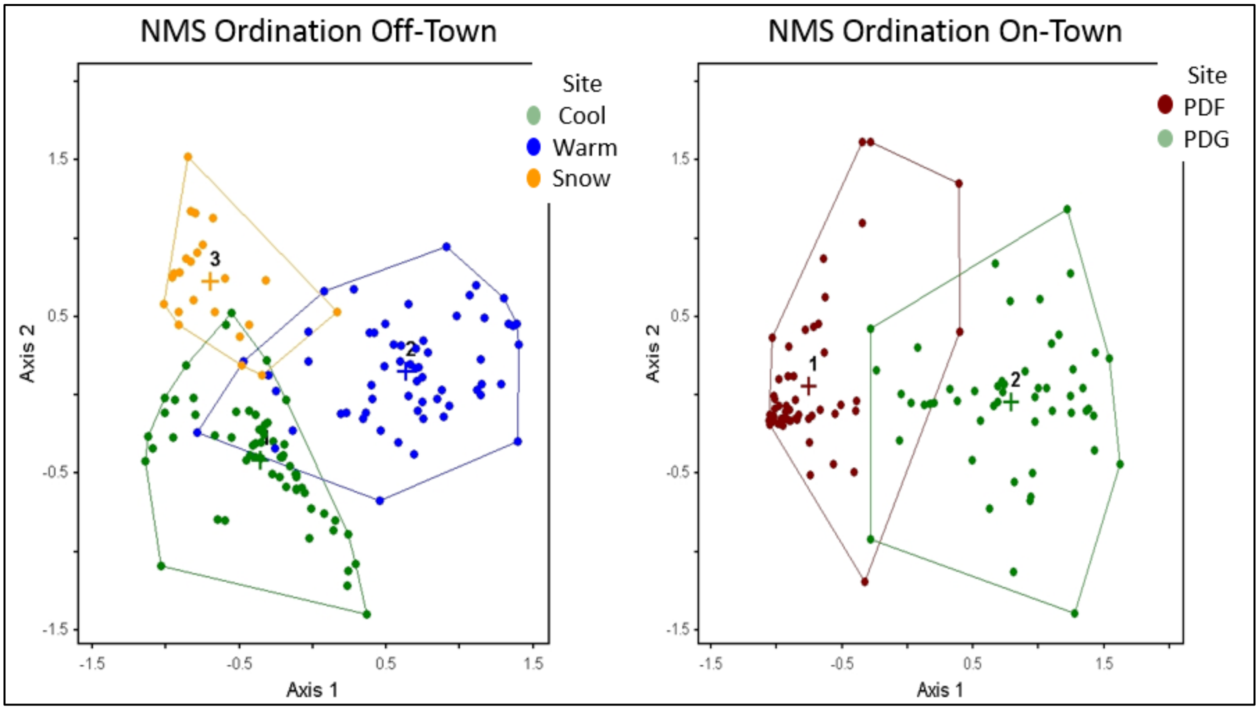

Figure 2.1. NMS ordination plots for plant communities located on and off of prairie dog towns, based on plant cover by species data collected in 2016 on the study site in north central South Dakota. Plant communities on prairie dog towns are grass-dominated (PDG) and forb-dominated (PDF); plant communities in off-town areas are cool season grass-dominated (COOL), warm season grass-dominated (WARM), and snowberry-dominated (SNOW).

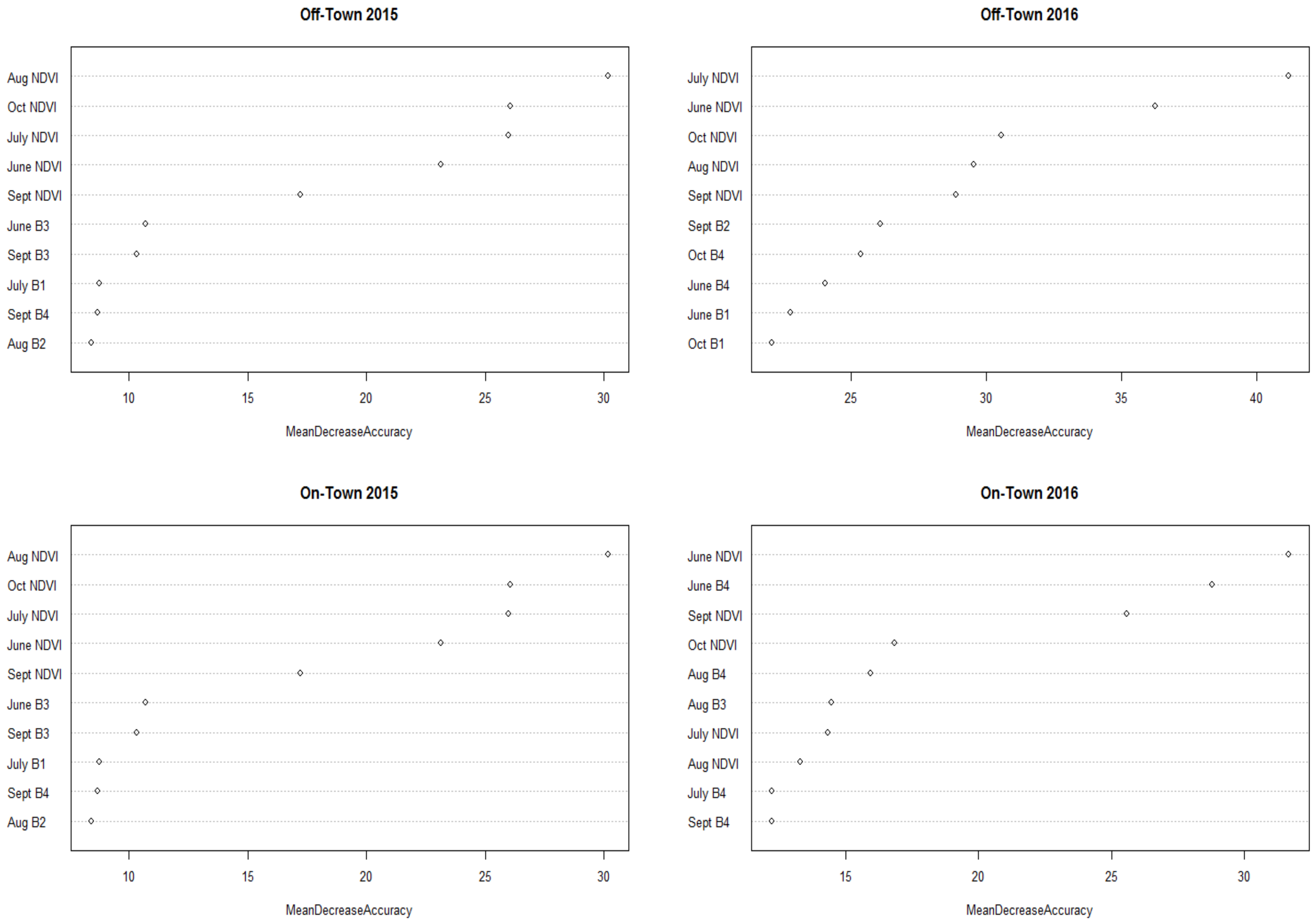

Figure 2.2: Variable importance reported as mean decrease in accuracy. Ten most important variables are shown, with B1 and B4 corresponding to spectral bands 1 and 4 respectively from Pleiades image. Variable importance is determined by the model output as the decrease in accuracy due to the exclusion of that variable during the out of bag error calculation process. Higher mean decrease in accuracy variables are more important in classifying the data.

Table 2.3: Out of Bag misclassification error rates (%) for each plant community for 2015, 2016, and combined year random forest models.

Plant Community[1]	2015 Model	2016 Model	2015-2016 Combined Model
COOL	0.20%	0.20%	0.03%
SNOW	2%	2%	0.60%
WARM	3%	5%	0.70%
PDG	0.30%	0.20%	0.07%
PDF	0.90%	0.70%	0.30%

[1] Plant communities on prairie dog towns are grass-dominated (PDG) and forb-dominated (PDF); plant communities in off-town areas are cool season grass-dominated (COOL), warm season grass-dominated (WARM), and snowberry-dominated (SNOW).

Table 2.4: Percent of pixels within each area (prairie dog town and off-town) for each plant community that remain unchanged and are changed between class belonging between 2015 and 2016 models.

Community Location	Transitions[1]	Percent of Total Area Pixels
Prairie Dog Town	Unchanged Pixels	93.3
	PDG ↔ PDF	6.7
Off-Town	Unchanged Pixels	75.7
	COOL ↔ SNOW	14.1
	COOL ↔ WARM	6.7
	SNOW ↔ WARM	3.5

[1] Plant communities on prairie dog towns are grass-dominated (PDG) and forb-dominated (PDF); plant communities in off-town areas are cool season grass-dominated (COOL), warm season grass-dominated (WARM), and snowberry-dominated (SNOW).

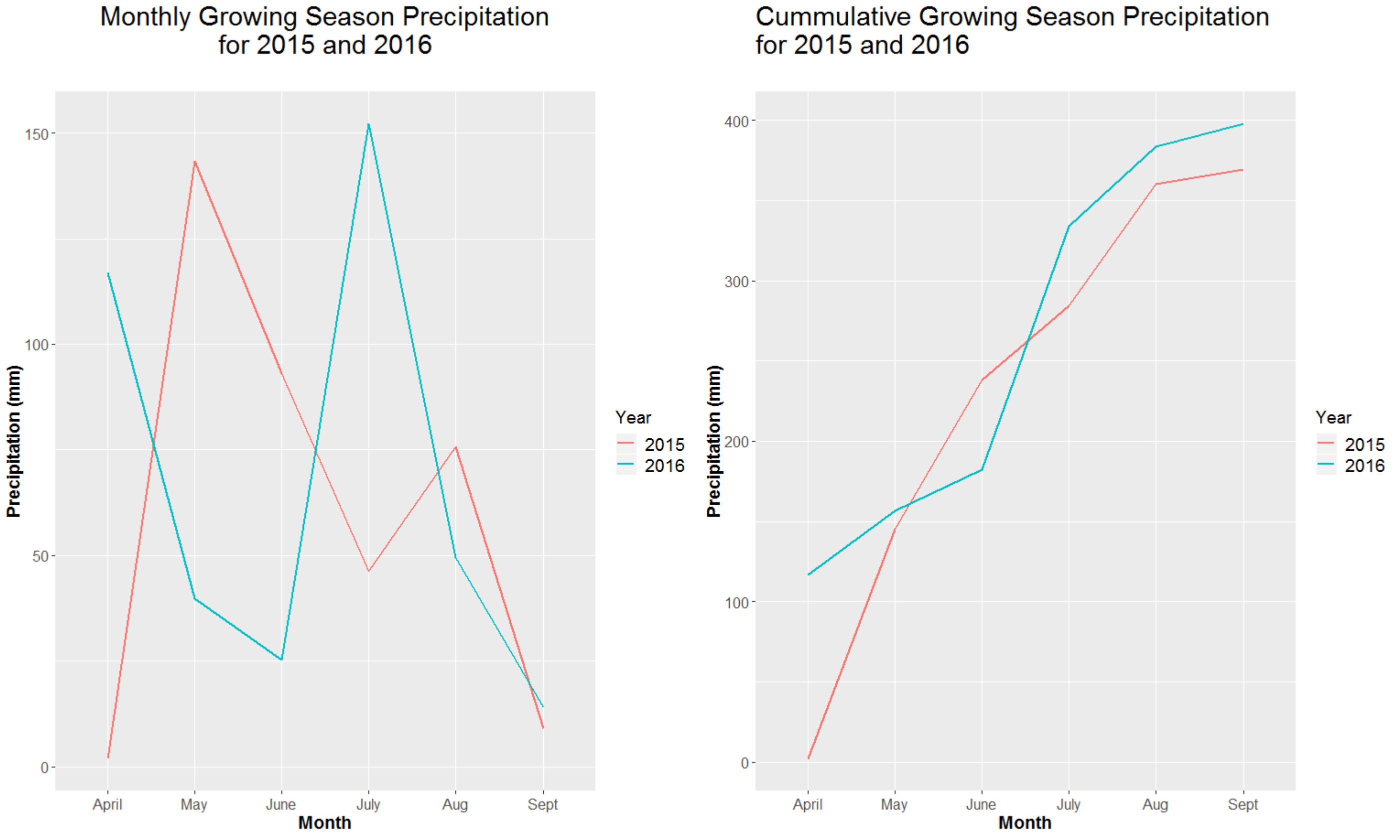

Figure 2.3: Monthly and cumulative growing season precipitation patterns for 2015 and 2016 recorded at a weather station located on the study area in north central SD (45.737296 N, -100.657540 W)(South Dakota Mesonet 2018).

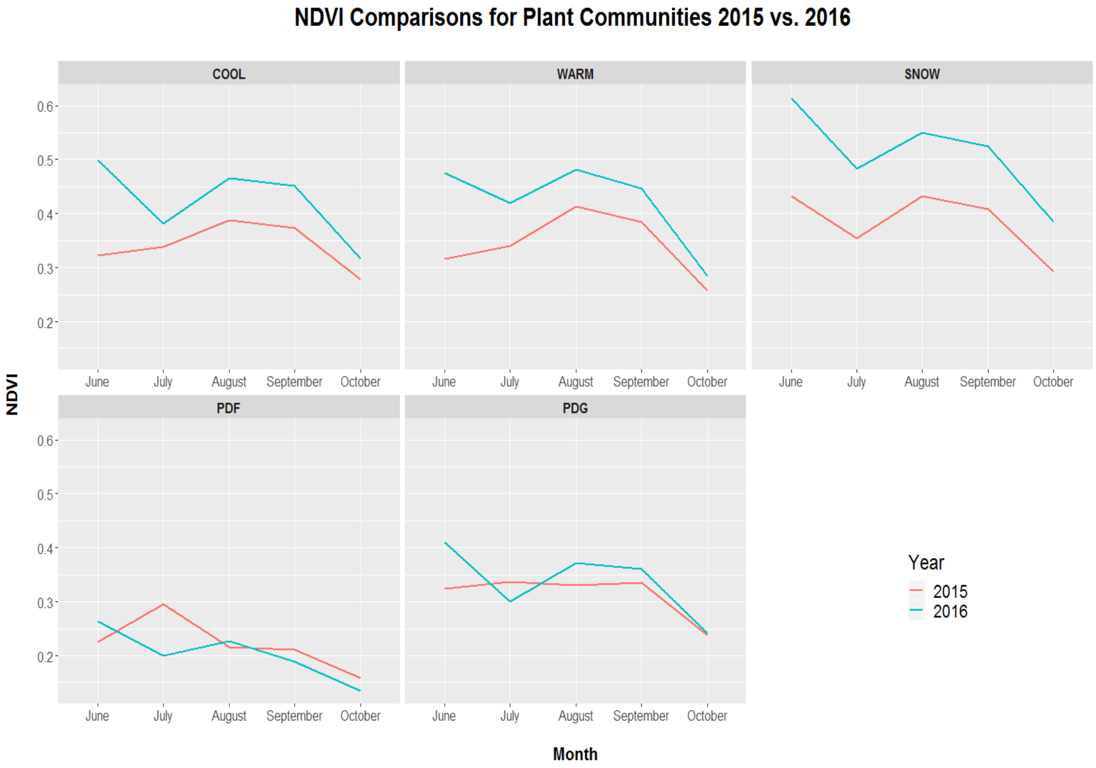

Figure 2.4: Comparison of mean monthly NDVI for training polygons in five plant communities on the study site in north central SD. Plant communities on prairie dog towns are grass-dominated (PDG) and forb-dominated (PDF); plant communities in off-town areas are cool season grass-dominated (COOL), warm season grass-dominated (WARM), and snowberry-dominated (SNOW).

