Changes in grassland songbird abundance and diversity in response to grazing by bison and cattle in the northern mixed-grass prairie

by

Maggi Sue Sliwinski

A Thesis Submitted to the Faculty of Graduate Studies of
The University of Manitoba
in Partial Fulfillment of the Requirements for the Degree of

Master of Natural Resources Management

Natural Resources Institute
Clayton H. Riddell Faculty of Environment, Earth, and Resources
University of Manitoba
Winnipeg, Manitoba
August 2011

Copyright © August 2011 by Maggi Sliwinski

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

*****

COPYRIGHT PERMISSION

Changes in grassland songbird abundance and diversity in response to grazing by bison and cattle in the northern mixed-grass prairie

By

Maggi Sue Sliwinski

A Thesis submitted to the Faculty of Graduate Studies of The University of

Manitoba in partial fulfillment of the requirements for the degree

Of Master of Natural Resources Management (M.N.R.M)

© 2010 by Maggi Sue Sliwinski

Permission has been granted to the Library of the University of Manitoba to lend or sell copies of this thesis, to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film, and to University Microfilms Inc. to publish an abstract of this thesis/practicum.

This reproduction or copy of this thesis has been made available by authority of the copyright owner solely for the purpose of private study and research, and may only be reproduced and copied as permitted by copyright laws or with express written authorization from the copyright owner.

ABSTRACT

There is little information comparing the impacts of bison and cattle grazing in the northern mixed-grass prairies; understanding which grazer to use for management is important. I collected data in sites grazed by bison or cattle using point counts to survey the songbird community, and habitat structure measurements. I used generalized- and non-linear mixed models to determine the relationships between grazers and habitat or songbird communities. Bison and cattle grazing caused changes in habitat structure, including decreased vegetation height and litter depth. Sprague's pipits declined more steeply with bison grazing than with cattle grazing. 0.4 AUM/ha was an important threshold, because chestnut-collared longspurs increased in abundance at this stocking rate, and grasshopper sparrows decreased in abundance at this stocking rate. Either grazer is appropriate for managing for grassland birds. There is also an opportunity to encourage surrounding landowners to manage their lands for the benefit of wildlife.

ACKNOWLEDGEMENTS

I would like to first thank my funding agencies, because without their support this research would not have been possible. Parks Canada, the World Wildlife Fund, University of Manitoba, Natural Sciences and Engineering Research Council, Canadian Foundation for Innovation, Manitoba Research Innovations Fund, the Clayton H. Riddell Endowment Fund, and the Government of Manitoba each generously supported my research.

I would like to thank the biologists and staff at Grasslands National Park for their valuable input to my study and their support in the logistical matters of running a large-scale project. In particular, I want to thank Wes Olson for initially taking me to where the bison were, and Rob Sissons for spending lots of time with me on determining what needed to be done. Also, Lander Anderson and Bryn Tetreau, and the rest of Asset Management crew, were essential for maintaining logistical and mechanical functions during my two field seasons.

My committee members, John Wilmshurst, grassland ecologist with Parks Canada, and John Markham, associate professor of Biological Sciences at the University of Manitoba, provided valuable advice on the writing of my thesis. I am indebted to my advisor, Nicky Koper, for her extensive input and advice throughout the research process.

Finally, I want to thank my field assistants for their tireless efforts: Barb Carleton, Rebecca Deatsman, Emily Pipher, Alexis Richardson, Sheila Taillon, Adrienne Tastad, Bonnie Timshel, and Jesse Watkins. I would like to especially thank Tonya Lwiwski for the first ten days of field work when I was frantically choosing study sites with little prior knowledge of the area.

TABLE OF CONTENTS

ABSTRACT i

ACKNOWLEDGEMENTS ii

LIST OF TABLES v

LIST OF FIGURES vii

1.0 INTRODUCTION 1

1.1 BACKGROUND 1
1.2 PROBLEM STATEMENTS 3
1.2.1 Biodiversity and Grazing Management Area Study *3*
1.2.2 Bison/Cattle Study *4*
1.3 RESEARCH QUESTIONS AND OBJECTIVES 5
1.4 RESEARCH HYPOTHESES 6
1.4.1 Biodiversity and Grazing Management Area Study *6*
1.4.2 Bison/Cattle Study *7*
1.5 PROJECT SIGNIFICANCE 8
1.6 LIMITATIONS 9

2.0 LITERATURE REVIEW 13

2.1 GRASSLAND SONGBIRD HABITAT ASSOCIATIONS 13
2.1.1 Baird's Sparrow (Ammodramus bairdii) *13*
2.1.2 Chestnut-collared Longspur (Calcarius ornatus) *14*
2.1.3 Grasshopper Sparrow (Ammodramus savannarum) *15*
2.1.4 Horned Lark (Eremophila alpestris) *15*
2.1.5 McCown's Longspur (Calcarius mccownii) *16*
2.1.6 Savannah Sparrow (Passerculus sandwichensis) *17*
2.1.7 Sprague's Pipit (Anthus spragueii) *17*
2.1.8 Vesper Sparrow (Pooecetes gramineus) *18*
2.1.9 Western meadowlark (Sturnella neglecta) *19*
2.2 HISTORICAL AND MODERN GRAZING PATTERNS 20
2.3 EFFECTS OF GRAZING ON VEGETATION AND HABITAT STRUCTURE 23
2.4 EFFECTS OF GRAZING ON SONGBIRDS 26
2.5 DIFFERENCES BETWEEN BISON AND CATTLE: GRAZING AND BEHAVIOR 29
2.6 RESEARCH GAPS IN MIXED-GRASS PRAIRIE 32
2.6.1 Cattle Grazing Studies *33*
2.6.2 Bison/Cattle Comparison Studies *35*

3.0 METHODS 39

3.1 STUDY DESIGN 39
3.2 STUDY AREA 42
3.3 FIELD METHODS 48
3.3.1 Bird Surveys *48*
3.3.2 Habitat structure *49*
3.3.3 Grazing Intensity *50*
3.4 STATISTICAL ANALYSIS 51
3.4.1 Biodiversity and Grazing Management Area *52*

3.4.2 West Block Bison Grazing *54*
3.4.3 Bison/Cattle Comparisons *56*

4.0 EFFECTS OF CATTLE STOCKING RATE ON SONGBIRDS AND HABITAT STRUCTURE OF THE MIXED-GRASS PRAIRIE **58**

4.1 ABSTRACT 58
4.2 INTRODUCTION 59
4.3 METHODS 63
4.3.1 Study Site *63*
4.3.2 Field Methods *65*
4.3.3 Statistical Analysis *66*
4.4 RESULTS 70
4.4.1 Habitat structure *70*
4.4.2 Songbird Abundance and Diversity *78*
4.4.3 Songbird Community *87*
4.5 DISCUSSION 88
4.6 MANAGEMENT IMPLICATIONS 95

5.0 IMPACTS OF BISON GRAZING ON SONGBIRDS AND HABITAT OF THE MIXED-GRASS PRAIRIE **97**

5.1 RESULTS 97
5.1.1 Habitat structure *97*
5.1.2 Songbird Abundance and Diversity *101*
5.1.3 Songbird Community *104*
5.2 DISCUSSION 104
5.3 MANAGEMENT IMPLICATIONS 107

6.0 ARE IMPACTS ON MIXED-GRASS PRAIRIE SONGBIRDS AND HABITAT DIFFERENT BETWEEN BISON GRAZING AND CATTLE GRAZING? **109**

6.1 ABSTRACT 109
6.2 INTRODUCTION 110
6.3 METHODS 112
6.3.1 Study site *112*
6.3.2 Field methods *114*
6.3.3 Statistical methods *115*
6.4 RESULTS 117
6.4.1 Habitat structure *117*
6.4.2 Songbird Abundance and Diversity *122*
6.5 DISCUSSION 128
6.6 MANAGEMENT IMPLICATIONS 132

7.0 MANAGEMENT CONSIDERATIONS **134**

8.0 LITERATURE CITED **138**

APPENDIX I. **151**

APPENDIX II. **153**

APPENDIX III **155**

LIST OF TABLES

Table 1. Stocking rates in the Biodiversity and Grazing Management Area and adjacent Mankota Community Pastures, 2009-2010. 46