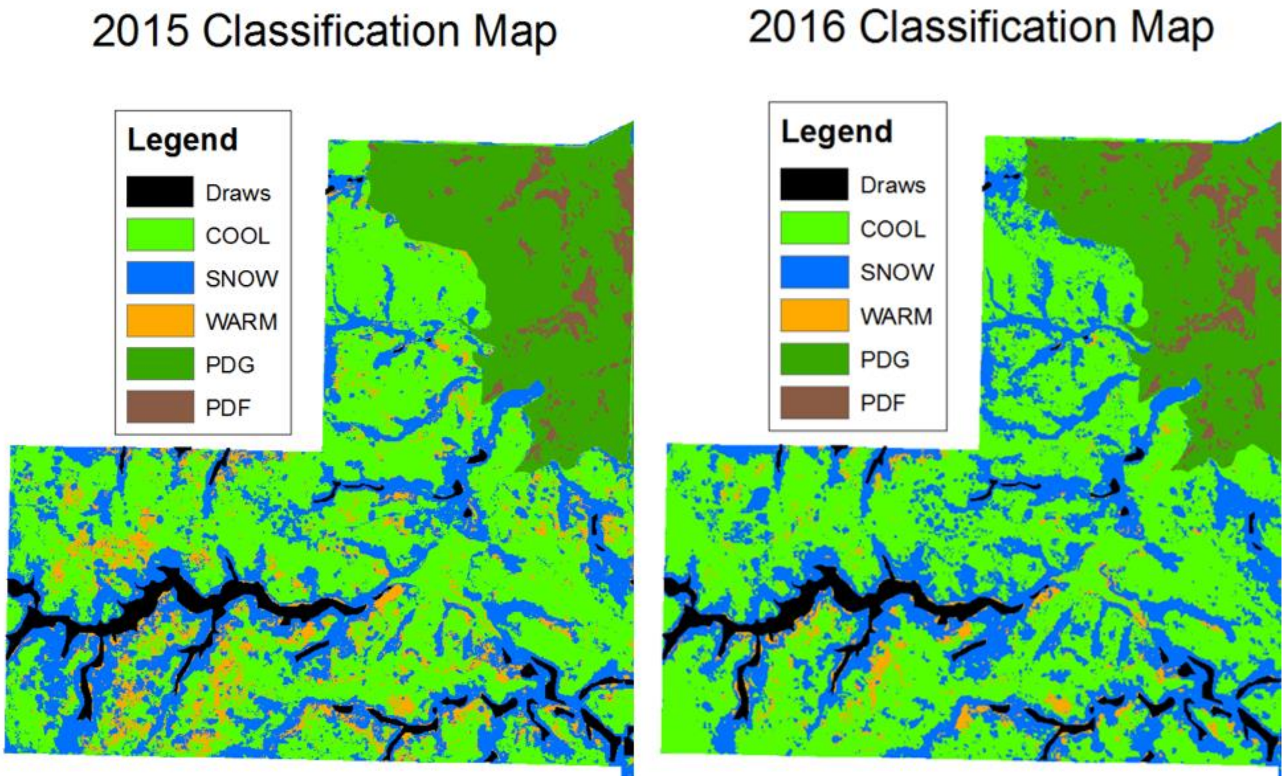

Figure 2.5: Random forest classification maps from 2015 and 2016 of one pasture in the study area in north central South Dakota. Plant communities on prairie dog towns are grass-dominated (PDG) and forb-dominated (PDF); plant communities in off-town areas are cool season grass-dominated (COOL), warm season grass-dominated (WARM), and snowberry-dominated (SNOW).

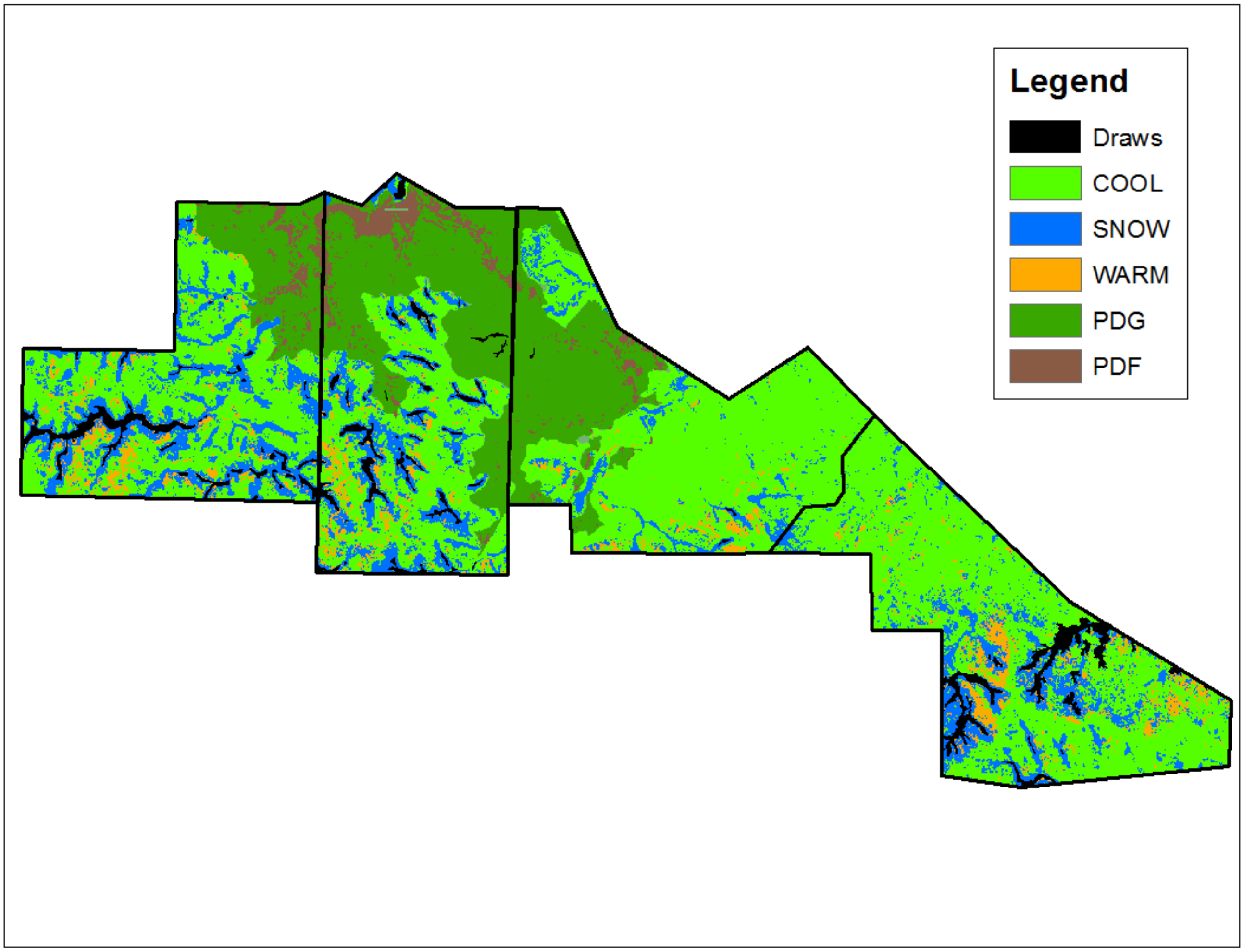

Figure 2.6: Final random forest generated thematic map of the entire study site in north central South Dakota produced from the combined 2015-2016 imagery data. Plant communities on prairie dog towns are grass-dominated (PDG) and forb-dominated (PDF); plant communities in off-town areas are cool season grass-dominated (COOL), warm season grass-dominated (WARM), and snowberry-dominated (SNOW).

Chapter 3: Technical Note: A Method to Streamline Processing of Livestock GPS Collar Data

This paper is currently in print in *Rangeland Ecology & Management* under the citation:

Brennan, J., Johnson, P., & Olson, K. (2019). Technical Note: Method to Streamline Processing of Livestock Global Positioning System Collar Data. *Rangeland Ecology & Management*, *72*, 615-618

Chapter 4: Grazing Behavior, Forage Quality, And Intake Rates Of Livestock Grazing Pastures Occupied By Prairie Dogs

Abstract

Prairie dogs have long been seen as competing with cattle. Prairie dogs can reduce the carrying capacity on rangelands by up to 50% through direct consumption of vegetation and by clipping plants to improve predator detection. Studies have shown that forage quality and digestibility are greater on prairie dog towns than off-town, however research is lacking that quantifies rates of forage and nutrition intake by cattle. In 2012-2016, a study was conducted in northcentral South Dakota to evaluate livestock grazing behavior, diet quality, and forage intake on three plant communities in pastures occupied by prairie dogs. Plant communities studied were grass-dominated on-town sites (PDG), forb-dominated on-town sites (PDF), and grass dominated off-town sites (NPD). Three pastures with varying levels of prairie dog occupation (0%, 20%, and 40%) were studied. Pasture stocking rates were adjusted to account for the level of forage removed by prairie dogs (50% of on-town forage removed). Each pasture was grazed by a separate herd of yearling steers, a random subset of which were fitted with GPS collars equipped with motion sensors to determine graze locations. Daily time spent grazing was estimated for each plant community and averaged by month for each pasture. Forage quality and intake were estimated using ruminally-fistulated steers that were allowed to graze in 30 minute increments in temporary exclosures within each plant community and pasture for June, July, and August of each year. Rumen diet samples were weighed and analyzed for OM, CP, NDF, and ADL. Intake was calculated as the rate of OM per minute and multiplied by average monthly grazing time based on GPS collar data. Livestock grazing preference decreased linearly on grass dominant sites on-town and increased linearly for off-town sites through the growing season. CP content was significantly higher (P = 0.002) on the PDF sites versus the PDG and NPD sites, however, few other differences in forage quality were evident between spatially dominant PDG and NPD communities. OM intake rates were similar between PDG and NPD communities, however PDF intake rates were reduced 59% compared with off-town sites. Results from this study indicate that grass dominant communities on prairie dog colonies should be considered as valuable for grazing livestock, but older core areas of prairie dog towns provide no nutritive value to foraging animals. Livestock performance was higher on prairie dog colonized pastures, suggesting that increased diet diversity within pastures colonized by prairie dogs may be beneficial to grazing livestock provided forage quantity isn't limited. Results from this study will inform land managers of potential forage contributions of on-town and off-town plant communities in pastures colonized by prairie dogs.

Introduction

Black-tailed prairie dogs have been identified as a keystone species in prairie ecosystems and ecosystem engineers providing habitat to other plant and wildlife species (Davidson et al. 2010; Kotliar et al. 1999). They also increase biotic diversity and the diversity of community structure while playing an important role in ecosystem function (Hopson et al. 2015). In semi-arid grasslands of the southwest, black-tailed prairie dogs were shown to increase essential ecosystem services of water infiltration rates, carbon storage rates, and soil stabilization (Martinez-Estevez et al. 2013). Prairie dog colonies are, however, also viewed as being very detrimental to beef production systems by limiting carrying capacity of rangelands.

Prairie dogs reduce available forage through direct consumption, clipping plants to increase predator detection, building soil mounds, and changing species composition (Derner et al. 2006). Colonization by prairie dogs and subsequent increases in grazing pressure can shift plant communities from mid-grass dominant to those characterized by high cover of perennial shortgrasses and annual forbs (Winter et al. 2002). Because graminoids are extensively used by prairie dogs, they eventually lose their competitive advantage over other functional groups (Detling 1998). Older core areas of prairie dog towns are often characterized by high percentage bare ground, low vegetation production, and dominance by annual forb and dwarf shrub species; areas more recently colonized typically remain grass dominated (Guenther and Detling 2003, Coppock et al., 1983). A shift in plant communities in the Northern Great Plains from mid-grass to shortgrass or annual forb domination has a potentially large, negative impact on livestock production.

Cattle and prairie dogs exhibit high dietary overlap, up to 60% in a mixed-grass prairie, which is a cause of concern for livestock producers (Miller et al. 2007). Derner et al. (2006) showed that an increase in prairie dog town size within pastures led to a decrease in cattle weight gains, however the decrease was not proportional to the increase in colony size. Although forage quantity is often limited, plant nutrient content and forage digestibility are improved within prairie dog town sites (Coppock et al. 1983). Through repeated defoliation, vegetation on prairie dog towns is often maintained in an immature state, with higher nutritive content (Olson et al. 2016). Johnson-Nistler et al. (2004) measured forage quantity and quality on northern mixed grass prairie in Montana, and found that sites occupied by prairie dog towns were characterized by a decrease in standing crop biomass and standing crop crude protein; concentration of crude protein in vegetation on colonized sites was, however, higher.

Livestock are able to select a balanced diet given suitable choices on rangelands that contain a diverse array of plant species and growth stages with varying levels of nutritional value (Provenza 1991). At low levels of colonization, livestock diets may be improved as they select a diet from a variety of mature and immature forages on- and off-town. Alternatively, dry matter intake may be limited in pastures with high levels of occupation, likely negating any potential gains in dietary quality. While limited research exists on prairie dog impacts on forage quality, abundance, and impact on livestock weight gains, even less research has evaluated how prairie dogs impact livestock grazing behavior, nutrient intake, and performance.

Understanding cattle grazing behavior can improve opportunities to manage prairie dog occupied pastures for better livestock performance and optimization of rangeland health. Guenther and Detling (2003) reported cattle selection of prairie dog sites differed little from random use, however the largest percentage of pasture colonized in their study was 10.7%. Within the Chihuahua desert grasslands, researchers reported that cattle preferentially grazed on prairie dog colonies in the fall and winter grass dormancy season and spent most of their time foraging at off colony sites in the summer (Sierra-Corona et al. 2015). Studies on livestock grazing behavior on prairie dog towns, however, are limited and further research is needed to understand how changes in forage quality may be driving changes in grazing behavior across multiple growing seasons.

In 2012 a large, multi-state, multi-institution, collaborative project was initiated with the overall goal of increasing food security for the people on the Standing Rock

Sioux Reservation in North Dakota and South Dakota by improving livestock production on rangelands with extensive prairie dog occupation. A major component of that effort was to study livestock use of on- and off-town plant communities to determine their preferences and to evaluate the quality and quantity of forages that cattle obtain from the different plant communities on the pastures. Objectives of this study were to 1) evaluate relationships between on- and off-town plant communities and cattle grazing locations to identify patterns and trends in livestock grazing behavior throughout the growing season, 2) evaluate diet nutrient composition and intake by cattle on plant communities on- and off-town over the grazing season, and 3) study livestock performance in response to level of prairie dog occupation within the pastures.