Table 2. Dependent and independent variables used to analyze songbird and habitat structure data in the East Block of Grasslands National Park, 2006-2010. 54

Table 3. Mean and standard deviation of habitat structure variables that varied by year in the East Block of Grasslands National Park, 2006-2010 72

Table 4. Non-linear mixed-effects models and parameter estimates for AIC-selected models for habitat structure variables in the East Block of Grasslands National Park, 2006-2010 73

Table 5. Mean and standard deviation of songbird abundances and diversity measures that varied by year in the East Block of Grasslands National Park, 2006-2010 79

Table 6. Non-linear mixed-effects models and parameter estimates for AIC-selected models for songbird abundance and diversity measures in the East Block of Grasslands National Park, 2006-2010 80

Table 7. Sorensen's quantitative similarity index for songbird communities in the East Block of Grasslands National Park, 2006-2010 87

Table 8. Comparisons of Sorensen's quantitative indices for the East Block of Grasslands National Park and the Mankota Community Pastures, 2006, 2009-2010 88

Table 9. Generalized-linear mixed-effects models and parameter estimates for AIC-selected models for habitat structure variables in the West Block of Grasslands National Park, 2009-2010 98

Table 10. Mean and standard deviation of habitat structure variables that varied significantly by year in the West Block of Grasslands National Park, 2009-2010 99

Table 11. Generalized-linear mixed-effects models and parameter estimates for AIC-selected models for songbird abundance and diversity in the West Block of Grasslands National Park, 2009-2010 102

Table 12. Mean and standard deviation of songbird abundance and diversity measures that varied significantly by year in the West Block of Grasslands National Park, 2009-2010 102

Table 13. Sorensen's binary and quantitative similarity indices for songbirds in comparing ungrazed sites and sites grazed heavily by bison 2009-2010 104

Table 14. Generalized-linear mixed-effects models and parameter estimates for AIC-selected models for habitat structure variables in the East and West Blocks of Grasslands National Park, 2009-2010 118

Table 15. Mean and standard deviation of habitat structure variables that varied significantly by year in the East and West Blocks of Grasslands National Park, 2009-2010 119

Table 16. Mean and standard deviation of habitat structure variables that significantly by grazer species in the East and West Blocks of Grasslands National Park, 2009-2010 119

Table 17. Generalized-linear mixed-effects models and parameter estimates for AIC-selected models for songbird abundance and diversity measures in the East and West Blocks of Grasslands National Park, 2009-2010 124

Table 18. Mean and standard deviation of songbird species that varied significantly by year in the East and West Blocks of Grasslands National Park, 2009-2010 125

Table 19. Mean and standard deviation of songbird species that varied significantly by grazer species in the East and West Blocks of Grasslands National Park, 2009-2010 125

LIST OF FIGURES

Figure 1. Map of Biodiversity and Grazing Management Area 45

Figure 2. Map of the study sites in the West Block of Grasslands National Park 47

Figure 3. Photos of patties in Grasslands National Park 51

Figure 4. Effects of stocking rate on habitat structure in the East Block of Grasslands National Park 74-77

Figure 5. Effects of stocking rate on songbirds in the East Block of Grasslands National Park 81-84

Figure 6. Effects of stocking rate on songbird diversity in the East Block of Grasslands National Park 85-86

Figure 7. Effects of bison grazing on habitat structure in the West Block of Grasslands National Park 100

Figure 8. Effects of bison grazing on songbirds and diversity in the West Block of Grasslands National Park 103

Figure 9. Effects of and interactions between bison and cattle grazing on habitat structure in the East and West Blocks of Grasslands National Park 120-121

Figure 10. Effects of and interactions between bison and cattle grazing on songbirds and diversity in the East and West Blocks of Grasslands National Park 126-127

1.0 INTRODUCTION

1.1 BACKGROUND

The North American prairies were once grazed by free-roaming herds of bison (*Bison bison*) likely numbering in the millions (Brennan and Kuvlesky 2005). Descriptions of what the prairies looked like prior to European settlement indicate that it was a mosaic of habitats: some patches would have been grazed recently while others were not grazed for years or even decades due to feedback loops among bison, vegetation re-growth, fire, and climate (Collins and Barber 1985, Brennan and Kuvlesky 2005). A number of changes have taken place on the prairies preventing restoration to their pre-settlement conditions (Brown and McDonald 1995). Homesteading in the late 1800s and early 1900s allowed breaking of native prairie for agriculture on a large scale for the first time, which reduced the overall extent of the prairies (Samson and Knopf 1994, Davis et al. 1999, Askins et al. 2007). The natural disturbance regime provided by the interaction of bison and fire was replaced with cattle (*Bos taurus*) ranching, which entails moderate stocking rates and homogenous grazing for the greatest economic benefit to the ranching industry (Bailey et al. 1996, Askins et al. 2007, Derner et al. 2008). Of similar importance to the replacement of bison was the suppression of wildfires, which interacted with grazing and climate factors to create a shifting mosaic of vegetation types (Fuhlendorf et al. 2010). These changes impacted the grazing patterns that had been present on the prairies for thousands of years (Brennan and Kuvlesky 2005, Towne et al. 2005), and are likely culprits for grassland bird population declines that have been detected over the past 40 years of the Breeding Bird Survey (Knopf 1994, Herkert 1995).

In light of these changes to the prairies, it is important to understand how grazing by free-roaming bison was ecologically different from cattle grazing on the prairies, as well as how to appropriately manage cattle grazing for the benefit of wildlife. With the research presented here, I asked two questions: how would songbirds respond to a range of stocking rates in the mixed-grass prairies of Saskatchewan, as stocking rates are an important and influential management tool for livestock grazing, and how do bison and cattle grazing compare as ecological drivers on the mixed-grass prairies?

Bison grazing was historically variable in space and time and therefore provided many different habitat niches to support a large diversity of birds across the landscape (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006), although there is little knowledge of the patterns in songbird abundance and diversity prior to European settlement. Studies have shown that bison and cattle have different behaviors and grazing patterns (England and DeVos 1969, Plumb and Dodd 1993) that can result in different effects on vegetation and habitat structure at both local and landscape scales, and therefore may result in differing impacts on grassland birds (Ellis et al. 1976). However, research has also shown that cattle can be an ecologically and economically appropriate substitute for bison (Plumb and Dodd 1993), although their impact on the grassland birds is not well understood (Derner et al. 2009). It is believed that by using stocking rates as a tool to facilitate changes in habitat structure, cattle can be used as a tool to manage for grasslands species (Anderies et al. 2002, Derner et al. 2009). Because managers of Grasslands National Park are interested in reintroducing a disturbance regime to land within the park, it has become important to understand how minimally managed bison and strictly managed cattle herds affect songbirds and their habitat, how stocking rates

can be used to manage for species at risk, how bison and cattle differ and which species may be better suited to the park's management goals (Brown and McDonald 1995, Parks Canada 2006). Further, because cattle ranching occurs on much of the remaining native mixed-grass prairies and is an important economic activity that is also compatible with wildlife management (Willms and Jefferson 1993, Brown and McDonald 1995, Derner et al. 2009), ranchers may benefit from research aimed at using stocking rates to manage for wildlife.

1.2 Problem Statements

The following problem statements are divided into the two studies that are presented here. First is the Biodiversity and Grazing Management Area study, which is the portion of the study taking place in the East Block of Grasslands National Park assessing the use of stocking rates for wildlife management. Second is the Bison/Cattle study, which is the portion of the study comparing bison in the West Block of the park with cattle in the East Block of the park.