Methods

All procedures involving animals were approved by the SDSU Institutional Animal Care and Use Committee (Approval no. 12-027A & 15-039A).

Study Area

The study area (45.74N, 100.65W) was located near McLaughlin, South Dakota on a northern mixed-grass prairie ecosystem. Predominant soils at the site were clays and loams. Ecological Sites (ES) and the plant communities they support varied widely. Loamy and Clayey were the predominant ES at the site, with inclusions of Dense Clay, Shallow Clay, Clayey, and Thin Claypan (Barth et al. 2014). Vegetation on the site was largely native, including western wheatgrass (*Pascopyrum smithii* Rydb.), green needlegrass (*Nassella viridula* Trin.), and needle-and-thread (*Hesperostipa comata* Trin. & Rupr), intermixed with blue grama (*Bouteloua gracilis* Willd. Ex Kunth), buffalograss

(*Bouteloua dactyloides* Nutt.), and sedges (*Carex* spp.). Kentucky bluegrass (*Poa gracilis* Boivin & Love) was an invasive exotic of concern at the site. Plant communities on areas occupied by prairie dog towns on the site were largely dominated by western wheatgrass and shortgrasses intermixed with patches of bare ground and annual forb-dominated areas. Common forbs on prairie dog towns included annuals such as prostrate knotweed (*Polygonum aviculare* L.), fetid marigold (*Dyssodia papposa* Vent.), and dwarf horseweed (*Conyza ramosissima* Cronquist), as well as perennials such as scarlet globemallow (*Sphaeralcea coccinea* Nutt.).

A weather station has been maintained on site from May 2013 operated by South Dakota Mesonet (South Dakota Climate and Weather, 2017). Climate data from 2012 until April 2013 was acquired from a nearby weather station in Mobridge, SD (40 km east, U.S. Climate Data, 2017). Precipitation totals were compared between the Mobridge weather station and the onsite weather station for similarity in 2014-2016; average yearly difference between the sites was 71 mm, with the Mobridge site consistently having higher estimates. Historical (1981-2010) mean annual precipitation at the Mobridge weather station was 414 mm (U.S. Climate Data, 2017). Total annual (Jan.-Dec.) precipitation (mm) for 2012-2016 was 350.5, 496.8, 460.5, 427.2, and 456.7, respectively.

Experimental Procedures

Three pastures at the study site, each approximately 200 ha in size, were established to have varying levels of prairie dog occupation (0%, 20%, 40%). Total area of the pastures occupied by prairie dog colonies was 122 ha. Boundaries of prairie dog towns were mapped using a handheld GPS unit. The 0% colonized pasture was maintained at that level over the duration of the study. Pasture boundaries were established to include similar proportions of landscape features such as ecological sites and topography. Pastures were grazed continuously by yearling steers from June until early October; stocking rate was set to achieve 50% total (cattle + prairie dog) utilization. Previous research on prairie dog colonies within western South Dakota has demonstrated cattle utilize only half as much forage on a prairie dog town compared to the same ES off-town (Gabrielson 2009; Stoltenberg 2004). Pastures were stocked for similar grazing pressure (animal unit month [AUM]) based on expected forage availability on and off prairie dog towns, adjusted for the percentage of pasture colonized. Formula for calculating total available forage was:

$$Available\ Forage\ Off\ Town = Production\ Off\ Town \times Utlization \times \big(Allotment \times (1 - \%\ Colonization)\big)$$

$$Availble\ Forage\ On\ Town = (Production\ Off\ Town \times 0.5) \times Utlization \times (Allotment \times \%\ Colonization)$$

$$Total\ Available\ Forage = Availble\ Forage\ On\ Town + Available\ Forage\ Off\ Town$$

Stocking rates for pastures with 0%, 20%, and 40% prairie dog occupation were 0.8, 1.03, and 1.36 ha/AUM, based on mean steer body weight of 357 kg with a grazing season of 4.33 months (Table 4.1).

Three plant communities of interest were identified in the study: grass-dominated off-town locations (i.e. no prairie dogs; **NPD**), annual forb-dominated sites on-town (i.e. prairie dog forb; **PDF**), and grass-dominated sites on-town (i.e. prairie dog grass; **PDG**). Plant community location was mapped using remotely sensed high resolution satellite imagery (Brennan et al. 2019). Remote sensing analysis generated a thematic raster map of plant communities for the study site. For the pasture with 20% level of colonization, the proportion of each plant community was: 81% NPD, 16% PDG, and 3% PDF. For the pasture with 40% level of colonization, the proportion of each plant community was: 58% NPD, 36% PDG, and 6% PDF.

Livestock Behavior

Locations and behavior of cattle were determined through the use of Lotek 3300LR GPS collars (Lotek Wireless, New Market, Ontario, Canada) equipped with motion sensors to discriminate between graze and non-graze locations. The collars were set to record a location fix and average motion sensor reading every 5 minutes. Livestock GPS data were collected every year from 2012 through 2016. Within each pasture, a subset of steers was outfitted with collars and allowed to graze freely. The number of steers collared per pasture varied from n = 2 to n = 6 depending on collar failure. Steers were gathered into corrals monthly to download data and charge batteries. A classification tree algorithm was used to determine whether a GPS fix was classified as a graze or non-graze location based on methods described by Augustine and Derner (2013).

Using the ‘extract’ function from Program R, the pixel value (NPD, PDG, and PDF) was extracted from the thematic plant community map for each GPS fix. Total number of daily graze fixes within each plant community was calculated for each steer and multiplied by fix interval (5 minutes) to get an estimate of the total daily time spent grazing for each steer in each pasture and plant community within a pasture. For each steer, daily preference indexes (PI) were calculated for each plant community. Daily time spent grazing within a given plant community was divided by the total daily time spent grazing to calculate the proportion of daily time spent grazing for each plant community. Preference index was calculated by dividing daily proportion of grazing time in each plant community by the percentage of the pasture the plant community occupied. An example would be an animal in the 20% colonized pasture that spent 500 minutes grazing for a given day, and 80 of those minutes were in the PDG plant community. This would result in 16% of the total time spent grazing that day on the PDG plant community. Dividing this by the proportion the PDG plant community occupied in that pasture (16%) would yield a PI of 1. A PI of 1 indicates the resource was being used in proportion to its availability; a PI greater than 1 indicates preference and a PI less than 1 indicates a resource was not preferred. Daily PI data were averaged by month for June, July, August, and September for each steer within each pasture and plant community.

Diet Quality

Six ruminally cannulated steers were used to determine the nutritive quality and rate of intake of forage consumed by steers grazing in the PDF, PDG, and NPD plant communities. Sampling took place over the span of one week in each of June, July, and August for 2012-2016. Temporary electric fence enclosures were constructed on PDF, PDG, and NPD plant communities within each pasture the day prior to sampling. Enclosure sizes were approximately 625 m^2. Two weeks prior to the sampling and when not being used for data collection, the cannulated steers were put in experimental pastures consisting of forage similar to the forage to be sampled. Steers were held in temporary pastures (each much larger than the sampling enclosures) during the week of sampling.

At dawn on each sampling day, steers were herded into corrals and their rumens evacuated based on techniques described by Lesperance et al. (1960) and Olson (1991). Each steer was then transported to and allowed to graze in an enclosure for 30 minutes.

Typically three steers were used to sample each enclosure during each sampling period. Time spent grazing within the enclosure was recorded. Steers were taken back to the corrals and all newly grazed masticate was removed from the rumen. Masticated samples were immediately weighed following collection for rate of intake calculations. A subsample was collected and frozen for diet analysis. Rumens were rinsed and each steer was transported to a second enclosure and allowed to graze for 30 minutes. Steers were again returned to the corrals and masticated samples from the second bout of sampling were removed and weighed, and a subsample was collected and frozen. After two enclosures were sampled per day per steer, the rumen contents that had been removed at the beginning of the day were replaced. Over the week of sampling, NPD, PDG, and PDF in each pasture were sampled once.

Frozen samples were lyophilized and ground to pass a 2-mm screen in a Standard Wiley Mill, No. 3 (Arthur H. Tomas Co., Philadelphia, PA, USA). Samples were analyzed for determination of DM, OM, CP (AOAC 1990), NDF, ADL (Goering and Van Soest 1970), and IVOMD (Tilley and Terry 1963). All results for diet quality are reported on an OM basis.

Intake

Rate of forage intake (g OM/min) was estimated using the weighed masticated sample from each cannulated steer sampling. Masticated sample weights were converted to grams OM and divided by the duration of grazing during the sampling period (typically 30 minutes) to give rate of intake. Crude protein intake rate (g CP/min) was estimated by multiplying the rate of OM intake by the percentage of crude protein on an

OM basis. Digestible OM intake (DOMI) rate (g DOMI/min) was estimated by multiplying the rate of OM intake by the percentage of IVOMD.

Total daily forage intake for each month, pasture, and plant community was calculated based on a method described by Chacon et al. (1976) and modified to use GPS collars instead of vibracorders to calculate grazing time. Daily grazing time (minutes) was estimated by averaging steer grazing time from GPS collars for each pasture, plant community, month, and year. Average daily grazing time was multiplied by the rate of forage intake for each corresponding pasture, plant community, month, and year to estimate total daily forage intake (g OM/day). Additionally, average daily grazing time was multiplied by rate of CP intake and rate of DOMI to estimate total daily CP intake (g CP/day) and total daily DOMI (g DOMI/day).

Preference indexes were estimated by dividing the daily forage intake for each year, month, pasture, and plant community by the sum of total daily forage intake for the corresponding sampling period to get a proportion of intake harvested from each plant community. This proportion was then divided by the percentage of the pasture the plant community occupied to calculate intake PI. An example would be an animal in the 20% colonized pasture that consumed an estimated 10,000 g OMI in a day, and 1600 g of the OMI was from the PDG plant community. This would result in 16% of the total daily OMI coming from the PDG plant community. Dividing this by the proportion the PDG plant community occupied in that pasture (16%) would yield a PI of 1. Intake PI was additionally calculated for CP intake and DOMI.

Animal Performance

At the beginning and end of each grazing season, unshrunk steer body weights were recorded on two consecutive days for calculation of individual animal performance and production. Steers were allowed to graze forage on site for a minimum of one week prior to initial weights being recorded to allow gut fill to be adapted to pasture forage. Average daily gains (ADG) were calculated for each animal (kg/head/day). Total pasture production (kg/ha) was also calculated to evaluate the tradeoffs between animal performance and production per unit of land as a result of reduced stocking rates to accommodate forage removed by prairie dogs.

Statistical Analyses

All statistical analysis was done using SAS (SAS Institute, Cary, NC). At the onset of the project, the goal was to study livestock interactions with prairie dogs at a larger ranch scale. Thus, to keep pastures large enough to be at ranch scale, there was only one replicate pasture for each level of prairie dog colonization (0%, 20%, and 40%). Due to the duration of the study (5 years), there was replication through time.

Total daily time spent grazing was analyzed by averaging estimated daily steer grazing times for each year, pasture, and month. Pasture had three levels (0%, 20%, and 40% prairie dog colonization) and month had 4 levels (June, July, August, and September). Total daily grazing time was analyzed using Proc Mixed. Pasture, month, and their two-way interaction were fixed effects and year was a random effect. Grazing time PI data was analyzed by averaging estimated daily steer PI across each year, pasture, plant community, and month. Only pastures at 20% and 40% colonization were analyzed for PI, as PI could not be calculated in a pasture with 100% NPD. PI data was analyzed using Proc Mixed, with PI as the response variable. Pasture, plant community, month, and all two- and three- way interactions were fixed effects in the model and year was a random effect. Contrasts statements were used to test two specific treatment comparisons: 1) on- versus off-town plant communities (PDG & PDF vs. NPD) and 2) grass versus forb plant communities (NPD & PDG vs. PDF). Additionally, orthogonal polynomial contrasts statements were used to test PI for each plant community for a significant linear, quadratic, or cubic relationship with month.

Diet metrics (CP, NDF, ADL, and IVOMD) were averaged by year, pasture, plant community, and month and analyzed using Proc Mixed. Pastures at 20% and 40% colonization were analyzed for diet metrics, as the 0% colonized pasture did not contain PDF and PDG plant communities. Diet metric was the response variable and pasture, plant community, month, and all two- and three- way interactions were fixed effects in the model. Diet metrics were analyzed using the same model as PI above.

Differences between NPD plant community diet metrics were analyzed between 0%, 20%, and 40% colonized pastures using Proc Mixed to test whether off-colony sites differed in forage quality between prairie dog and non-prairie dog occupied pastures. Pasture, month, and two-way interactions were fixed effects in the model, and year was a random effect. Month was specified as a repeated measure. Orthogonal polynomial contrasts statements were used to test whether each diet metric had a significant linear or quadratic relationship with month.

Intake measurements included rate, total daily, and PI for OM, CP, and DOMI. Measurements were averaged by year, pasture, plant community, and month and analyzed using Proc Mixed using the model previously described for PI. Pastures at 20%

and 40% colonization were analyzed for intake measurements, as the 0% colonized pasture did not contain PDF and PDG plant communities. Differences between the 0%, 20%, and 40% colonized pastures for OM, CP, and IVOMD intake rates and total daily OM, CP, and DOM intake for the NPD plant community were analyzed using Proc Mixed using the model previously described for diet quality metrics. Total daily intake for the 20% and 40% pastures were estimated by summing intake estimates across on- and off-town plant communities.

Livestock performance (ADG) and production (kg/ha) were averaged by year and pasture for the 0%, 20%, and 40% colonized pastures. Data was analyzed using Proc Mixed with pasture as a fixed effect and year as a random effect. Orthogonal polynomial contrasts statements were used to test whether performance and production had a significant linear or quadratic relationship with level of colonization (0%, 20%, or 40%).

For all models the Kenward-Roger option was used to estimate denominator degrees of freedom. When repeated measures were involved, the variance-covariance matrix was chosen in an iterative process wherein best fit was chosen based on the Bayesian Information Criterion. Least square means and standard errors were generated.

Results and Discussion

Livestock Behavior

For total time spent grazing, there were no significant interactions (P = 0.64) or main effects for pasture (P =0.44) or month (P =0.09). Overall average grazing time spent each day (least square means) was 7.45, 7.85, and 7.55 hours (SEM = 0.23) for the 40, 20, and 0 % occupied pastures, respectively. In his review of the literature, Kilgour et al. (2012) found that cattle spend between 6.8 and 13 hours grazing per day depending of forage quality and quantity. Studies have shown that livestock grazing times increase as available forage decreases (Chacon and Stobbs 1976; David et al. 1985; Scarnecchia et al. 1985). Lack of differences in grazing time between pastures and months, plus the relatively low time spent foraging on average, suggest that adequate forage was available in all pastures regardless of percent occupation by prairie dogs. The stocking rate imposed in this study that accounted for the percentage of forage removal attributed to prairie dogs likely meant cattle in these pastures did not need to increase grazing time in response to limited forage due to prairie dog competition.

Results from the grazing behavior PI analysis indicated a significant two-way interaction between pasture and plant community ($P = 0.0005$, Table 4.2) and between plant community and month ($P < 0.0001$, Table 4.3). Contrasts statements indicated that there was a significant difference between on-town and off-town plant communities for the 20% occupied pasture but not the 40% occupied pasture. The primary driver in the interaction appears to be PDG in the 20% occupied pasture, which exhibited a higher preference (1.58) than other plant communities. Habitat type preference is useful as long as it is used on a relative scale allowing habitats to be ranked (Aebischer et al. 1993). Several studies have used preference indexes (forage ratios) as a measurement of food selectivity (Jacobs 1974; Krueger 1972; Manning et al. 2017), however sensitivity of preference indexes to changes in areas with smaller proportions of habitat can potentially over-inflate importance. This may partially explain differences in pasture response. The smaller percentage of PDG in the 20% pasture may cause that community to be more sensitive to changes that are occurring relative to the 40% colonized pasture. In both the 20% and 40% colonized pastures, contrasts statements show that livestock significantly preferred grass plant communities over forb plant communities. Our results indicate that livestock are primarily selecting grass dominant sites over forb dominant sites within pastures containing prairie dogs. Previous research has shown that cattle primarily consumed graminoids in all seasons, and forbs contributed between 5-15% of cattle diets in a mixed-grass prairie (Hanley and Hanley 1982; Plumb and Dodd 1993). The PDF plant community represents older core areas within prairie dog colonies that have typically undergone the most severe disturbance. Grasses and grass-like cover is low (<10%), and species which do persist are primarily forb and shrub species (Hendrix 2018). Total plant species diversity has been shown to be reduced on older prairie dog towns, and dominated by fringe sage (*Artemisia frigida* Willd.) (Coppock et al. 1983). Plants able to sustain prolonged grazing pressure associated with these older core areas may be high in defense chemicals as a mechanism to deter herbivory, which would further deter livestock grazing of these sites.

Over the duration of the grazing season, NPD preference increased linearly with time while PDG preference decreased linearly with time (Table 4.3). The significant cubic relationship for PDF across months indicated that cattle had a preference for the forb community early in the grazing season, which leveled off near 1 in the middle, and the forb community was avoided at the end of the grazing season. The proportion of PDF plant community (3% and 6%) within the pastures may be small enough that PI values could be skewed. Livestock preferred grazing on-town locations relative to their abundance early in the grazing season, however, preference shifted toward off-town locations over time. Seasonal grazing fluctuations were also reported by Sierra-Corona et al. (2015), where livestock showed strong preference for foraging on prairie dog towns in fall and winter and spent most of their time foraging off colony in the summer in a Chihuahua desert grassland. These results and ours differed from Guenther and Detling (2003) who reported no significant seasonal differences (June- mid-August) for cattle grazing on prairie dog colonies during intensive surveys. Guenther and Detling (2003) indicated through road side surveys that cattle significantly selected for prairie dog towns, however, they concluded that the magnitude of the effect was small and likely differed little from random use. Within our study, cattle showed a preference for the PDG plant community, but similarly the magnitude of the effect was not that large.

Diet Quality

All diet metrics had a significant main effect of month (table 4.4). There was an overall decline in forage quality through time characterized by linear decreases in CP (also displayed a quadratic response) and IVOMD, and linear increases in NDF and ADL. Within a northern mixed grass prairie, Johnson et al. (1998) reported a linear decline in CP and IVOMD, whereas NDF and ADF increased linearly with advancing season (June-December). Within our study NDF had no other significant relationship besides month (P =0.037). Similarly, Johnson-Nistler et al. (2004) reported no significant difference in NDF between colonized and uncolonized sites for any plant functional group. ADL (P =0.008) and IVOMD (P =0.032) had significant pasture x plant community interactions (Table 4.2). Contrasts indicated a significant difference between grass and forb communities for ADL, with the PDF community having higher ADL than the two grass communities. Research has shown that dicots have higher lignin content than monocots (Boufennara et al. 2012), which is likely the cause of higher ADL values on the PDF community. Contrasts comparisons between on-town and off-town for ADL were mixed, with only the 20% occupied pasture having a significant difference, likely the result of higher ADL within the PDF community for that pasture. IVOMD had a significant contrast between on- versus off-town for the 40% occupied pasture. Mixed results for IVDMD of on- and off-colony forage samples were also reported by Augustine and Springer (2013), with differences and magnitude of effect varying between sites and whether standing dead biomass was included in the sample. No difference for IVDMD was observed by Johnson-Nistler et al. (2004) comparing forage on- and off- colony. Though statistically significant, differences between the 20% and 40% pastures for IVOMD were likely the result of sampling variability and were not biologically significant.

CP was the only diet metric with a significant plant community main effect (P =0.002). Least square means were: 12.2, 12.4, and 16.2 (SEM=0.82) for the NPD, PDG, and PDF plant communities, respectively. Contrasts indicated CP was different between on- and off-town (P = 0.01) and between grass and forb sites (P = 0.0004). Previous research has shown CP and nitrogen content on-colony to be higher compared to off-colony vegetation (Augustine and Springer 2013; Chipault and Detling 2013; Coppock et al. 1983; Johnson-Nistler et al. 2004). While these results appear similar to those observed in our study, the main difference was that the higher CP content was only associated with the forb dominant sites on-colony in our study. The main driver between CP content on-town versus off-town was higher CP content of the PDF community, which comprised a relatively small proportion of total area on prairie dog towns, with virtually no difference between the two grass communities. Connell et al. (2019) reported that CP content was 1.4 times higher in western wheatgrass samples on prairie dog colonies, and was significantly greater than on off colony sites throughout the growing season (June-August). It is likely that differences in our results and those of others may be attributed to the methods used in determining forage quality. Previous studies of the quality of forages on prairie dog towns have relied on clipping vegetation by hand, whereas this study examined the forage selected and consumed by cattle. Several studies have shown fistula samples contain significantly more protein than hand clipped samples due to animals' ability to select higher quality diets (Kiesling et al. 1969; Bredon et al. 1967; Weir and Torell 1959). They do this, in part, by initially removing the uppermost layer of vegetation composed primarily (>80%) of leaves (Chacon and Stobbs 1976). Thus it is likely that hand-clipped vegetation samples do not accurately represent what is actually removed by grazing livestock. The moderate to low stocking rates maintained on the prairie dog occupied pastures in this study ensured that forage was not limiting, and fistulated steers were likely able to select a higher quality diet than what was generally available to them, even in off-town locations.

Comparisons of CP, NDF, ADL, and IVOMD for the NPD community in the 0%, 20%, and 40% colonized pastures show no significant difference between pasture ($P > 0.05$ for all comparisons). This indicates there was no difference between pastures for off-town forage quality, regardless of whether a pasture was colonized or not. For all off-town diet metrics across all 3 pastures, there was a significant month main effect ($P < 0.05$), with a linear decline in CP and IVOMD, a linear increase in NDF, and a quadratic increase in ADL over time. Forage quality declines throughout the growing season are expected as vegetation matures over time.

Intake

All intake measurements had a plant community main effect ($P < 0.05$), and no ($P > 0.05$) main effects of pasture, month, or interactions (Table 4.5). For OM, CP, and DOM intake rates, there were significant contrasts between on- versus off-town communities and grass versus forb communities. The main driver of differences in on- versus off-town was the lower intake rate for the PDF plant community (9.86 g OM/min). Little difference existed between mean intake rates for PDG and NPD. These results indicate that animals grazing grass-dominated sites on-town were able to consume forage, CP, and digestible OM at similar rates compared with off-town locations. Though CP content was higher in the PDF plant communities, the relatively low production and high bare ground associated with these older core areas of prairie dog towns were depressing intake rates for OM, CP, and DOM.

Comparisons of total daily intake of OM, CP, and DOM indicate that cattle were getting a greater amount of their diet from off-town NPD communities versus the on-town communities. Given that intake rates were similar between NPD and PDG communities, the difference in total daily intake can be attributed to more time spent grazing off-town due to a greater abundance (total area) of that plant community. For the PDF plant community, total OM and CP intake least square means were numerically negative, and all total daily intake values on PDF were not different from zero. DOMI for the PDF community was less than 1% of total DOMI from the 3 communities combined. Previous research has shown that free ranging cattle prefer locations in pastures with higher than average CP and lower than average NDF (Ganskopp and Bohnert 2009). Within our study, there was no difference in NDF between the three plant communities. Though the PDF plant community had significantly higher CP content compared to the grass dominant communities, intake results indicate that forb dominant sites within prairie dog colonies provide little to no nutrient value to grazing livestock. The low production and high bare ground associated with older core areas of prairie dog colonies would likely depress intake rates to the point of negating any benefits received from an increased CP content associated with these communities. Within our study site, the percentage of pasture comprised of the PDF plant community was relatively small, but rangelands occupied by prairie dogs with a significant amount of older core areas would likely see a large reduction of carrying capacity for livestock production.

Estimation of intake is difficult due to changes in environmental factors, feed quality, and animals' physiological state (Coleman et al. 2014). Coleman (2005) noted that variability among animals given the same diet, particularly a forage diet, may be quite high, ranging from 10 to 30% of the mean. Empirical equations for predicting intake typically only account for 50-70% of the variation in intake, often with relatively high standard errors (Galyean and Gunter 2016). Given the difficulties in measuring intake, especially as it applies to free ranging animals, data reported in Table 4.5 was likely not a true estimate of daily intake for yearling steers grazing in the pastures. However, relative differences among means are reflective of pasture, plant community, and monthly effects on intake. Reports of estimated cattle forage intake on prairie dog colonies are lacking in the literature, making direct comparisons of observations difficult. However, total estimated daily OM intake was 8.93 kg/day within prairie dog occupied pastures. Beginning steer weights over the entire project averaged 325 kg/steer and ending weights averaged 424 kg/steer, so daily intake as a percentage of body weight ranged from 2.1% to 2.7%, which was within expectations for free ranging livestock (Coleman et al. 2014; National Academies of Sciences and Medicine 2016).

Expressing total daily intake as a PI, however, showed there was no difference for intake preference between on-town and off-town communities. Contrast statements comparing grass versus forb communities indicated significant differences for OM, CP, and DOM intake PI. For the PDF plant community, 95% confidence intervals (CI) of the mean for OMI PI were 0.36-0.83. CI values that didn't overlap 1 for PDF indicate that forage consumption was strongly avoided on this community. For the NPD plant community, the 95% CI was 0.82 – 1.02, a CI overlapping 1 suggests that OMI from off-town locations was in proportion to what was available to them. The CI for the PDG plant community for OM PI was 1.01-1.49, and indicated that livestock slightly to heavily preferred getting a larger proportion of their diet from grass dominant sites on-town. Diet data from our study showed little difference in forage quality between PDG and NPD plant communities, therefore it was unlikely that livestock were showing preference for on-town grass dominant sites based on increased quality. Research has shown that cattle showed a preference for and were able to maximize daily energy intake on short patches due to the reduction of senescent leaves of low quality forage (Devries and Daleboudt 1994; Hodgson et al. 2009). Johnson-Nistler et al. (2004) observed up to 7 times more standing dead forage present on uncolonized sites compared to colonized areas, mainly attributed to prairie dogs clipping vegetation which greatly reduced the amount of grasses that reached maturity. Reduction in standing dead material may allow grazing steers to harvest forage more efficiently on PDG communities because the need for sorting is reduced.

Comparisons between NPD intake rates for the 0%, 20%, and 40% colonized pastures displayed no relationship ($P > 0.05$) with pasture, month, or their interaction (data not shown). Comparisons between total daily intake for OM, CP, and DOM between the 0%, 20%, and 40% occupied pastures had no significant pasture effect or interactions ($P>0.05$), and only a significant month effect for total daily OM intake ($P = 0.03$). Least square means of total daily OMI by month were: 8508, 11371, and 11377 g (SEM = 2168g) for June, July, and August, respectively. The lack of significant differences between pastures demonstrated that cattle were able to consume a similar amount of forage, CP, and DOM intake across pastures with varying levels of colonization when stocking rate was adjusted for prairie dog forage removal.

Livestock Performance and Production

There was a pasture effect ($P = 0.0025$) for livestock performance (ADG). Least square means were 0.74, 0.86, and 0.85 kg/hd/day (SEM = 0.03) for the 0, 20, and 40% pastures, respectively. Polynomial contrasts for ADG across level of colonization indicated significant linear ($P = 0.0015$) and quadratic effects ($P = 0.049$). Long term average gain (ADG) estimates (1969-2002) for livestock grazing low, good, and excellent condition range within the northern great plains were 0.70, 0.77, and 0.73 kg/hd/day (Dunn et al. 2010). Lack of differences in diet quality and intake rates between the spatially dominant NPD and PDG plant communities suggests that animal performance should be similar across pastures with and without prairie dog colonization. One potential explanation for the difference in ADG observed is that livestock may benefit from increased diet diversity associated with prairie dog colonies. Previous research has shown that forbs contributed 15% of cattle diets in June and July and 5-10% of diets from August to September (Plumb and Dodd 1993). Prairie dogs have been shown to significantly increase plant species richness and diversity, often through increasing forb species biomass on-town versus off-town (Fahnestock and Detling 2002). Geaumont et al. (2019), in analyzing species assemblages and community structure between on-town and off-town locations, revealed a definitive contrast in vegetation, and concluded that having both habitats on the landscape increases plant diversity at broader scales. At the landscape scale, access to both on- and off-town plant communities may increase diet diversity available to free ranging livestock. Additionally, plant community shifts on-town towards those dominated by shortgrass species have been documented (Agnew et al. 1986; Koford 1958), and are probably attributable to the high grazing resistance of blue grama and buffalograss (Derner et al. 2006). Higher percentages of warm season grasses on-town may further increase diet diversity by expanding the seasonality of high quality forages within pastures occupied by prairie dogs.

Secondly, within the context of most grazing studies, climate and stocking rate should be considered. Augustine and Springer (2013) predicted in a shortgrass steppe and northern mixed-grass prairie that competition between prairie dogs and cattle is likely with below average precipitation, and facilitation dominates with above average precipitation. Given that rainfall at our study site for four out of five years was above average, forage on-town was likely not a constraining factor and facilitation between prairie dogs and cattle may have occurred. Numerous studies on rangelands have shown that lower stocking rates can lead to increased individual animal performance (e.g.

Derner et al. 2008; Dunn et al. 2010; Holechek et al. 1998). Stocking rate for the current study was established for production expectations for an average year. Higher than average precipitation for all years except the first, however, likely resulted in higher forage production than average. Stocking rates were reduced in colonized pastures to account for the amount of forage removed by prairie dogs, but there was no adjustment for increased production both on- and off-town. Thus, colonized pastures were likely stocked at an effectively lighter rate than the 0% occupied pasture, possibly leading to differences observed in ADG.