1.2.1 Biodiversity and Grazing Management Area Study

Most studies that have assessed the impact of livestock on the prairies focus on floristic diversity (Collins and Barber 1985, Collins 1987, Collins et al. 1998) or ecosystem processes (Biondini et al. 1998, Damhoureyeh and Hartnett 1997). Previous large-scale cattle grazing experiments all used categorical classifications of grazing intensity (i.e. low, medium, high grazing, or 10% and 50%, etc), and lacked pre-treatment data (Koper et al. 2008). Two key recent papers highlighted the impact of cattle grazing on birds in the mixed-grass prairie, and suggested that grazing can be used for management of those birds, but they were both literature reviews and did not provide any

new empirical evidence suggesting the benefits or drawbacks of using cattle, and did not address the specific manner in which cattle should be managed (Saab et al. 1995, Derner et al. 2009). In northern mixed-grass prairie, the Biodiversity and Grazing Management Area (BAGMA) experiment is unique because no previous study has used a gradient of stocking rates as a continuous variable, which allows for the detection of thresholds in the response variables. In this thesis, I define a threshold as a point at which there is a change in the slope of the response variable that indicates that an ecologically significant change occurred at that stocking rate. Further, pre-treatment data were collected to distinguish between pre-existing environmental patterns and the effects of grazing on habitat structure and songbirds. This study will allow me to determine how cattle can be used for wildlife management both inside Grasslands National Park but also on public and private ranchlands (Koper et al. 2008).

1.2.2 Bison/Cattle Study

Several studies have found that bison and cattle grazing have different effects on habitat structure and/or grassland birds (i.e. Coppedge and Shaw 1997, Griebel et al. 1998, Hart 2001, Hickman et al. 2004, Towne et al. 2005, Fuhlendorf et al. 2010), but few have been done on mixed-grass prairie, and most of these have been complicated by limitations of the study design. Some of the studies were done on very small pastures (Plumb and Dodd 1993), or on pastures that had been burned recently (Plumb and Dodd 1993, Griebel et al. 1998, Lueders et al. 2006). Other studies controlled for differences in bison and cattle behavior by managing them similarly (Towne et al. 2005), and conclusions drawn from these studies may not reflect bison and cattle behavior in their typical management regimes (Bailey et al. 1996, Coppedge and Shaw 1998, Biondini et

al. 1999). Further, studies from tallgrass or short-grass prairies should not be extrapolated to mixed-grass prairies because of differences in climate and soil types (Madden et al. 2000).

To compare bison and cattle in a way that reflects typical herd behavior of bison as a conservation tool and cattle as used for production of beef in southwestern Saskatchewan, the bison must be minimally managed and effectively free-roaming while the cattle must be managed in a manner typical to ranching in the region. The study presented here compared bison that had been reintroduced to the West Block of Grasslands National Park and were minimally managed to cattle that were reintroduced in the East Block of the park as part of BAGMA and were managed similarly to those on commercial cattle operations, to understand how these two species' impacts differed in relation to habitat and songbirds.

1.3 Research Questions and Objectives

There were three main questions in this study. My first question was "how does a range of cattle stocking rates impact habitat structure, songbird abundance, and songbird diversity?" The second question I asked was "what are the impacts of effectively free-roaming bison on habitat structure, songbird abundance, and songbird diversity?" The final question was "how do the impacts of bison and cattle grazing differ in their effects on habitat structure and songbirds?" Four objectives were met to reach the three overarching questions:

1. Determined abundance and diversity of songbirds and habitat structure indices in habitats grazed by cattle (2006-2010) and bison (2009-2010).

2. Analyzed and compared abundance and diversity indices and habitat structure among pastures of varying cattle stocking rates to understand how stocking rates affect songbirds and habitat.
3. Assessed whether bison grazing impacted habitat structure, songbird abundance, or songbird diversity.
4. Analyzed and compared abundance and diversity indices and habitat structure between bison and cattle (for 2009-2010) to understand the differences or similarities that existed.

1.4 RESEARCH HYPOTHESES

1.4.1 Biodiversity and Grazing Management Area Study

Null hypothesis: A range of stocking rates will not cause a change in bird abundance, diversity, or habitat structure.

Alternate hypothesis: A range of stocking rates will cause a range of responses in songbird abundance, diversity, and habitat structure.

I expected to support the alternate hypothesis because grazing removes vegetation from a pasture, and therefore impacts the habitat structure by decreasing vegetation height, vegetation density, and litter accumulation. At high enough stocking rates in dry mixed-grass prairie, cattle may also reduce litter depth by consuming dead vegetation after the live vegetation has been completely grazed. This change in habitat structure should increase with increased stocking rates and with increased grazing duration (i.e. higher grazing intensity). Because songbirds typically choose their breeding habitat based on innate preferences for a particular range of habitat structure, songbirds should respond to the change in habitat structure caused by increasing grazing intensity by increasing or

decreasing in abundance. It follows that cattle stocking rates can be manipulated to impact habitat structure for the benefit of a given songbird species. For example, McCown's longspurs have a habitat preference for short grass and bare ground, and would have likely followed behind dense bison herds and therefore would inhabit a pasture with heavy grazing intensity, while Sprague's pipits have a preference for taller vegetation and would likely inhabit lightly grazed areas. By implementing a range of stocking rates in a group of pastures, cattle grazing should cause a range of responses in the habitat structure and therefore in the songbird community.

1.4.2 Bison/Cattle Study

Null hypothesis: Bison and cattle will not differ enough in grazing regimes to affect songbird abundance, diversity, or habitat structure differently.

Alternate hypothesis: Differences in grazing regimes between bison and cattle will be great enough to affect songbird abundance, diversity, and habitat structure differently.

Bison grazing preferences and behaviors are different from those of cattle; these differences include a stronger preference for graminoids, wallowing, horning, and increased digestion times. Also, bison are typically managed as wild animals and are not provided supplemental feed or minerals, and are allowed to roam freely across large areas without fencing, while cattle are most often fenced into smaller pastures and provided feed and water to encourage even grazing distribution. If these differences in cattle and bison grazing, behaviors, and management result in differences in habitat structure between bison and cattle grazing areas, then songbird abundance and diversity will be different in pastures grazed by bison and grazed by cattle, due to songbird habitat

preferences. For example, given that bison can graze closer to the ground than cattle and also create bare patches by wallowing, I might expect the litter component in bison grazed areas to be shorter, which will be preferred more strongly by chestnut-collared longspurs. Alternatively, Sprague's pipits should be less strongly affected by cattle grazing than by bison grazing because they prefer taller and denser vegetation. If the differences in cattle and bison grazing and behaviors are not large enough to result in different habitat structures between bison-grazed and cattle-grazed paddocks, then songbird abundance and diversity should not be different in habitats grazed by bison and habitats grazed by cattle.

1.5 PROJECT SIGNIFICANCE

According to the proposed management plan for Grasslands National Park (GNP), and as a requirement for all national parks in Canada, the main goal of management is to achieve ecological integrity within the park (Parks Canada 2009). To achieve this goal, the park is beginning to reintroduce a disturbance regime similar to the one that was historically present. First, bison were reintroduced to the West Block in 2006 and can freely graze over 18,000 ha. Second, the Biodiversity and Grazing Management Area research project was begun in 2006 to assess the benefits of using cattle and stocking rates as a management tool for wildlife and as a possible alternative to bison.

Cattle are likely an appropriate management tool that can be used to benefit grassland species, including birds (Hart 2001, Derner et al. 2009). Stocking rates can be easily managed to alter the effects of grazing so that they benefit some species over others (Koper et al. 2008). However, bison were the most abundant large herbivore on the prairies prior to settlement, and it has been shown that bison and cattle grazing (Peden et

al. 1974, Plumb and Dodd 1993, Towne et al. 2005) and behaviors (Hartnett et al. 1997, Knapp et al. 1999) are different. How these differences in management and behavior may affect grassland species is poorly understood. Further, understanding the impact of very different management strategies for bison and cattle is important to understand the benefits or drawbacks of choosing one over the other (Plumb and Dodd 1993, Towne et al. 2005). This study will provide pertinent information for the park to develop a grazing management plan, and may also be useful for neighboring landowners who wish to manage their operations in an ecologically sound manner.

1.6 LIMITATIONS

The purpose of this study is to compare songbird abundance and diversity between habitats grazed by cattle or bison, and as such the survey method of choice is the point count. There is some uncertainty as to whether or not point counts are an accurate predictor of habitat quality, or if they should simply be used to measure relative abundance (Van Horne 1983, Bock and Jones 2004). According to Bock and Jones (2004), human disturbances or competition from conspecifics in otherwise optimal habitat can cause individuals to choose suboptimal habitat, and therefore a simple count of birds is not an accurate indicator of habitat quality and therefore of reproductive success. However, a review of the literature revealed that in the majority of cases, point counts were in fact a good estimate for habitat quality (Bock and Jones 2004). Another study suggested that birds may move away from a plot upon arrival of the observer (Lueders et al. 2006). However, there is no reason that individuals of a species in different treatments should behave differently, and this error is likely the same in all areas

and should not cause an error in analyzing the data based on relative abundances (Lueders et al. 2006).

One additional limitation of point counts is that they do not allow for detecting species that sing at different times of day, because the counts are typically started at sunrise and completed within four hours. This may leave out at least two species that sing consistently at other times of day. For instance, the horned lark predominantly sings before dawn (Beason 1995). The horned lark's ground song was heard 1.7 hours prior to sunrise, and ended within fifteen minutes of sunrise (Beason 1970 in Beason 1995), and the flight song occurred most commonly around noon (Pickwell 1931). The McCown's longspur is known to sing throughout the day (Mickey 1943), and possibly more after the early morning hours (With 1994). One study showed that only 16% of McCown's longspurs were detected between 0500 and 0700 (Porter and Ryder 1974 in With 1994).

A limitation of the bison/cattle comparison study is that the natural disturbance regime is not actually present in the West Block of Grasslands National Park, because fire has not yet been reintroduced to that ecosystem. Fire is thought to have been an important component in the evolution of the Great Plains (Brennan and Kuvlesky 2005, Fuhlendorf et al. 2010). However, fire may not be as important in the mixed-grass prairie as it is in the tallgrass prairie, because the mixed-grass prairie is limited by climate (Pylypec and Romo 2003), whereas the tallgrass prairie is not limited by climate and would succeed to a shrub or forest ecosystem without frequent fires (Askins et al. 2007). Further, precipitation in the study area is approximately 350 mm per year (Parks Canada 2006), and one review paper stated that areas with less than 400 mm had only infrequent historical wildfires (Oesterheld et al. 1999). The local ranching population also

disapproves of fire in the dry mixed-grass prairie because fires are a threat to croplands, livestock, and infrastructure, and if the park decides to reintroduce fire, it may be many years before it can be done on a large enough scale to be ecologically relevant. Therefore, the study presented here was the best representation of what is likely to occur for the near future in the region and perhaps what is historically accurate.

The bison/cattle comparison study has an additional limitation in that it was begun four years after bison reintroduction to the West Block, while the cattle portion of the study began immediately after introduction of cattle. To partially account for this limitation, this study used ungrazed areas of the park in both the West Block and East Block as controls. I also included an interaction between grazing pressure, grazer species (bison or cattle), and year, to test if this difference in years grazed caused any differences between the grazer species. Finally, there were a limited amount of songbird data from 2004 (approximately half of the bison plots in 2009) that were used in the analysis to test for pre-existing distributions in songbird abundance in the different areas of the West Block. These data allowed me to understand any effects of bison grazing that were detected in the context of bird distributions prior to grazing due to inherent variability in the habitat structure of different areas of the West Block (Underwood 1994).

A note on the organization of the thesis:

Because there are three separate questions being addressed in this thesis, the sandwich format was chosen for the presentation of the results and discussion. Chapter 4 presents a manuscript for future publication on the Biodiversity and Grazing Management Area, chapter 5 presents information on bison grazing that will be useful for park managers, and chapter 6 presents a manuscript for future publication on the Bison/Cattle comparison study. Chapter 7 presents a set of management implications that stems from these three studies combined.

2.0 LITERATURE REVIEW

2.1 GRASSLAND SONGBIRD HABITAT ASSOCIATIONS

2.1.1 Baird's Sparrow (Ammodramus bairdii)

The presence of a Baird's sparrow is considered an indication of high-quality prairie, and it was probably one of the most common birds on the prairie prior to European settlement (Green et al. 2002). The Baird's sparrow is one of the endemic species of the mixed-grass prairies of the Great Plains (Ahlering et al. 2009), and is now rare across its range. The species was once listed as at risk in Canada, but was removed from this list in 1996; the species' status will be reviewed in 2012 by the Committee on the Status of Endangered Wildlife in Canada candidate species list (COSEWIC 2010). Arrival on the breeding grounds is in early May and departure for their wintering grounds in the southern US starts in mid- to late-September (Green et al. 2002).

The Baird's sparrow avoids areas that are overgrown with woody or exotic vegetation, but they are amenable to using cultivated lands with remaining taller vegetation that are similar in structure to their preferred native habitat (Owens and Myres 1973, Green et al. 2002, Madden et al. 2000). Mixed-grass and fescue prairies are their native habitat. Baird's sparrows prefer prairies with few shrubs, a relatively large amount of litter retained from previous years, little bare ground, and low disturbance from agriculture or grazing (Owens and Myres 1973, Green et al. 2002). Relatively low height and density of vegetation is preferred upon arrival on the breeding grounds and for nest site selection, likely because foraging is easier in this habitat (Ahlering et al. 2009), but most studies have shown that the species nests in areas with moderately tall and dense vegetation with moderate litter, but low visual obstruction (Kantrud and Kologiski 1983,

Madden et al. 2000, Davis 2004). Grazing intensity was not shown to dramatically impact Baird's sparrows' abundance, but they were still attracted more to pastures with taller vegetation and lower shrub cover (Davis et al. 1999). Baird's sparrows are probably area sensitive, as they do not occur on small pastures (Davis 2004).

2.1.2 Chestnut-collared Longspur (Calcarius ornatus)

Chestnut-collared longspurs are endemic to the short- and mixed-grass prairies of North America, preferring sites that have been heavily grazed or recently disturbed by fire (Hill and Gould 1997). Populations of the chestnut-collared longspur are declining, and the Committee on the Status of Endangered Wildlife in Canada has proposed that the chestnut-collared longspur be listed as threatened under the Species at Risk act (COSEWIC 2010). Spring arrival on the breeding grounds begins in March and extends through May, and departure for the wintering grounds begins mid-September and extends through early October (Hill and Gould 1997).

This species prefers areas of low density and sparse vegetation, very little litter accumulation, and native pastures over seeded pastures (Davis et al. 1999). It also has a greater affinity to shorter vegetation and increased bare ground than other species including Sprague's pipits, Baird's sparrows, and Savannah sparrows (Davis 2005), while larger-scale habitat characteristics were similar to other songbirds in that there was taller and denser vegetation (Davis 2005). One other important feature that this species may select for is the presence of cow or bison patties, which may assist in concealing the open nests from predators or sun and wind (Davis 2005). Chestnut-collared longspurs are also area sensitive, selecting only larger patches of grassland (Davis 2004).

2.1.3 Grasshopper Sparrow (Ammodramus savannarum)

The grasshopper sparrow is not endemic to the Great Plains, as it breeds from coast to coast (Vickery 1996). This species has been declining dramatically (Herkert 1994), and is listed on the subcommittee candidate list of the Committee on the Status of Endangered Wildlife in Canada for Alberta and Saskatchewan (COSEWIC 2010). Grasshopper sparrows are also likely to be area sensitive, and are only found on larger tracts of their preferred habitat (Herkert 1994, Davis 2004).

The grasshopper sparrow prefers sites that are more densely vegetated with more shrubs in the mixed-grass prairie (Vickery 1996), although a separate study showed that grasshopper sparrows were associated with pastures that have a lower density of shrubs (Davis 2004). Grasshopper sparrows were found to occupy transitional areas between shrubsteppe and grasslands (Kantrud and Kologiski 1983). A study in the mixed-grass prairie of North Dakota showed that grasshopper sparrows had large overlap in habitat associations with Baird's sparrows and bobolinks, and that they preferred moderate vegetation height and moderate litter accumulation (Madden et al. 2000). Davis (2004) also found that grasshopper sparrows preferred intermediate habitat structures and avoided areas with tall and dense vegetation and areas with low and sparse vegetation.