Livestock production (kg/ha) displayed a significant pasture effect ($P < 0.001$). Least square means were: 31.6, 28.7, and 21.4 (SEM=2.0) for the 0, 20, and 40% pastures, respectively. Results from the livestock production analysis indicated a significant quadratic effect ($P = 0.033$) of production versus level of colonization. Stocking rates adjusted for level of colonization had a direct impact on differences observed in livestock production. The quadratic effect observed in production demonstrated that increased ADG on the 20% colonized pasture may have offset some of the production loss associated with the lower stocking rate. Derner et al. (2006) reported cattle weight gains were significantly impacted by level of prairie dog colonization, though differences in production were not evident until colonization exceeded 30% of the pasture. The quadratic relationship between production and level of colonization, as well as those observed from Derner et al. (2006) indicate that livestock production may not be proportionally impacted at low levels of prairie dog colonization.

Management Implications

Producers who manage pastures occupied by prairie dogs have difficult choices to make about maintaining high production and healthy grasslands. Pastures occupied by prairie dogs are commonly stocked (acres per AUM) regardless of the level of colonization. Within this study, stocking rates adjusted for percentage of colonization ensured that forage was not limited and thus reduced competition between livestock and prairie dogs, likely driving some of the responses observed in livestock grazing preference and diet selection. Results from our study, however, indicate that different plant communities associated with prairie dog colonies have different values for livestock. Grass dominant areas on-town were preferred and contributed more to nutrient intake than expected and should be considered valuable by livestock producers. Older core areas of prairie dog towns, however, had little to no nutritive value to grazing livestock, and large areas of this plant community would likely depress nutrient intake by foraging animals. Animal performance results indicate that one benefit of low levels of prairie dog colonization to livestock production may be increased ADG, potentially due to increased diet diversity and seasonality. Though difficult to assess in our study due to reduced stocking rates in colonized pastures, livestock production may only be minimally impacted by prairie dogs at low levels of colonization. Control efforts in these cases may not be beneficial relative to cost, especially if prairie dog towns occupy lower productivity sites within pastures. In pastures with high levels of prairie dog occupation and large proportions of core, bare ground and annual forb dominated communities, livestock production will likely be negatively impacted and grass resources overgrazed if pastures are stocked without regard to level of occupation.

Literature Cited

Aebischer, N.J., Robertson, P.A., & Kenward, R.E. (1993). Compositional Analysis of Habitat Use From Animal Radio-Tracking Data. *Ecology, 74*, 1313-1325

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

AOAC (1990). Official Methods of Analysis. 15th Ed. In. Arlington, VA: Assoc. Off. Anal. Chem.

Augustine, D.J., & Derner, J.D. (2013). Assessing Herbivore Foraging Behavior with GPS Collars in a Semiarid Grassland. *Sensors, 13*, 3711-3723

Augustine, D.J., & Springer, T.L. (2013). Competition and facilitation between a native and a domestic herbivore: trade-offs between forage quantity and quality. *Ecological Applications, 23*, 850-863

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, 78*, 2054-2060

Boufennara, S., López, S., Bousseboua, H., Bodas, R., & Bouazza, L. (2012). Chemical composition and digestibility of some browse plant species collected from Algerian arid rangelands. *Spanish Journal of Agricultural research 10*, 88-98

Bredon, R. M., T. Torell, D., & Marshall, B. (1967). Measurement of Selective Grazing of Tropical Pastures Using Esophageal Fistulated Steers. *Journal of Range Management, 20*, 319-320

Brennan, J., Johnson, P., & Hanan, N. (2019). Comparing Stability in Random Forest Models to Map Northern Great Plains Plant Communities Using 2015 and 2016 Pleiades Imagery. *Biogeosciences Discuss., 2019*, 1-28

Chacon, E., & Stobbs, T.H. (1976). Influence of progressive defoliation of a grass sward on the eating behaviour of cattle. *Australian Journal of Agricultural Research, 27*, 709-727

Chacon, E., Stobbs, T.H., & Sandland, R.L. (1976). Estimation of herbage consumption by grazing cattle using measurements of eating behaviour. *Grass and Forage Science, 31*, 81-87

Chipault, J.G., & Detling, J.K. (2013). Bison selection of prairie dog colonies on shortgrass steppe. *Western North American Naturalist, 73*, 168-176

Coleman, S.W. (2005). Predicting forage intake by grazing ruminants. *In 'Proceedings of 2005 ruminant nutrition symposium, Florida.* 72-99

Coleman, S.W., Gunter, S.A., Sprinkle, J.E., & Neel, J.P.S. (2014). BEEF SPECIES SYMPOSIUM: Difficulties associated with predicting forage intake by grazing beef cows. *Journal of Animal Science, 92*, 2775-2784

Connell, L.C., Porensky, L.M., & Scasta, J.D. (2019). Prairie Dog (Cynomys ludovicianus) Influence on Forage Quantity and Quality in a Grazed Grassland-Shrubland Ecotone. *Rangeland Ecology & Management, 72*, 360-373

Coppock, D.L., Detling, J.K., Ellis, J.E., & Dyer, M.I. (1983b). Plant-herbivore interactions in a North American mixed-grass prairie : I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia, 56*, 1-9

David, L.S., Anastasios, S.N., & Malechek, J.C. (1985). Effects of Forage Availability on Grazing Behavior of Heifers. *Journal of Range Management, 38*, 177-180

Davidson, A.D., Ponce, E., Lightfoot, D.C., Fredrickson, E.L., Brown, J.H., Cruzado, J., Brantley, S.L., Sierra-Corona, R., List, R., Toledo, D., & Ceballos, G. (2010). Rapid response of a grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock. *Ecology, 91*, 3189-3200

Derner, J.D., Detling, J.K., & Antolin, M.F. (2006). Are livestock weight gains affected by black-tailed prairie dogs? *Frontiers in Ecology and the Environment, 4*, 459-464

Derner, J.D., Hart, R.H., Smith, M.A., & Waggoner, J.W. (2008). Long-term cattle gain responses to stocking rate and grazing systems in northern mixed-grass prairie. *Livestock Science, 117*, 60-69

Detling, J.K. (1998). Mammalian herbivores: ecosystem-level effects in two grassland national parks. *Wildlife Society Bulletin, 26*, 438-448

Devries, M.F.W., & Daleboudt, C. (1994). Foraging strategy of cattle in patchy grassland. *Oecologia, 100*, 98-106

Dunn, B.H., Smart, A.J., Gates, R.N., Johnson, P.S., Beutler, M.K., Diersen, M.A., & Janssen, L.L. (2010). Long-Term Production and Profitability From Grazing Cattle in the Northern Mixed Grass Prairie. *Rangeland Ecology & Management, 63*, 233-242

Fahnestock, J.T., & Detling, J.K. (2002). Bison-prairie dog-plant interactions in a North American mixed-grass prairie. *Oecologia, 132*, 86-95

Gabrielson, M.L. (2009). Effects of Black-tailed Prairie Dogs (Cynomys ludovicianus) and Cattle on Vegetation Composition and Disappearance in the Mixed-Grass Prairie (M.S. Thesis). South Dakota State University

Galyean, M.L., & Gunter, S.A. (2016). Predicting forage intake in extensive grazing systems. *Journal of Animal Science, 94*, 26-43

Ganskopp, D.C., & Bohnert, D.W. (2009). Landscape nutritional patterns and cattle distribution in rangeland pastures. *Applied Animal Behaviour Science, 116*, 110-119

Geaumont, B.A., Hovick, T.J., Limb, R.F., Mack, W.M., Lipinski, A.R., & Sedivec, K.K. (2019). Plant and Bird Community Dynamics in Mixed-Grass Prairie Grazed by Native and Domestic Herbivores. *Rangeland Ecology & Management, 72*, 374-384

Goering, H.K., & Van Soest, P.J. (1970). *Forage Fiber Analyses (apparatus, Reagents, Procedures, and Some Applications)*. U.S. Agricultural Research Service

Guenther, D.A., & Detling, J.K. (2003). Observations of cattle use of prairie dog towns. *Journal of Range Management, 56*, 410-417

Hanley, T., & Hanley, K. (1982). Food Resource Partitioning by Sympatric Ungulates on Great Basin Rangeland. *Journal of Range Management, 35(2)*, 152-158

Hendrix, M.R. (2018). Black-tailed Prairie Dog (Cynomys ludovicianus) State-and-Transition Model for Loamy Ecological Sites in MLRA 62 in Custer State Park, South Dakota (M.S. thesis). South Dakota State University

Hodgson, J., Capriles, J.M.R., & Fenlon, J.S. (2009). The influence of sward characteristics on the herbage intake of grazing calves. *The Journal of Agricultural Science, 89*, 743-750

Holechek, J.L., Pieper, R.D., & Herbel, C.H. (1998). *Range management: principles and practices*. Upper Saddle River, New Jersey, USA: Prentice-Hall

Hopson, R., Meiman, P., & Shannon, G. (2015). Rangeland dynamics: investigating vegetation composition and structure of urban and exurban prairie dog habitat. *Peerj, 3*

Jacobs, J. (1974). Quantitative measurement of food selection. *Oecologia, 14*, 413-417

Johnson-Nistler, C.M., Sowell, B.F., Sherwood, H.W., & Wambolt, C.L. (2004). Black-tailed prairie dog effects on Montana's mixed-grass prairie. *Journal of Range Management, 57*, 641-648

Johnson, J.A., Caton, J.S., Poland, W., Kirby, D.R., & Dhuyvetter, D.V. (1998). Influence of season on dietary composition, intake, and digestion by beef steers grazing mixed-grass prairie in the northern great plains. *Journal of Animal Science, 76*, 1682-1690

Kiesling, H.E., Nelson, A.B., & Herbel, C.H. (1969). Chemical Composition of Tobosa Grass Collected by Hand-Plucking and Esophageal-Fistulated Steers. *Journal of Range Management, 22*, 155-159

Kilgour, R.J., Uetake, K., Ishiwata, T., & Melville, G.J. (2012). The behaviour of beef cattle at pasture. *Applied Animal Behaviour Science, 138*, 12-17

Koford, C.B. (1958). *Prairie dogs, whitefaces, and blue grama*. Wildlife Society

Kotliar, N.B., Baker, B.W., Whicker, A.D., & Plumb, G. (1999). A Critical Review of Assumptions About the Prairie Dog as a Keystone Species. *Environmental Management, 24*, 177-192

Krueger, W.C. (1972). Evaluating Animal Forage Preference. *Journal of Range Management, 25*, 471-475

Lesperance, A.L., Bohman, V.R., & Marble, D.W. (1960). Development of Techniques for Evaluating Grazed Forage1. *Journal of Dairy Science, 43*, 682-689

Manning, J., Cronin, G., González, L., Hall, E., Merchant, A., & Ingram, L. (2017). The Behavioural Responses of Beef Cattle (Bos taurus) to Declining Pasture Availability and the Use of GNSS Technology to Determine Grazing Preference. *Agriculture, 7*, 45

Martinez-Estevez, L., Balvanera, P., Pacheco, J., & Ceballos, G. (2013). Prairie Dog Decline Reduces the Supply of Ecosystem Services and Leads to Desertification of Semiarid Grasslands. *Plos One, 8*

Miller, B.J., Reading, R.P., Biggins, D.E., Detling, J.K., Forrest, S.C., Hoogland, J.L., Javersak, J., Miller, S.D., Proctor, J., Truett, J., & Uresk, D.W. (2007). Prairie dogs: An ecological review and current biopolitics. *Journal of Wildlife Management, 71*, 2801-2810

National Academies of Sciences, E., & Medicine (2016). *Nutrient Requirements of Beef Cattle: Eighth Revised Edition*. Washington, DC: The National Academies Press

Olson, K.C. (1991). Diet Sample Collection by Esophageal Fistula and Rumen Evacuation Techniques. *Journal of Range Management, 44*, 515-519

Olson, K.C., Schauer, C., Engel, C., Kincheloe, 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

Plumb, G.E., & Dodd, J.L. (1993). Foraging Ecology of Bison and Cattle on a Mixed Prairie - Implications for Natural Area Management. *Ecological Applications, 3*, 631-643

Provenza, F.D. (1991). Behavior and nutrition are complementary endeavors. *Okalahoma Agric. Exp. Sta. Misc. Rep. MP-133*, 157-169

Scarnecchia, D., L. , Anastasios, S.N., & Malechek, J.C. (1985). Effects of Forage Availability on Grazing Behavior of Heifers. *Journal of Range Management, 38*, 177-180

Sierra-Corona, R., Davidson, A., Fredrickson, E.L., Luna-Soria, H., Suzan-Azpiri, H., Ponce-Guevara, E., & Ceballos, G. (2015). Black-Tailed Prairie Dogs, Cattle, and the Conservation of North America's Arid Grasslands. *Plos One, 10*

South Dakota Climate and Weather, 2017 *South Dakota Climate and Weather Mesonet at SDSTATE* Available at: https://climate.sdstate.edu/archive/ (2017), Accessed 1st Dec 2017

Stoltenberg, M. (2004). Effects of prairie dogs on plant community composition and vegetation disappearance in Mixed-Grass Prairie (M.S. Thesis). South Dakota State University

Tilley, J.M.A., & Terry, R.A. (1963). A two-stage technique for the in vitro digestion of forage crops. *Grass and Forage Science, 18*, 104-111

US Climate Data, 2017. Climate Mobridge - South Dakota and Weather Averages Mobridge. Available at: www.usclimatedata.com/climate/mobridge/south-dakota/united-states/ussd0227. Accessed 1st Dec 2017.

Weir, W.C., & Torell, D.T. (1959). Selective Grazing by Sheep as Shown by a Comparison of the Chemical Composition of Range and Pasture Forage Obtained by Hand Clipping and that Collected by Esophageal-Fistulated Sheep. *Journal of Animal Science, 18*, 641-649

Winter, S.L., Cully, J.F., & Pontius, J.S. (2002). Vegetation of prairie dog colonies and non-colonized short-grass prairie. *Journal of Range Management, 55*, 502-508

Table 4.1: Stocking rates variables for three experimental pastures on the study site near McLaughlin, South Dakota. The pastures had varying levels of prairie dog colonization. Stocking rates were adjusted to account for the amount of forage removed by prairie dogs (50%) based on level of colonization.

% Colonization[a]	Area (ha)	Head[b]	Stocking rate (ha/AUM[c])
0	203	75	0.80
20	193	55	1.03
40	209	45	1.36

[a] Level of prairie dog colonization of the pasture
[b] Number of cattle in the pasture
[c]AUM calculate as the: (# of head) x (duration of grazing) x (animal unit equivalent), where the duration of grazing was 4.33 months and the animal unit equivalent for average weight of steers was 357kg/454 kg.

Table 4.2: Livestock grazing behavior preference index (PI) and forage diet quality (ADL and IVOMD) least square means and standard errors for results with a significant pasture x plant community interaction ($P < 0.05$) evaluated on the study site near McLaughlin, South Dakota. The study was conducted from 2012 to 2016. Pastures with two levels of prairie dog colonization (20% and 40%) were analyzed. Plant communities of interest in the study included grass-dominated sites on prairie dog towns (PDG), forb-dominated sites on prairie dog towns (PDF) sites, and grass-dominated sites off prairie dog towns (NPD).