2.1.4 Horned Lark (Eremophila alpestris)

The horned lark is native to North America, and its breeding range extends from central Mexico as far north as Alaska (Beason 1995). Distribution of the horned lark within its breeding range is dependent on suitable habitat and therefore this species' abundance varies widely (Beason 1995). The northern populations of the horned lark migrate south during the winter, but they can arrive in Saskatchewan as early as February

(Beason 1995), and the peak breeding season may be as early as May (Owens and Myres 1973). This species increased in abundance as lands across North America were converted to agriculture, which provided suitable habitat often in the form of summer fallow (cropland that is left unseeded for a summer and therefore is mostly bare ground) (Hurley and Franks 1976, Beason 1995). Horned larks have declined since agricultural lands have been abandoned and returned to forest (Beason 1995). It is not a listed or candidate threatened or endangered species in Canada in Saskatchewan (COSEWIC 2009, 2010, Government of Canada 2009).

Horned larks prefer open grasslands with short and sparse vegetation or bare ground, and also nest in deserts and agricultural areas (Beason 1995, Dinkins et al. 2003). In one study, the horned lark was the only songbird of nine studied that was found using summer fallow habitats and seeded pasture habitats, and horned larks were most abundant in cultivated pastures (Owen and Myres 1973). In fact, in this study horned larks only bred on cultivated and grazed plots, which have low grass heights and more bare ground (Owens and Myres 1973).

2.1.5 McCown's Longspur (Calcarius mccownii)

McCown's longspurs are a bird of the open prairies (With 1994). Arrival in the spring begins in April, and the birds begin to group up in August for the migration to their wintering grounds in the southern US and Mexico (With 1994). This species is listed as special concern under the Canada Species at Risk Act (COSEWIC 2009).

This species is restricted to short-grass prairies and areas in mixed-grass prairies that resemble short-grass because of disturbances such as heavy grazing and/or fire (With 1994). McCown's longspurs prefer to nest at sites with sparse vegetation, little litter

accumulation, short-grass species such as blue grama grass (*Bouteloua gracilis*), cactus, and some mid-height grasses and shrubs (With 1994). The species is rarely found on idle grassland that has taller and denser vegetation (Kantrud 1981).

2.1.6 Savannah Sparrow (Passerculus sandwichensis)

Savannah sparrows are broadly distributed and breed across most of North America in open habitats (Wheelwright and Rising 2008). This species migrates south to the southern United States and Mexico for the winter (Wheelwright and Rising 2008). Savannah sparrows may be area sensitive: in one study, only larger tracts of their preferred habitat were used (Herkert 1994), but in another study this species' abundance was inversely related to or independent of patch size (Davis 2004). The Savannah sparrow is not a listed or candidate species in Canada (Government of Canada 2009, COSEWIC 2010).

Savannah sparrows inhabit a wide range of open habitat types, including native prairies, grassy meadows, cultivated fields, edges of salt marshes, tundra, lightly grazed pastures, and coastal grasslands (Wheelwright and Rising 2008). They tend to avoid areas with heavy tree cover, but perch on shrubs while singing (Swanson 2003, Wheelwright and Rising 2008). Local characteristics for site selection include little bare ground, high litter accumulation, and old and decaying cow dung (Davis 2005). The cow dung allows for vegetation to be thick due to fertilization of the soil (Davis 2005). This species also prefers tall vegetation, even if on the edges of cultivated fields (Owens and Myres 1973).

2.1.7 Sprague's Pipit (Anthus spragueii)

The Sprague's pipit is one of the few bird species endemic to North American grasslands, and is also one of the least understood due to its cryptic behavior and

markings (Robbins and Dale 1999). The Sprague's pipit has experienced large declines over its entire range (Robbins and Dale 1999), and is currently listed as a threatened species under the Canada Species at Risk Act (Government of Canada 2009). Spring arrival for the Sprague's pipit is typically the end of April through the middle of May, and it begins migration to its wintering grounds of the southern United States and Mexico in late September (Robbins and Dale 1999).

Breeding habitat of the Sprague's pipit is in dry, open grasslands with very low shrub cover (Robbins and Dale 1999). They prefer to nest in grasses of medium height (shorter than anything available in tallgrass prairie) and litter depth, and avoid non-native species such as crested wheatgrass and smooth brome (Wilson and Belcher 1989, Davis et al. 1996). Pipits run or walk to forage, and as breeding habitat is also used as foraging habitat, they avoid dense litter that can be difficult to move through (Harris 1933, Robbins and Dale 1999, Madden et al. 2000). Pipit nests are built out of medium length dried grasses (litter) and often have a dome over top made of live grasses around the nest (Robbins and Dale 1999). Sprague's pipits are area sensitive; one study found that they were only observed on pastures of at least 30 ha, and that the minimum area requirement (patch size at which Sprague's pipits reached 50% of its predicted maximum abundance) was 145 ha (Davis 2004).

2.1.8 Vesper Sparrow (Pooecetes gramineus)

The vesper sparrow resides in open rangelands where it is relatively common and breeds across the northern half of the United States and the southern portion of Canada from coast to coast. It winters in the southern US and Mexico (Jones and Cornely 2002). Migrating birds arrive on the breeding grounds starting in mid-April and leave for the

wintering grounds starting in September (Dechant et al. 2003). The vesper sparrow is not a listed or candidate species in Canada (Government of Canada 2009, COSEWIC 2010).

Vesper sparrows prefer dry grasslands with a few shrubs for perching on to sing and a small amount of bare ground, but are considered a moderate generalist as they are found in a variety of habitats including native prairie, shrublands, old fields, and even woodland edges (Jones and Cornely 2002, Dechant et al. 2003). Areas of dry habitat with short, sparse, and patchy vegetation are preferred by vesper sparrows (Dechant et al. 2003). This species may be negatively associated with vegetation height, as it was found to prefer shorter vegetation in one study (Davis and Duncan 1999).

2.1.9 Western meadowlark (Sturnella neglecta)

The western meadowlark is a very common bird of the prairie region, with a range extending from the northern Great Plains to the Pacific Ocean (Davis and Lanyon 2008). It breeds in the southern half of Canada (as north as central Alberta) and most of the United States from the Pacific Ocean to approximately the eastern edge of Kansas (Davis and Lanyon 2008). Western meadowlarks winter as far south as central Mexico, but a large portion of its breeding range overlaps with its wintering range. They migrate from the northern-most portion of their range starting in mid-October, and return starting in March and April (Davis and Lanyon 2008). The western meadowlark is not a listed or candidate species in Canada (Government of Canada 2009, COSEWIC 2010).

The western meadowlark is most common on native prairie and lands under perennial cover, and least common on cropland (Davis and Duncan 1999). Western meadowlarks prefer areas with moderate grass cover, litter, and forbs (Wiens and Rotenberry 1981, Madden et al. 2000), but avoid areas with tall and dense vegetation

(Wiens 1969, Madden 1996, Fritcher et al. 2004). The western meadowlark has large territories relative to other grassland species, but it is unclear whether they are area sensitive (Davis 2004, Johnson and Igl 2001).

2.2 HISTORICAL AND MODERN GRAZING PATTERNS

The lack of precipitation is the primary factor in maintaining mixed-grass prairie and limiting the system from succeeding to a forested state, but grazing and fire were also important drivers of the ecosystem (but see page 11, Milchunas et al. 1988, Askins et al. 2007). The feedback loops between climate, bison grazing, and fire led to a landscape with a mosaic of habitat patches in every stage of succession, which provided habitat for twenty-six species of obligate grassland birds (Askins et al. 2007). Declines of nearly all of these obligate songbirds are likely due to land settlement, agriculture, and the suppression of fires (Davis et al. 1999); in Saskatchewan, only 24% of the original native prairie remains (Askins et al. 2007). The near-extinction of the bison and their replacement with cattle on the landscape also led to a subtle shift in grass and forb densities and dominance on the remaining native prairie, which has likely contributed to the decline in songbird populations (Askins et al. 2007).