		Plant Community				Contrasts[a]	
	Pasture[b]	NPD	PDG	PDF	SEM[c]	On vs Off	Grass vs. Forb
PI[d]	20%	0.93	1.58	1.08	0.1	<0.0001	0.015
	40%	0.92	1.02	0.74	0.09	0.5232	0.0008
ADL[e]	20%	5.56	5.45	9.06	0.53	<0.0001	<0.0001
	40%	6.67	5.52	7.65	0.53	0.805	0.0074
IVOMD[f]	20%	60.45	61.69	57.67	2.54	0.704	0.144
	40%	54.04	61.36	61.05	2.54	0.001	0.15

[a] Contrast: On Vs. Off compares NPD vs PDG & PDF, Grass vs. Forb compares NPD & PDG vs. PDF.

[b] Pasture indicates level of prairie dog colonization.

[c] Maximum SEM provided

[d] PI (preference index) calculated as the percentage of daily time spent grazing within the plant community divided by the percentage of area the plant community occupied within the pasture.

[e] ADL is % acid detergent lignin on an organic matter basis

[f] IVOMD is in vitro organic matter digestibility

Table 4.3: Livestock grazing behavior (PI) least square means and standard errors for results with a significant plant community x month interaction ($P < 0.05$) evaluated on the study site near McLaughlin, South Dakota. The study was conducted during the summers from 2012 to 2016. Plant communities of interest in the study included grass-dominated sites on prairie dog towns (PDG), forb-dominated sites on prairie dog towns (PDF) sites, and grass-dominated sites off prairie dog towns (NPD).

		Month					Contrasts[a]		
	Plant Community	Jun	Jul	Aug	Sep	SEM[b]	Linear	Quad.	Cubic
PI[c]	NPD	0.796	0.865	0.953	1.1	0.065	0.001	0.321	0.761
	PDG	1.726	1.45	1.185	0.856	0.134	<0.0001	0.756	0.814
	PDF	1.358	0.903	0.978	0.412	0.08	<0.0001	0.323	0.0006

[a] Orthogonal polynomial contrasts to determine whether the relationship between plant community and month was linear, quadratic, or cubic

[b] Maximum SEM provided

[c] PI (preference index) calculated as the percentage of daily time spent grazing within the plant community divided by the percentage of area the plant community occupies within the pasture.

Table 4.4: Forage diet quality least square means and standard errors for results of the month main effect ($P < 0.05$) evaluated on the study site near McLaughlin, South Dakota. The study was conducted during the summers from 2012 to 2016. Forage quality samples were collected through the use of ruminally cannulated steers for June, July, and August of each year.

	Jun	Jul	Aug	SEM[a]	Linear[b]	Quad.[b]
CP[c]	16.2	12.66	11.93	0.748	<0.0001	0.0011
NDF[d]	72.31	73.94	76.25	2.09	0.032	0.76
ADL[e]	5.91	6.9	7.24	0.25	<0.0001	0.71
IVOMD[f]	64.98	58.04	55.11	1.94	<0.0001	0.133

[a] Maximum SEM provided

[b] Orthogonal polynomial contrasts to determine whether the relationship between plant community and month is linear or quadratic.

[c] CP is % crude protein content on an organic matter basis

[d] NDF is % neutral detergent fiber on an organic matter basis

[e] ADL is % acid detergent lignin on an organic matter basis

[f] IVOMD is % in vitro organic matter digestibility

Table 4.5: Livestock intake least square means and standard errors for results with a significant plant community main effect ($P < 0.05$) evaluated on the study site near McLaughlin, South Dakota. The study was conducted from 2012 to 2016. Forage intake rates were collected through the use of ruminally cannulated steers grazing plant communities of interest. Plant communities of interest in the study included grass-dominated sites on prairie dog towns (PDG), forb-dominated sites on prairie dog towns (PDF) sites, and grass-dominated sites off prairie dog towns (NPD). Total daily intake was estimated by multiplying intake rate by average time spent grazing within that plant community estimated from GPS collars. Intake preference index (PI) calculated as the proportion of total daily intake from each plant community adjusted for the proportion of the pasture the plant community occupied.

	Plant Community				Contrasts[a]	
	NPD	PDG	PDF	SEM	On vs. Off	Grass vs. Forb
Intake Rate (g/min)						
OM[b]	24.22	22.68	9.86	3.21	0.0002	<0.0001
CP[c]	2.78	2.66	1.54	0.49	0.0019	0.0001
DOM[d]	13.74	13.77	5.95	2.22	0.0042	<0.0001
Total Daily Intake (kg)						
OM	6.00	2.94	-0.41	1.08	<0.0001	<0.0001
CP	0.69	0.34	-0.03	0.14	0.0005	0.0013
DOM	3.49	1.57	0.04	0.66	<0.0001	<0.0001
Intake PI						
OM	0.92	1.25	0.60	0.12	0.962	0.0004
CP	0.91	1.25	0.77	0.15	0.375	0.0492
DOM	0.89	1.31	0.59	0.13	0.5921	0.0003

[a] Contrast: On Vs. Off compared NPD vs PDG & PDF, Grass vs. Forb compared NPD & PDG vs. PDF.

[b] OM is organic matter

[c] CP is crude protein content on an organic matter basis

[d] DOM is digestible organic matter

Chapter 5: Developing A Systems Approach for Addressing The Prairie Dog – Livestock Conflict

Abstract

Numerous controversies exist regarding competition and conflict between wildlife species and livestock. One of the more controversial conflicts is that between prairie dogs and cattle, which has broad impacts on conservation and agricultural production. From a conservation perspective, prairie dogs are viewed as ecosystem engineers providing habitat to a number of species by altering vegetation structure and composition and increasing biodiversity. From an agricultural viewpoint, prairie dogs compete with cattle for forage resources, reducing the carrying capacity on rangelands. Increasingly, rangeland management has sought to incorporate historical disturbance regimes into management strategies to improve heterogeneity on the landscape. Although fire and large ungulate grazing have been the focus, heterogeneity associated with prairie dog occupation of rangelands may be a logical extension of that effort. Regardless, it is crucial that management and conservation strategies on rangelands occupied by prairie dogs account for concerns of livestock producers if they are to be adopted, especially on private lands. The overall goal of this paper is to approach the prairie dog-cattle conflict from a systems perspective to understand the potential benefit of having both on-town and off-town plant communities for plant diversity, wildlife, and livestock production. Our study demonstrates that plant communities on-town can differ significantly from off-town communities in northern mixed-prairie, however, the presence of both plant communities within a pasture can increase diversity at broader landscape scales. This is important because, while prairie dog towns support a variety of wildlife species, there are

many species that require greater vegetation structure. Those species require plant communities not found on prairie dog towns. Accommodating the array of habitat structure needed by the suite of wildlife on grasslands, then, requires incorporation of a wide variety of disturbance regimes on the landscape. From a livestock production perspective, our study suggests that the inclusion of prairie dogs within a pasture may increase diet diversity through shifting plant species composition, which may potentially be beneficial for grazing livestock provided forage quantity isn't limited. Incorporation of a prairie dog-livestock management framework requires active management of both species to reduce competition and prevent degradation. Though certain wildlife species, such as black-footed ferrets, may require extensive prairie dog colonies for habitat, benefits to biodiversity can still be realized on pastures containing relatively small areas of prairie dog towns, which may minimize impacts to livestock production.

Introduction

Rangeland ecosystems often sit at the nexus of balancing economic and conservation goals. Within the United States, rangelands and grasslands occupy roughly 29% of the land use area, and of that an estimated 52% is privately owned (Nickerson et al. 2011). The majority of rangelands around the world are utilized for agricultural purposes, primarily livestock grazing, which is sometimes seen as being in conflict with environmental goals. Critical to the use and preservation of rangelands is the sustainability of these landscapes from an economic agricultural perspective, as well as from a conservation perspective. Numerous studies have looked at conflicts, whether perceived or real, between domestic livestock and wildlife (Atickem and Loe 2014; Augustine and Derner 2012; de Souza et al. 2018; Hegel et al. 2009; Ranglack et al.

2015; Thomas 1996). One of the more controversial species that sits at the heart of livestock-wildlife conflicts is the prairie dog. Its presence on the landscape sparks tremendous controversy, especially regarding potential implications for conservation goals and livestock production.

Throughout much of the 20th century, prairie dog colonies have been subject to extensive control measures to reduce their numbers in order to minimize their competition for forage with grazing livestock (Sierra-Corona et al. 2015). Estimates of prairie dog town extent prior to European settlement vary widely and are based on early 20th century data with no evidence to support pre-settlement population numbers (Vermeire et al. 2004). Although disagreements of extent of rangelands occupied occur, control efforts have no doubt limited their expanse over the past century as wide-spread eradication efforts have sought to reduce occupation to increase rangeland productivity for cattle (Weltzin et al. 1997). In 1998, a petition was filed to list black tailed prairie dogs as a threatened species under the Endangered Species Act, with the US Fish and Wildlife Service (USFWS) concluding that listing may be warranted. As a response to potential listing, a multistate cooperative effort, including South Dakota, was established to create management plans to prevent federal listing of the species, with minimum acreages set to maintain long-term self-sustaining prairie dog populations. Of the 411,000 acres of prairie dog colonies within the state of South Dakota, an estimated 38% are located on private lands (Cooper and Gabriel 2005), demonstrating the need for livestock producer cooperation in accomplishing conservation goals.

From a conservation perspective, prairie dogs have been identified as a keystone species, and are often seen as ecosystem engineers providing habitat for a number of other plant and wildlife species (Davidson et al. 2010; Kotliar et al. 1999). They are known to increase biotic diversity and community structure while playing an important role in ecosystem function (Hopson et al. 2015). Smith and Lomolino (2004) argued that the importance of conservation of prairie dogs goes beyond that of a single species and is an important strategy for preserving the prairie ecosystem. In semi-arid grasslands of the southwest, prairie dogs were shown to increase essential ecosystem services of water infiltration rates, carbon storage rates, and soil stabilization (Martinez-Estevez et al. 2013). Additionally, prairie dogs create habitat for a number of other wildlife species through providing refuge via burrow systems and by altering existing vegetation structure and composition.

From an agricultural perspective, many concerns exist over the impact of prairie dogs on plant biomass production and consequently livestock production. Prairie dogs reduce the carrying capacity of rangelands through consumption of forage and clipping vegetation to increase predator detection. Cattle and prairie dogs exhibit a high dietary overlap, up to 60% in a mixed-grass prairie, which is a cause of concern for livestock producers (Miller et al. 2007). Within the shortgrass steppe, Derner et al. (2006) showed that livestock weight gains were negatively correlated to an increase in prairie dog colonization, though the decrease in gains was not in proportion to the increase in colonization. Numerous studies have shown prairie dogs significantly reduce herbaceous biomass compared with off-colony sites (Augustine and Springer 2013; Gabrielson 2009; Johnson-Nistler et al. 2004; Stoltenberg 2004), however, it has been argued that this decrease in forage quantity can somewhat be offset by an increase in forage quality on-town (Augustine and Springer 2013; Connell et al. 2019; Coppock et al. 1983b).

Recently within the field of rangeland management, there has been substantial interest in increasing heterogeneity on rangelands. Heterogeneity in plant communities and vegetation structure has tremendous value in providing increased ecosystem services and habitat for a variety of wildlife species. Previous research has evaluated pyric herbivory as a management strategy to increase plant community and structural heterogeneity, leading to benefits for both wildlife species and livestock production (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004; Augustine and Derner 2014). There is also interest in utilizing livestock grazing to increase heterogeneity on the landscape to create a mosaic of habitats available to wildlife (Derner et al. 2009). In the absence of historical disturbances on the landscape such as fire, it has been hypothesized that prairie dog colonies can effectively create habitat conditions for species such as mountain plovers, because the effects on vegetation structure are more stable in space and time (Augustine and Derner 2012). Because of the large percentage of private ownership of grasslands, strategies involving prairie dogs to promote heterogeneity are unlikely to be adopted by ranchers if livestock production is negatively affected. Therefore the need exists to develop a framework which can balance the potential biodiversity benefits associated with prairie dogs with the concerns of livestock producers.

Prairie dogs and cattle are often portrayed as being in direct competition for achieving conservation and production goals. The fact remains that the majority of rangelands occupied by prairie dogs are also used for livestock grazing, and the two species are inextricably linked together within an agro-ecological system. While the debate over prairie dogs on rangelands has primarily been framed as on- versus off-town, and livestock versus prairie dogs, this issue would benefit from evaluation using a systems perspective. Within a given pasture, presence of both on-town and off-town plant communities may provide the greatest potential ecosystem benefit. Additionally the scale and age at which colonies exist on the landscape will have a direct impact on the value of prairie dogs to provide increased plant species diversity, wildlife habitat, and livestock diet diversity.

Plant communities

One of the largest sources of concern for livestock producers regarding prairie dogs is the reduction in biomass on-town compared to off-town. In our study, there was 37% less standing crop biomass in the prairie dog only treatment compared to the cattle only graze treatment (Table 1.3). Within the northern mixed-grass prairie, Johnson-Nistler et al. (2004) reported a 60% reduction in standing crop biomass and Augustine and Springer (2013) reported a 63% reduction in commonly grazed species biomass on colonized compared to uncolonized sites. Not all studies in the Great Plains, however, have documented reductions in biomass on-colony compared to off-colony. In the shortgrass prairie of Colorado, Augustine and Springer (2013) reported no statistical differences in biomass between on-town and off-town sites. Within the mixed-grass prairie sagebrush ecotone in Wyoming, Connell et al. (2019) reported no difference in aboveground herbaceous biomass between praririe dog colonies and sites without prairie dogs across three growing seasons. While the results of these studies indicate that the impact of prairie dogs on vegetation production may differ between ecosystems, studies in the northern mixed-grass prairie suggest that significant reductions in biomass production due to prairie dogs are likely.

One of the two major drivers of biomass reduction on-town is the removal of a large proportion of forage by prairie dogs due to either direct consumption or through clipping of vegetation to aid in predator detection. Gabrielson (2009) observed that, of total forage removed on-colony, 83% was attributed to prairie dogs, with the additional 17% attributed to cattle. Stoltenberg (2004) estimated that upwards of 90% of the forage disappearance due to prairie dogs during the growing season is the result of non-consumptive clipping (Stoltenberg 2004). The second driver of biomass reduction on-town is plant community change. In the northern mixed-grass prairie, colonization tends to increase the prevalence of grazing tolerant shortgrasses. On-town sites are characterized by a decrease in C3 grasses, such as western wheatgrass and green needlegrass, and an increase in C4 grasses, primarily buffalograss and blue grama. Shifts in plant communities on-town to those dominated by shortgrass species have been documented (Agnew et al. 1986; Koford 1958), and are probably attributable to the high grazing resistance of blue grama and buffalograss (Derner et al. 2006). Replacement of mid-grasses with shortgrasses is likely a major cause of biomass reduction observed in this ecosystem compared with other grassland sites. Additionally, older core areas of prairie dog towns are often characterized by high percentage bare ground, low vegetation production, and dominance by annual forb and dwarf shrub species; areas more recently colonized typically remain grass dominant (Guenther and Detling 2003, Coppock et al., 1983a). The relative proportion of prairie dog towns consisting of older core areas may have a more dramatic effect on biomass production, forage availability, and species diversity at the pasture and colony scale than simply forage removal attributed to prairie dogs.