The grazing patterns present in pre-settlement times differ from what occurs today. Herds of thousands of bison roamed the prairies and essentially applied a rest-rotational or deferred grazing system, which caused some areas to be grazed heavily and repeatedly, and allowed other areas to be undisturbed for years or even decades (Coughenour 1991, Hartnett et al. 1997, Brennan and Kuvlesky 2005). Plains bison declined drastically, nearly to extinction, due to over-hunting in the mid-1800s (Boyd and Gates 2006), but were saved from extinction by the foresight of individuals and

conservation organizations that established private herds (Boyd and Gates 2006). There are approximately 500,000 bison in North America today; 95% of these are raised for commercial purposes, and only the remaining 5% are in conservation herds across Mexico, the United States, and Canada (Boyd and Gates 2006). It is suggested that bison herds will have conservation value only when they inhabit large geographic ranges, and that the herds should be of sufficient size to maintain population viability (Boyd and Gates 2006). Larger geographic areas for bison to roam and year-round presence on the prairies would allow them to act more naturally, and to select grazing sites based on innate preferences (Coughenour 1991).

Current grazing patterns of cattle are very different from patterns displayed by bison in pre-European settlement times. Cattle are fenced into smaller pastures and they are moved periodically to encourage uniform grazing, which creates a landscape of more homogeneous vegetation heights and densities than would be present on prairies impacted by natural bison grazing (Knopf 1996, Askins et al. 2007). However, cattle can increase habitat heterogeneity when stocked at low intensities in larger pastures because they graze more selectively (Hart et al. 1988). The goal of most cattle managers is to maximize forage utilization by the strategic placement of fencing, minerals, and water sources, to extract as much as is sustainably (and sometimes unsustainably) possible from an ecosystem (Coughenour 1991, Bailey et al. 1996, Fuhlendorf and Engle 2001), while bison are typically not given supplemental feed and are minimally managed (Knapp et al. 1999). Cattle and bison both spend more time at nutritionally superior sites (Bailey et al. 1996), but because cattle do not have the opportunity to select sites at large spatial scales in the way that free-roaming bison do, they may graze more heavily and continuously in

all areas of a given pasture to meet their nutritional requirements. Studies have shown that this effect may be exacerbated because beef production increases with increasing stocking rate and grazing pressure (Derner et al. 2008). This gives ranchers an economic incentive for over-grazing their lands, but by doing so they risk deterioration of rangelands and diminishing economic returns (Hart et al. 1988). These economic and ecological factors likely balance each other when land managers and ranchers are deciding how to manage their lands. Further, bison historically grazed a portion of the landscape to extreme lengths, creating patches with very little or no remaining vegetation (England and DeVos 1969), so there may be a wildlife benefit to allowing portions of ranchland to be heavily overgrazed, depending on which species are being managed for.

Even though there are large differences between the way that cattle are currently managed and the way that bison once roamed the prairies, cattle may be an appropriate substitute for bison when managing for grassland birds (Plumb and Dodd 1993, Knapp et al. 1999, Derner et al. 2009). However, some researchers suggest that this substitution will only be successful when management strategies are used that mimic historical grazing patterns (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006). The historical grazing patterns included all intensities of grazing (Hart and Hart 1997) and temporal and spatial variability (Hartnett et al. 1996), so it is important to maintain this grazing heterogeneity to maintain maximum species diversity (Vickery et al. 1999, Hart 2001). Further, other subtle differences between cattle and bison, along with different management regimes for both (Hartnett et al. 1997), may have an impact on whether or not cattle can be an ecological substitute for bison when managing for grassland birds and prairies in general.

2.3 Effects of grazing on vegetation and habitat structure

The first theory to explain the impacts of grazing on rangelands was the range succession model, proposed by Dyksterhuis (1949), which stated that rangelands have a single climax state in the absence of grazing, and that there is a continuous divergence from the climax state as grazing increases. However, this theory did not take into account many more variables that are present on rangelands and was therefore insufficient to explain the dynamics that are present. Two other models were proposed in the 1980s and are widely used to describe the impact of disturbances on rangelands. The first was the range model (also known as the MSL model), proposed by Milchunas and colleagues (1988), and the second was the state-and-transition model, proposed by Westoby and colleagues (1989).

The main strength of the state-and-transition model was that it challenged range managers to develop a model that was suitable for their specific location (Cingolani et al. 2005). The MSL model, on the other hand, used two site characteristics to predict the site's response to grazing: site productivity (mainly precipitation), and evolutionary history of grazing (Milchunas et al. 1988, Cingolani et al. 2005). In the arid mixed-grass prairie with a long history of grazing, the MSL model predicts that plant diversity will be highest at low to moderate grazing intensities, and will begin to decrease at higher grazing intensities (Milchunas et al. 1988). In wet years in the mixed-grass prairie, such as in 2009 and 2010, the model predicts that highest diversity will be at moderate grazing intensities (Milchunas et al. 1988). This shows that the model proposed can be flexible depending on climatic patterns. It is now understood that the MSL range model is actually a special case of the state-and-transition model (Briske et al. 2003) and that the

two can be used together to inform an understanding of the dynamics present on rangelands. Cingolani and colleagues (2005) modified the MSL model to include non-equilibrium dynamics and irreversible changes in plant communities that allowed it to be better suited to a variety of situations present on rangelands.

The mixed-grass prairie has been maintained by low levels of precipitation, and also by grazing, fire, and low-quality soils (Askins et al. 2007). Precipitation, grazing, and fire were distributed variably through space and time, and this created a prairie with varying height and density of vegetation and litter accumulation (Askins et al. 2007). Herbivores such as bison and cattle modify habitat structure and plant communities in a variety of ways. Grazing reduces plant canopy height, changes plant morphology, creates grazing lawns, affects hydrology, compacts soils, and changes the rate of litter accumulation (Milchunas et al. 1989, Saab et al. 1995, Hartnett et al. 1997). Trampling by bison and cattle and wallowing by bison can also have impacts on ungrazed areas by compacting the soil and removing vegetation (Hartnett et al. 1997). Grazing also has direct impacts on the composition of plant species (Collins 1987, Anderson and Briske 1995), and therefore on habitat structure, due to the structure of plants selected for or avoided (Hartnett et al. 1996, Briske et al. 2005). For example, one study showed that cattle grazing decreased the cover of dominant grasses and increased the cover of ruderal forbs in tallgrass prairie, and the author speculated that bison, which strongly select for grasses, would cause even greater reduction of dominant grasses (Collins 1987). These impacts on specific species can affect habitat structure because taller species that are grazed will lose dominance, allowing short-stature species to increase in abundance (Anderson and Briske 1995). By reducing the abundance of dominant grasses, growth

and survival of subdominant species may increase, and diversity and evenness of the plant community may increase in the presence of herbivores (Cid et al. 1991, Hartnett et al. 1997).

In a study comparing plant diversity at a variety of grazing intensities, Collins and Barber (1985) found that diversity, richness, and evenness were highest on pastures that were lightly to moderately grazed. Other studies have also had similar results (i.e. Hartnett et al. 1996, Collins et al. 1998, Knapp et al. 1999). These studies are consistent with the intermediate disturbance hypothesis, which predicts that biodiversity will be higher in moderately disturbed systems because the dominance of any one species or group of species will be prevented, allowing other species to grow and survive (Grime 1973, Connell 1978). These results were also consistent with the MSL Model (Milchunas et al. 1988). However, others have concluded that diversity can both increase and decrease with grazing depending on the productivity of the grassland, the intensity of grazing, and the evolutionary history of grazing in the area (Milchunas et al. 1988, Cid et al. 1991, Milchunas et al. 1998, Bakker et al. 2006). Therefore, there are a number of different models that can be used to describe the effects of grazing on vegetation and community structure. In the mixed-grass prairie, the effects of grazing on plant communities depend on the degree of the disturbance, water availability, and history of past grazing events (Milchunas et al. 1988). Probably of most importance to bird communities, increased grazing intensity means increased plant removal (lower vegetation height), decreased standing dead vegetation, and decreased litter accumulation (Biondini et al. 1998, Gillen et al. 2000). Further, grazing at different intensities and in pastures of different size can change the impact on habitat structure because these

changes can influence grazer behavior and selectivity (Fuhlendorf and Smiens 1999, Briske et al. 2005). For example, grazing a small pasture at a high stocking rate will cause increased homogeneity, while grazing a large pasture at a low stocking rate will cause increased heterogeneity (Hart et al. 1993).

2.4 Effects of grazing on songbirds

In a review of the effects of grazing intensity on various floral and faunal communities on the shortgrass steppe of Colorado, the only group of animals found to have a shift in dominant species and community composition in response to grazing intensity was birds (Milchunas et al. 1998). This suggests that birds may be particularly sensitive to grazing treatments (Milchunas et al. 1998). Because various birds of the prairies have different habitat requirements (Saab et al. 1995, Askins et al. 2007), there is the need to manage grazing to provide suitable habitat for every species (Fuhlendorf and Engle 2001, Hart 2001). Managing for heterogeneity in the landscape is the best way to provide habitat for the bird species that inhabit the Great Plains (Fuhlendorf et al. 2006).

Songbirds are very sensitive to changes in litter depth and density, and grazing and fire are forces that have a large impact on litter (Fuhlendorf et al. 2006). A study done in tallgrass prairie found that landscapes treated with fire and grazing had the highest diversity of songbirds because there was the greatest diversity in litter accumulation, supporting a variety of songbirds. The typical management practice of encouraging homogeneous grazing of the landscape resulted in low species diversity (Fuhlendorf et al. 2006). Practices that maintain homogeneity of the landscape, which is the common goal in ranching operations (Bailey et al. 1996), are not capable of

maintaining the wide diversity of songbirds that were once present on the prairies (Fuhlendorf et al. 2006).

The brown-headed cowbird population has increased with the changing landscape in part because it is closely associated with grazing animals such as cattle (Robinson et al. 1995, Shaffer et al. 2003). This increased population poses a risk to songbirds because cowbird brood parasitism is increasing (Harnett et al. 1997). Because the landscape has changed so drastically and there is little chance that it will be returned to pre-settlement quality, the impact of cowbirds may not be manageable unless cowbird populations themselves are managed (reviewed in Shaffer et al. 2003). However, GNP may be a refuge for songbirds because it is a large, undisturbed area that cowbirds are less likely to inhabit (reviewed in Shaffer et al. 2003). The building of fences and introduction of cattle might provide an incentive for brown-headed cowbirds (reviewed in Shaffer et al. 2003) to enter and stay in BAGMA, and this impact will have to be carefully monitored.

Many studies have focused on the Sprague's pipit because it is a listed species (Government of Canada 2009). Sprague's pipits are sensitive to grazing, and they are usually found more frequently on pastures that are grazed lightly or moderately over pastures that are grazed heavily (Saab et al. 1995, Davis et al. 1999). However, chestnut-collared longspurs have the opposite habitat preferences of Sprague's pipits, preferring sparse vegetation and more bare ground (Davis et al. 1999, Davis 2005). Also of possible importance to chestnut-collared longspurs is the presence of cow or bison patties, which may aid in concealing adults, young, and nests (Davis 2005). These studies are highlighted to show that grazing impacts all songbirds differently, because of divergent

evolutionary paths leading each species to develop specific ranges of habitat preferences (Cody 1985).

The use of seral stages has been proposed as a model for determining songbird use of grasslands, and this may be an economically and logistically efficient tool (Fritcher et al. 2004). Seral stages are different communities and structures of grassland that can be maintained by disturbances such as grazing and fire (Lesica and Cooper 1999). For some species, such as McCown's longspurs, horned larks, and burrowing owls, an early seral stage, or one of low vegetation height, more bare ground, and less litter, is the ideal grassland condition (Fritcher et al. 2004). For others, a moderate seral stage is ideal. For example, western meadowlarks were found more often on areas of intermediate vegetation height and density (Fritcher et al. 2004). Grasshopper sparrows were found mostly on pastures of late seral stage, where grazing or fire had not occurred for a number of years (Fritcher et al. 2004). By understanding the preferences of songbirds for certain seral stages, it may become easy to manage grazing for the benefit of certain species, but more research is necessary to determine the efficacy of seral stages as a management tool (Fritcher et al. 2004). Alternatively, songbirds may be a potential indicator for the impact grazing is having on the landscape (Bock and Webb 1984), and whether or not grazing is having an ecologically relevant impact on the ecosystem. Because each songbird species has very particular habitat requirements, their presence or absence may indicate what effect grazing is having on the landscape.

These previous examples show that grazing treatments can have different effects on different songbirds. Also, the same grazing system applied in the tallgrass prairie can have vastly different results if applied in the short-grass or mixed-grass prairie (Saab et

al. 1995). There is not one treatment type that can solve the problem of declining songbird populations. As a rule, it is important that small sites are managed for species with similar habitat requirements, because a small area can only support the habitat and size requirements of certain grassland birds (Vickery et al. 1999). However, larger areas should be managed for heterogeneity (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006). Large-scale management that mimics historical grazing patterns to create a heterogeneous landscape will be important for the conservation of grassland species (Fuhlendorf et al. 2006). This will support the songbirds that once flourished under the intermittent and variable grazing of bison (Griebel et al. 1998, Vickery et al. 1999, Walk and Warner 2000).

2.5 DIFFERENCES BETWEEN BISON AND CATTLE: GRAZING AND BEHAVIOR

There are a small number of studies that have directly compared bison and cattle foraging preferences and behavior (reviewed in Hartnett et al. 1997), but most have been done in tallgrass prairies. There is no indication in the literature that any of the foraging preferences or behaviors would be different for the study site in this research. However, due to differences in species composition and water availability between tallgrass prairies and mixed-grass prairies, there may be important differences in the responses of plants and habitat structure between mixed-grass and tallgrass prairie. Inherent differences between bison and cattle, including morphology, social behaviors, physiology, and environmental tolerances, do cause dissimilarities in their grazing preferences and behaviors (Damhoureyeh and Hartnett 1997), which may have an important impact on habitat structure and therefore on grassland birds.

Bison and cattle both select for graminoids, but bison consistently consume more of them and select for them more strongly than cattle do, while cattle consume more forbs and browse than bison (Peden et al. 1974, Schwartz and Ellis 1981, Cid et al. 1991, Plumb and Dodd 1993, Damhoureyeh and Hartnett 1997). Further, cattle and bison both better digest the plant groups that they select for, which may be an evolutionary adaptation (Peden et al. 1974). Even these slight differences in plant preferences between bison and cattle may cause subtle but important changes on the prairies (Hartnett et al. 1997).

Horning and rubbing of objects such as trees and shrubs can have substantial impacts on the landscape of tallgrass prairies because of the presence or invasion of trees (Coppedge and Shaw 1997). Because there are very few trees on the mixed-grass prairie, trampling by cattle of any shrubs present may have similar effects on the mixed-grass landscape as bison horning and rubbing (Hartnett et al. 1997).

One activity bison exhibit that cattle do not is wallowing. Wallowing can cause a difference at the landscape level (Coppedge and Shaw 2000), because wallowing creates a solid depression in the ground that can be present on the prairie for over 125 years after bison have been removed (Knapp et al. 1999). The combination of bison grazing and wallowing may act together to limit the competitive dominance of a single species (Collins and Barber 1985), and because cattle do not wallow, there may be higher abundance of dominant species in cattle pastures. Bison wallowing increases plant species richness and heterogeneity in a patch in both active and inactive wallows (Polley and Collins 1984, Hartnett et al. 1997), and these patches of compacted and barren soil

can provide important habitat for prairie species that require wetter conditions because of the ability of wallows to hold water in the spring (Polley and Collins 1984).