Many studies have focused on the impact of prairie dogs on plant communities. Results from this study (Table 1.5) show that significant plant community composition differences occurred in every year of the study for all comparisons between on-town vs. off-town treatments. Though species richness is also dependent on ecological site, on-town sites tended to be characterized by higher species richness compared with off-town sites within the same ecological sites (Table 1.4). Prairie dogs have been shown to significantly increase plant species richness and diversity, resulting in a more even distribution of biomass among species on-town versus off-town (Fahnestock and Detling 2002). In shortgrass prairie, the total number of species, both annual and perennial, increased on-town versus nearby off-town sites (Bonham and Lerwick 1976). Increases in plant community richness and diversity, however, may not persist and may be dependent on colony age. Archer et al. (1987) reported that increases in diversity occurred in the first 3 years following colonization, but dropped to values similar to those on off-town sites after 4-6 years. Similarly, it has been observed that total number of plant species was greatest on younger versus older prairie dog towns, with the reduction in diversity on older colonized areas the result dominance of a single dwarf shrub species (Coppock et al. 1983). These results suggest that colony age has an impact on plant community composition, especially through a reduction in the competitive ability of graminoids due to increased utilization levels.

Numerous other research studies, have focused on differences between off-town and on-town plant communities (e.g. Agnew et al. 1986; Archer et al. 1987; Coppock et al. 1983; Fahnestock and Detling 2002), and demonstrate that a significant driver in plant community change on the landscape is presence or absence of prairie dogs. While these on- vs. off-town contrasts are important to make, within a grassland system the greatest benefit to diversity is the inclusion of both within a pasture. In our study (Table 1.6), a large percentage of species occur every year either on-town or off-town but not on both. Additionally, for the entire duration of the study (2012-2016), 46 species were only observed on-town and 17 only observed off-town out of a total 113 species observed throughout the 5 years of the study. This highlights the importance of thinking of on- and off-town communities as a system, as opposed to focusing on their differences as has occurred in most studies. Geaumont et al. (2019), in analyzing species assemblages and community structure between on-town and off-town locations, revealed a definitive contrast in vegetation, and concluded that having both habitats on the landscape increases plant diversity at broader scales. The potential benefit of having a heterogeneous landscape of plant communities and structures at the pasture scale may serve to improve both wildlife habitat and livestock forage resources.

Wildlife

Large scale prairie dog eradication programs limited the expanse of prairie dog colonies to the point of consideration for listing under the Endangered Species Act. Although conservation of prairie dogs as an individual species is important, much focus has been placed on the ability of prairie dogs to create habitat for other species associated with colonies. Protection of prairie dogs as a species has been suggested to provide a framework from single-species management to management of an ecological system (Miller et al. 1994). In their ecological review of black-tailed prairie dogs, Sharps and Uresk (1990) noted that their burrowing activities and feeding habits created habitat for 134 vertebrate wildlife species in South Dakota. Agnew et al. (1986) reported a greater abundance of rodent species on-town compared with off-town sites. Species such as swift foxes, golden eagles and other birds of prey, and black-footed ferrets rely heavily on prairie dogs as prey (Hillman 1979; Hillman and Sharps 1979; Sharps and Uresk 1990). Among the species most often studied as being associated with prairie dog colonies and dependent upon their impacts on the landscape are grassland nesting birds.

The importance of prairie dog colonization on grassland bird species has been documented for species such as mountain plover, burrowing owls, killdeer, horned larks, and lark sparrows, that benefit from pastures with short vegetation and ample bare ground, which are commonly associated with prairie dog towns (Augustine 2011; Augustine and Baker 2013; Geaumont et al. 2019). Although habitat requirements differ from species to species, one of the potential benefits of prairie dogs on the landscape is an increase in vegetation heterogeneity. Contemporary range management plans have focused on maximizing livestock production through the uniform use of plant communities, resulting in decreased vegetation heterogeneity with corresponding reductions in species richness and wildlife habitat (Derner et al. 2009; Fuhlendorf and Engle 2001). Knopf (1996) and Reynolds and Symes (2013) suggested that all bird species endemic to prairies evolved within a grazed grassland mosaic ranging in gradient from idle areas to excessively disturbed areas. Prairie dogs create large distinct patches within the grassland matrix resulting in a mosaic of plant community types (Whicker and Detling 1988). Agnew et al. (1986) observed that maximum plant height was consistently lower on prairie dog towns compared with off-town sites. Similarly, Connell et al. (2018) found that prairie dogs reduced vegetation height and visual obstruction by at least 54% compared with areas that had been undisturbed and those that had been burned in previous years, and concluded that prairie dogs are critical drivers of variation in vegetation structure on the landscape.

While the presence of prairie dogs on the landscape may provide a benefit to some grassland nesting birds, their impacts on plant communities may also be detrimental to other species of concern. Species such as the lesser prairie chicken, upland sandpiper, and grasshopper sparrow rely on concealment in taller vegetation structure for nesting in rangelands (Derner et al. 2009; Herse et al. 2018). Connell et al. (2018) reported that sagebrush (*Artemesia tridentata*) was reduced by 76-81% on sites with prairie dogs when compared to undisturbed sites. Like prairie dogs, sagebrush is also considered a keystone species, and a reduction in shrub densities may negatively affect populations of sage-obligate species such as sage grouse (Beck et al. 2012). Although mountain plover density is positively correlated with prairie dog colonies, Duchardt et al. (2019) documented mountain plover densities decline towards the center of extremely large colonies as distance to colony edge exceeded 800 m. Duchardt et al. (2019) suggested that plovers may avoid areas that are too sparse in vegetation structure, potentially due to reduced insect biomass (Schneider et al. 2006).

Results from these studies demonstrate that while prairie dogs may provide habitat for a large number of other species, management for prairie dogs alone may not be most beneficial to biodiversity at the landscape scale. The scale at which prairie dog colonies exist on the landscape, colony age, and plant communities they support may determine the extent to which habitat is suitable for other wildlife. At one extreme, is the habitat requirement and scale for the black-footed ferret, where colonies in excess of 10,000 individuals are needed to sustain 10 breeding pairs of black-footed ferrets, and colonies over 4,300 ha may be necessary for successful reintroduction (Dobson and Lyles 2000; Jachowski et al. 2011). However, the value of black-footed ferret habitat on prairie dog towns may be somewhat dependent on the plant communities present. Jachowski et al. (2008) found, at large scales, areas of high vegetation cover supported greater densities of prairie dogs and thus better suitability for ferret habitat. They concluded that management of vegetation might be able to improve habitat for ferrets by creating large high density areas of prairie dogs.

It is clear from these studies that the importance of prairie dogs in supporting wildlife habitat in grassland ecosystems is not uniform. Not all wildlife species benefit from the presence of prairie dog towns, including those that require tall or moderate vegetation structure. They may, however, be beneficial for species requiring short vegetation structure (e.g. mountain plovers), have prairie dogs as a primary food source (e.g. black-footed ferrets), or utilize burrows and mounds (e.g. burrowing owls). Size of prairie dog towns can alter the benefits to some wildlife species, with very large towns of more limited value to plover densities and large, barren core areas of less value to black-footed ferrets due to limited prairie dog densities compared to better vegetated perimeter areas. Prairie dog towns are not all the same and their vegetation is typically not uniform. Established prairie dog towns can include a wide variety of plant communities (Hendrix 2019), each of which likely is of differing value to wildlife species utilizing prairie dog colonies. Active management of prairie dog colonies to develop/maintain a variety of plant communities may be necessary to provide the greatest benefit to wildlife while mitigating impacts to livestock production.

Livestock Diets and Competition for Resources

Although there may be large impacts on livestock production associated with prairie dog colonization and conservation, very little research exists where livestock-prairie dog interactions have been specifically studied. Understanding cattle grazing behavior can improve opportunities to manage prairie dog occupied pastures for better livestock performance and to optimize rangeland health, yet relatively few studies have looked at the effects and interactions of cattle grazing behavior and forage intake within prairie dog occupied pastures. Guenther and Detling (2003) indicated through road side surveys that cattle significantly selected for prairie dog towns; however, they concluded that the magnitude of the effect was small and likely differed little from random use. Within the Chihuahua desert grasslands, researchers reported that cattle preferentially grazed on prairie dog colonies in the fall/winter grass dormancy season and spent most of their time foraging at off colony sites in the summer (Sierra-Corona et al. 2015). In our study (Table 4.3), livestock had a higher preference for grazing on-town early in the season, but grazing behavior shifted towards off-town locations as the growing season progressed. Guenther and Detling (2003) reported that there was no significant difference between cattle foraging rates (bites/min) between off-town and on-town sites, and Sierra-Corona et al. (2015) showed that prairie dog colonies can provide favorable grazing habitat for cattle. We obtained similar results for forage intake rates for grass-dominated sites on- and off-town, however intake rates were depressed for forb-dominated sites on-town (table 4.5). Results from these studies suggest that grass dominated sites on prairie dog colonies should be considered as valuable forage for grazing livestock by producers; however, the value of forage resources on-town is not evenly distributed spatially. Older core areas of prairie dog towns provide little to no value to grazing livestock, and, as colonies age, the greater proportion of older core areas will greatly limit forage quantity and depress forage intake rates, thus impacting livestock production.

Research conducted looking at prairie dog impacts on livestock production has primarily focused on the impacts of prairie dogs on forage quantity and quality. Numerous studies within the northern mixed-grass prairie have shown prairie dogs significantly reduce herbaceous biomass compared with off-colony sites (Augustine and Springer 2013; Gabrielson 2009; Johnson-Nistler et al. 2004; Stoltenberg 2004). Our study demonstrates that on-town sites grazed only by prairie dogs had 37% less standing crop biomass compared to off-town sites grazed by cattle (Table 1.3). Other northern mixed-grass prairie studies have documented as much as 60% less biomass on-town compared to off-town (Augustine and Springer 2013; Johnson-Nistler et al. 2004). Though it is generally recognized within the northern mixed-grass prairie that prairie dogs reduce forage quantity, conservationists often argue that this may be offset by increases in forage quality. Connell et al. (2019) reported a significant increase in crude protein (CP) content (1.4 x higher) for western wheatgrass samples across June, July, and August, and a significant increase in CP content only in June for composite samples. Grant-Hoffman and Detling (2006) measured plant nitrogen content in four dominant species, and found virtually no differences in nitrogen content between grass species on-town and off-town in southwest Colorado. Augustine and Springer (2013) studied differences in forage quality across 4 prairie dog complexes in the shortgrass and mixed-grass prairies, and found significantly greater forage nitrogen on-town versus off-town

(1.41% compared to 1.08%); differences in forage digestibility were, however, site specific. Johnson-Nistler et al. (2004) measured forage quality on a northern mixed-grass prairie, and found that plants on sites occupied by prairie dog towns were characterized by an increase in percentage crude protein, however they also showed a decrease in total standing crop crude protein when compared to off-town sites and no differences in forage digestibility. In our study, CP content in cattle diets was greater in forb-dominated communities on-town, with virtually no difference between grass-dominated sites on- and off-town; forage digestibility results were inconsistent (Table 4.2). The importance of highlighting these studies is to demonstrate that potential increases in forage quality are not universal and vary across studies, seasons, sites, local weather conditions, plant species, and other factors. It is also important to note that in most of these studies forage quality measurements were made on hand-clipped samples. In our study, measurements were made on forage actually consumed by cattle; several studies (Kiesling et al. 1969; Bredon et al. 1967; Weir and Torell 1959) have demonstrated that diets selected by cattle are of higher quality than the overall quality of forage on offer. Vermeire et al. (2004), noted that for livestock grazing prairie dog colonies, realizing the benefits of increased forage quality still depends on the amount of forage available, and forage quantity becomes more limited as colonies age and occupy greater portions of an area, potentially impacting livestock production.

Cattle grazing in prairie dog occupied pastures in Oklahoma gained less weight annually than in pastures without prairie dogs (O’Meilia et al. 1982). While this result was not statistically significant, the estimated cost to the producer was between $13.76-$23.81 per steer. Derner et al. (2006) reported cattle weight gains were significantly impacted by level of prairie dog colonization, although differences were not evident until colonization exceeded 30% of the pasture. Results from our study (Chapter 4) indicate that cattle grazing in pastures with prairie dogs had higher average daily gains (kg/hd/day). Minimal differences in forage quality were observed on our study site between the grass-dominated off- and on-town communities that dominated the study area (forb-dominated communities on-town were only a minor component of the study area), making it difficult to make inferences regarding the influence of forage quality on animal performance. Stocking rates within our study were moderate, and adjusted for the proportion of pasture colonized by prairie dogs, which has a direct impact of livestock production (kg/ha). However, a significant quadratic effect of level of colonization (0%, 20%, and 40%) on production was observed, suggesting that at moderate stocking rates, low levels of prairie dog colonization may not impact livestock production. Within prairie dog occupied pastures, shifts in plant communities to those with higher forb diversity, greater abundance of grazing tolerant warm season grasses, and reduced standing dead material may provide a benefit to grazing livestock in terms of increased diet diversity compared with access only to non-prairie dog areas.

Results of these studies indicate that the relative impact of prairie dogs on livestock grazing behavior and production is a complex issue with tradeoffs occurring between forage production, forage quality, level of colonization, colony age, and climate. Despite these tradeoffs, the potential exists to manage cattle-prairie dog systems in a way that minimizes reductions in agricultural production, and provides management opportunities to increase biodiversity and heterogeneity on the landscape.

Managing Livestock - Prairie Dog Systems

Management of rangelands is undergoing a paradigm shift, from one focused on even utilization of forage resources so as to maximize livestock production, to one that recognizes the need for heterogeneity on the landscape to benefit biodiversity and wildlife habitat. Derner et al. (2009) proposed utilizing livestock as ecosystem engineers to achieve conservation objectives, providing land managers with the opportunity to reduce conflicts between conservation and livestock production goals on rangelands. Research has demonstrated that manipulation of timing and intensity of grazing can be used to improve sage-grouse populations and habitat (Monroe et al. 2017), improve forage quality for wintering elk (Vavra and Sheehy 1996), and maintain structural heterogeneity on the landscape following patch burning (Fuhlendorf and Engle 2001). Vavra (2005), in his review of livestock wildlife systems, concluded that if livestock continue to graze public lands, managers need to provide grazing systems that are both compatible with wildlife and produce economic return to livestock producers. It can also be argued that conservation groups working in grasslands will require partnerships with private landowners to achieve conservation goals at broader scales beyond public lands. In cases of single species management, targeted grazing systems can be used to meet specific habitat needs. The development, however, of a management framework that incorporates livestock production and development of habitat for wildlife, such as prairie dogs, has the potential to enhance and maintain whole ecological systems. Key to maintaining livestock - prairie dog systems is actively managing both species to reduce competition and prevent degradation.

From a livestock management perspective, reducing overgrazing may help to either prevent initial colonization or limit the expansion of existing prairie dog towns. Licht and Sanchez (1993) showed that prairie dog colonies were associated with cattle point attractants (watering tanks & supplemental feed sites), which are areas that typically see heavy use by livestock. In cases with a high proportion of prairie dog colonization within a pasture, stocking rates which do not account for forage removal attributed to prairie dogs may result in overgrazing and subsequently accelerate prairie dog expansion. Research has shown that taller vegetation height associated with deferred grazing might be an effective tool in discouraging prairie dog colony expansion (Cable and Timm 1987). Sites with shorter vegetation height provide much more suitable habitat for prairie dogs, as was pointed out by Truett et al. (2001) in their recommendations for selecting sites for translocating prairie dogs. Land managers concerned with encroachment or expansion of prairie dogs into uncolonized areas of pastures would be prudent to minimize heavy livestock grazing.

From a prairie dog management perspective, numerous methods exist for controlling or limiting prairie dog colonization, including poisoning. In an economic evaluation of prairie dog control in South Dakota, Collins et al. (1984) found that the cost of controlling prairie dogs was higher than the value of forage gained for livestock. Though not evaluated in the study, they suggested that a control program may be economically feasible if used to prevent the spread of prairie dogs. Hendrickson et al. (2016) suggested that the impact of prairie dogs on livestock production could be minimized if colonies were confined to less productive ecological sites. Hendrix (2018), in developing state and transition models for prairie dog towns within Custer State Park, found older core areas were considered undesirable for management due to losses of native grasses, increased bare ground and potential for erosion and exotic species invasion; older core areas also required large and typically expensive inputs to restore sites to a more desirable state. Chronic overgrazing is detrimental because it reduces primary productivity, impedes plant growth, and alters species composition (Krausman et al. 2009). Effective management of prairie dogs should seek to limit sites from becoming highly degraded, which in turn may help to limit the impact on plant communities, wildlife habitat, and livestock production.

The scale and age of colonies will likely play a role in evaluating compatibility between cattle and prairie dogs within an ecosystem. Pastures which contain smaller proportions of prairie dogs may be able to provide benefits to biodiversity and wildlife species. For example, Geaumont et al. (2019) found that the presence of prairie dogs in pastures grazed by cattle was more important to avian communities than level of prairie dog occupation. The importance of this study, then, demonstrates that while conservation of species such as the black-footed ferret may require vast colonies of prairie dogs, benefits to plant and bird biodiversity can still be realized within pastures containing smaller proportions of prairie dog towns. Low levels of colonization may not impact cattle production, and benefits may also be realized to grazing livestock through increased diversity in diet selection. Relegating a relatively small area (<20%) of a pasture to prairie dogs may be a more palatable option to land managers concerned over balancing wildlife conservation with losses in livestock production.

Literature Cited

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

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

Atickem, A., & Loe, L.E. (2014). Livestock-wildlife conflicts in the Ethiopian highlands: assessing the dietary and spatial overlap between mountain nyala and cattle. *African Journal of Ecology, 52*, 343-351

Augustine, D.J. (2011). Habitat Selection by Mountain Plovers in Shortgrass Steppe. *Journal of Wildlife Management, 75,* 297-304

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

Augustine, D.J. and J.D. Derner. 2014. Controls over the strength and timing of fire-grazer interactions in a semi-arid rangeland. *J. Appl. Ecol., 51*, 242-250

Augustine, D.J., & Derner, J.D. (2012). Disturbance regimes and mountain plover habitat in shortgrass steppe: Large herbivore grazing does not substitute for prairie dog grazing or fire. *Journal of Wildlife Management, 76,* 721-728

Augustine, D.J., & Springer, T.L. (2013). Competition and facilitation between a native and a domestic herbivore: trade-offs between forage quantity and quality. *Ecological Applications, 23*, 850-863

Beck, J.L., Connelly, J.W., & Wambolt, C.L. (2012). Consequences of Treating Wyoming Big Sagebrush to Enhance Wildlife Habitats. *Rangeland Ecology & Management, 65*, 444-455

Bonham, C. D.., & Lerwick, A. (1976). Vegetation Changes Induced by Prairie Dogs on Shortgrass Range. *Journal of Range Management, 29,* 221-225

Cable, K.A., & Timm, R.M. (1987). Efficacy of Deferred Grazing in Reducing Prairie Dog Reinfestation Rates. In, *Eigth Great Plains Wildlife Damage Control Workshop Proceedings*. Rapid City, SD

Collins, A.R., Workman, J.P., & Uresk, D.W. (1984). An Economic Analysis of Black-Tailed Prairie Dog [Cynomys ludovicianus] Control. *Journal of Range Management, 37,* 358-361

Connell, L.C., Porensky, L.M., & Scasta, J.D. (2019). Prairie Dog (Cynomys ludovicianus) Influence on Forage Quantity and Quality in a Grazed Grassland-Shrubland Ecotone. *Rangeland Ecology & Management, 72*, 360-373

Connell, L.C., Scasta, J.D., & Porensky, L.M. (2018). Prairie dogs and wildfires shape vegetation structure in a sagebrush grassland more than does rest from ungulate grazing. *Ecosphere, 9*, 19

Cooper, J., & Gabriel, L. (2005). South Dakota Black-Tailed Prairie Dog Conservation and Management Plan. In. https://gfp.sd.gov/UserDocs/nav/prairiedog-management-plan.pdf: South Dakota Game, Fish, and Parks

Coppock, D.L., Detling, J.K., Ellis, J.E., & Dyer, M.I. (1983). Plant-herbivore interactions in a North American mixed-grass prairie : I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia, 56*, 1-9

Davidson, A.D., Ponce, E., Lightfoot, D.C., Fredrickson, E.L., Brown, J.H., Cruzado, J., Brantley, S.L., Sierra-Corona, R., List, R., Toledo, D., & Ceballos, G. (2010). Rapid response of a grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock. *Ecology, 91*, 3189-3200

de Souza, J.C., da Silva, R.M., Goncalves, M.P.R., Jardim, R.J.D., & Markwith, S.H. (2018). Habitat use, ranching, and human-wildlife conflict within a fragmented landscape in the Pantanal, Brazil. *Biological Conservation, 217*, 349-357

Derner, J.D., Detling, J.K., & Antolin, M.F. (2006). Are livestock weight gains affected by black-tailed prairie dogs? *Frontiers in Ecology and the Environment, 4*, 459-464

Derner, J.D., Lauenroth, W.K., Stapp, P., & Augustine, D.J. (2009). Livestock as Ecosystem Engineers for Grassland Bird Habitat in the Western Great Plains of North America. *Rangeland Ecology & Management, 62*, 111-118

Dobson, A., & Lyles, A. (2000). Black-Footed Ferret Recovery. *Science, 288*, 985

Duchardt, C.J., Augustine, D.J., & Beck, J.L. (2019). Threshold responses of grassland and sagebrush birds to patterns of disturbance created by an ecosystem engineer. *Landscape Ecology, 34*, 895-909

Fahnestock, J.T., & Detling, J.K. (2002). Bison-prairie dog-plant interactions in a North American mixed-grass prairie. *Oecologia, 132*, 86-95

Fuhlendorf, S.D., & Engle, D.M. (2001). Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. *BioScience, 51*, 625-632

Fuhlendorf, S.D., and D.M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *J. Appl. Ecol., 41*, 604-614.

Gabrielson, M.L. (2009). Effects of Black-tailed Prairie Dogs (Cynomys ludovicianus) and Cattle on Vegetation Composition and Disappearance in the Mixed-Grass Prairie (M.S. thesis). South Dakota State University

Geaumont, B.A., Hovick, T.J., Limb, R.F., Mack, W.M., Lipinski, A.R., & Sedivec, K.K. (2019). Plant and Bird Community Dynamics in Mixed-Grass Prairie Grazed by Native and Domestic Herbivores. *Rangeland Ecology & Management, 72*, 374-384

Grant-Hoffman, M.N., & Detling, J.K. (2006). Vegetation on Gunnison's Prairie Dog Colonies in Southwestern Colorado. *Rangeland Ecology & Management, 59*, 73-79

Guenther, D.A., & Detling, J.K. (2003). Observations of cattle use of prairie dog towns. *Journal of Range Management, 56*, 410-417

Hegel, T.A., Gates, C.C., & Eslinger, D. (2009). The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. *Journal of Environmental Management, 90*, 222-235

Hendrickson, J.R., Johnson, P.S., Liebig, M.A., Sedivec, K.K., & Halvorson, G.A. (2016). Use of Ecological Sites in Managing Wildlife and Livestock: An Example with Prairie Dogs. *Rangelands, 38*, 23-28

Hendrix, M.R. (2018). Black-tailed Prairie Dog (Cynomys ludovicianus) State-and-Transition Model for Loamy Ecological Sites in MLRA 62 in Custer State Park, South Dakota (M.S. thesis). South Dakota State University

Herse, M.R., With, K.A., & Boyle, W.A. (2018). The importance of core habitat for a threatened species in changing landscapes. *Journal of Applied Ecology, 55*, 2241-2252

Hillman, C.N. (1979). Prairie Dog Distribution in Areas Inhabited by Black-Footed Ferrets. *American Midland Naturalist, 102*, 185-187

Hillman, C.N., & Sharps, J.C. (1979). Return of the swift fox to northern Great Plains. *Proceedings of the South Dakota Academy of Science, 57*, 154-162

Hopson, R., Meiman, P., & Shannon, G. (2015). Rangeland dynamics: investigating vegetation composition and structure of urban and exurban prairie dog habitat. *Peerj, 3*

Jachowski, D.S., Gitzen, R.A., Grenier, M.B., Holmes, B., & Millspaugh, J.J. (2011). The importance of thinking big: Large-scale prey conservation drives black-footed ferret reintroduction success. *Biological Conservation, 144*, 1560-1566

Jachowski, D.S., Millspaugh, J.J., Biggins, D.E., Livieri, T.M., & Matchett, M.R. (2008). Implications of black-tailed prairie dog spatial dynamics to black-footed ferrets. *Natural Areas Journal, 28*, 14-25

Johnson-Nistler, C.M., Sowell, B.F., Sherwood, H.W., & Wambolt, C.L. (2004). Black-tailed prairie dog effects on Montana's mixed-grass prairie. *Journal of Range Management, 57*, 641-648

Knopf, F.L. 1996. Prairie legacies-birds. Pages 135-148 *In*: F. B. Samson and F. L. Knopf (eds.), Prairie conservation: preserving North America’s most endangered ecosystem. Island Press. Covelo, California.

Koford, C.B. (1958). *Prairie dogs, whitefaces, and blue grama*. Wildlife Society

Kotliar, N.B., Baker, B.W., Whicker, A.D., & Plumb, G. (1999). A Critical Review of Assumptions About the Prairie Dog as a Keystone Species. *Environmental Management, 24*, 177-192

Krausman, P.R., Naugle, D.E., Frisina, M.R., Northrup, R., Bleich, V.C., Block, W.M., Wallace, M.C., & Wright, J.D. (2009). Livestock Grazing, Wildlife Habitat, and Rangeland Values. *Rangelands, 31*, 15-19, 15

Licht, D.S., & Sanchez, K.D. (1993). Association of Black-Tailed Prairie Dog Colonies with Cattle Point Attractants in the Northern Great-Plains. *Great Basin Naturalist, 53*, 385-389

Martinez-Estevez, L., Balvanera, P., Pacheco, J., & Ceballos, G. (2013). Prairie Dog Decline Reduces the Supply of Ecosystem Services and Leads to Desertification of Semiarid Grasslands. *Plos One, 8*

Miller, B., Ceballos, G., & Reading, R. (1994). THE PRAIRIE DOG AND BIOTIC DIVERSITY. *Conservation Biology, 8*, 677-681

Miller, B.J., Reading, R.P., Biggins, D.E., Detling, J.K., Forrest, S.C., Hoogland, J.L., Javersak, J., Miller, S.D., Proctor, J., Truett, J., & Uresk, D.W. (2007). Prairie dogs: An ecological review and current biopolitics. *Journal of Wildlife Management, 71*, 2801-2810

Monroe, A.P., Aldridge, C.L., Assal, T.J., Veblen, K.E., Pyke, D.A., & Casazza, M.L. (2017). Patterns in Greater Sage-grouse population dynamics correspond with public grazing records at broad scales. *Ecological Applications, 27*, 1096-1107

Nickerson, C., Ebel, R., Borchers, A., & Carriazo, F. (2011). Major Uses of Land in the United States, 2007. *USDA Economic Information Bulletin, 89*

O'Meilia, M.E.O., Knopf, F.L., & Lewis, J.C. (1982). Some Consequences of Competition between Prairie Dogs and Beef Cattle. *Journal of Range Management, 35*, 580-585

Ranglack, D.H., Durham, S., & du Toit, J.T. (2015). Competition on the range: science vs. perception in a bison-cattle conflict in the western USA. *Journal of Applied Ecology, 52*, 467-474

Reynolds, C., & Symes, C.T. (2013). Grassland bird response to vegetation structural heterogeneity and clearing of invasive bramble. *African Zoology, 48*, 228-239

Schneider, S.C., Wunder, M.B., & Knopf, F.L. (2006). Relationship Between Shrubs and Foods in Mountain Plover Habitat in Park County, Colorado. *The Southwestern Naturalist, 51*, 197-202, 196

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

Sierra-Corona, R., Davidson, A., Fredrickson, E.L., Luna-Soria, H., Suzan-Azpiri, H., Ponce-Guevara, E., & Ceballos, G. (2015). Black-Tailed Prairie Dogs, Cattle, and the Conservation of North America's Arid Grasslands. *Plos One, 10*

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

Stoltenberg, M. (2004). Effects of prairie dogs on plant community composition and vegetation disappearance in Mixed-Grass Prairie (M.S. thesis). South Dakota State University

Thomas, J.W. (1996). Sharing common ground - A way toward common solutions. *Sharing Common Ground on Western Rangelands: Proceedings of a Livestock/Big Game Symposium*, *343*, 6-8

Truett, J.C., Jo Ann, L.D.D., Matchett, M.R., Owens, E., & Seery, D. (2001). Translocating Prairie Dogs: A Review. *Wildlife Society Bulletin (1973-2006), 29*, 863-872

Vavra, M. (2005). Livestock grazing and wildlife: Developing compatibilities. *Rangeland Ecology & Management, 58*, 128-134

Vavra, M., & Sheehy, D.P. (1996). Improving elk habitat characteristics with livestock grazing. *Rangelands, 18*, 182-185

Vermeire, L.T., Heitschmidt, R.K., Johnson, P.S., & Sowell, B.F. (2004). The prairie dog story: Do we have it right? *Bioscience, 54*, 689-695

Weltzin, J.F., Dowhower, S.L., & Heitschmidt, R.K. (1997). Prairie dog effects on plant community structure in southern mixed-grass prairie. *Southwestern Naturalist, 42*, 251-258

Whicker, A.D., & Detling, J.K. (1988). Ecological Consequences of Prairie Dog Disturbances. *BioScience, 38*, 778-785