Another important difference between bison and cattle is that bison are less selective than cattle at smaller scales, meaning that bison do not spend time to search for patchily distributed forage classes, but bison are more selective at the larger patch scale (Damhoureyeh and Hartnett 1997, Hartnett et al. 1997). This may be because cattle do not have the opportunity to make landscape-scale habitat selection decisions because they are placed in smaller pastures than the bison (Coughenour 1991, Bailey et al. 1996). Even so, this is an important difference in the typical management strategies for bison and cattle that can affect habitat structure and grassland birds. This can be important because free-roaming bison may have the opportunity to choose certain landscape features in a way that has different impacts on the environment than if they did not have this choice (Bailey et al. 1996). Also, bison and cattle chose distinctive areas to graze when they were given the same choice: cattle chose moister areas, while bison chose drier areas (Peden et al. 1974). This is likely because cattle are more dependent on water than bison are, and therefore bison can have an impact on a much larger area of the landscape than cattle because they are not as restricted by the absence of water (Hartnett et al. 1997).

The morphology of the bison mouth is different from that of the cattle mouth and this difference allows bison to graze nearer to the ground than cattle, resulting in closer-cropped grazing lawns in bison pastures (Hartnett et al. 1997). This results in sharper boundaries between grazed and ungrazed areas in the bison pastures than would be seen in cattle pastures (Knapp et al. 1999).

The differences in management strategies may have significant consequences for wildlife on the prairies, as mentioned above. In historical times, free-roaming bison in herds of thousands were capable of all but destroying a localized area, causing severely overgrazed areas and contaminating water bodies with urine, feces, and dead bison. The bison would then move on, leaving these areas to recover and be used by other wildlife (England and DeVos 1969, Hart and Hart 1997). The return interval may have been between eight and thirty-five years in some areas (Malainey and Sherriff 1996, Parks Canada 2004), allowing for a mosaic of landscape types to be available. Cattle managed for production purposes are not usually allowed to severely overgraze the grassland and are not kept at densities such that waterways are flooded with excrement, but are instead encouraged to graze rangelands uniformly (Temple et al. 1999, Askins et al. 2007). This means that any wildlife reliant on overgrazed areas (such as prairie dogs, juvenile burrowing owls, and McCown's longspurs), or undergrazed areas (such as Sprague's pipit and Baird's sparrows) will have less suitable habitat available across the prairies (Temple et al. 1999). Bison, on the other hand, may create this habitat as a function of their grazing strategies.

2.6 Research Gaps in Mixed-grass Prairie

The following sections focus on studies done in the mixed-grass prairie region of the Great Plains, because studies from tallgrass prairie and short-grass prairie should not be extrapolated to mixed-grass prairie due to vegetation and climatic differences (Madden et al. 2000).

2.6.1 Cattle Grazing Studies

Because cattle grazing is an important management tool for prairie habitat (Fuhlendorf and Engle 2001, Derner et al. 2009), understanding how cattle grazing can be managed for the benefit of songbirds is important. A number of studies assessing the impacts of cattle grazing on habitat and songbirds have been done, but most of these contained flaws in the study design that makes them less useful for designing a grazing management scheme for Grasslands National Park or the surrounding lands.

A study was conducted in North Dakota, USA in mixed-grass prairie, to assess the impacts of cattle grazing on ecosystem processes such as nitrogen cycling, above- and below-ground net primary production, and plant species cover and density (Biondini et al. 1998). The study began in 1988 and continued through 1995, and included three replications of ungrazed control, moderate grazing, and heavy grazing, in nine pastures of 13.2 ha. The study found that no differences in species composition or density could be attributed to grazing intensity. Only one difference was found between grazing treatments, and this was the near-disappearance of a single species of forb in the heavy grazing treatment. Above-ground net primary production also showed no consistent patterns between grazing treatments; only standing dead biomass, biomass nitrogen, and litter biomass changed significantly with increased grazing. The authors conclude that grazing intensity only affects grassland ecosystems within the context of the climate, and that grasslands are resilient to changes in grazing (Biondini et al. 1998).

Davis and colleagues (1999) conducted a study in the northern mixed-grass prairie of southern Saskatchewan, and a component of the study was to determine whether various stocking rates influenced the occurrence of three endemic songbirds.

Grazing intensity was estimated by a range ecologist, and was divided into idle (ungrazed for at least two years), light, moderate, and heavy grazing. This study was forced to use presence/absence instead of abundance data because the species of interest were detected in too few plots. The data indicated that grazing intensity had little influence on the occurrence of Baird's sparrows and chestnut-collared longspurs, but that Sprague's pipits occurred less frequently on heavily grazed pastures. However, idle sites were removed from data analyses because of a lack of pastures that were ungrazed. With a lack of control sites, it becomes difficult to interpret the results properly.

A study done in the southern mixed-grass prairie by Gillen and colleagues (2000) assessed the impacts of stocking rate on floristic species composition and standing crop variables. The seven-year study had six pastures of 65 ha that were stocked at rates between 23 and 51 AUD/ha (animal unit days per hectare), with 25 AUD/ha considered the sustainable rate for the area. This study found little impact of stocking rate on floristic composition or on standing crop biomass, and the change in biomass was attributable to the higher demand for forage at higher stocking rates. The benefit of this study is that it used very high stocking rates for the area, but the main drawback is that it did not include ungrazed controls. The authors concluded that the mixed-grass prairie was resilient to all stocking rates, even at slightly lower than average rainfall during the first years of the study, and that many years of grazing prior to the study had already influenced the vegetation (Gillen et al. 2000). Of most importance here, the study did not evaluate the effects of stocking rate on songbird populations.

An important review paper was recently published that explains the importance of livestock as ecosystem engineers, and the manner in which conservationists and livestock

producers can be brought together for the management of prairie birds (Derner et al. 2009). This paper examines four birds of the prairies that encompass a wide range of habitat requirements, from heavily overgrazed to ungrazed, some of the species requiring a spectrum of habitat throughout their lifecycle. This study does not present any new empirical results, but it does highlight the importance of understanding how livestock grazing affects the landscape, and how it can be used for the management of birds (and presumably other wildlife).

Even with this number of studies, there is still the need to improve and add to the information these studies provided. None of these studies used a continuous independent variable, which would allow for the detection of important ecological thresholds in response to grazing pressure. Also, none of these studies were done at a spatial scale that is relevant to typical grazing management needs. Finally, most of these studies did not collect data prior to the treatment of sites, which would allow for detection of ecological variation that existed prior to treatment. This last shortcoming is probably the most important because ecological variation in the mixed-grass prairie can be high. My study attempted to fill these gaps by using a continuous independent variable (stocking rate), large spatial scale (300-ha pastures), and collection pre- and post-treatment data.

2.6.2 Bison/Cattle Comparison Studies

Several studies have found that bison and cattle grazing have different effects on habitat structure and/or grassland birds, but the design or location of these studies makes them unsuitable to Grasslands National Park and its information requirements for management. The following paragraphs outline some of the research that has been done in mixed-grass prairies on songbirds and habitat, and relevant literature gaps.

Griebel and colleagues (1998) conducted a study comparing the effects of bison plus fire and cattle on grasslands in the Sandhill Prairies of Nebraska, USA. The bison plus fire pasture was 3200 ha and was grazed year long at 1.2 AUM/ha. The four, 800-ha cattle pastures were unburned, and were grazed season long at 1.0 AUM/ha. This study used survey transects to detect songbirds and conduct vegetation surveys: transects were 250m long and each had 10 points located 25m apart. After treatments, vegetation height and density were similar in the bison plus fire and cattle enclosures, but more bird species were encountered in the bison plus fire treatment. The key problem with interpreting the results of this study is that portions of the bison pasture were burned, while none of the cattle pastures were burned. This study provides information on the interactions of bison grazing and fire, but confounds the comparisons between the cattle and bison, because both grazers preferentially graze burned areas (Vinton et al. 1993, Coppedge and Shaw 1998, Biondini et al. 1999). Also, the Sandhills have been considered distinct from typical mixed-grass prairie (WWF 2001). My study leaves out the effects of fire because, even though fires may have been an important part of the natural disturbance regime (but see page 11, Askins et al. 2007), having four treatments for both bison and cattle (unburned/ungrazed, burned/grazed, unburned/grazed, burned/grazed) is beyond the scope of my project.

Lueders and colleagues (2006) compared the effects of bison and cattle management regimes on breeding birds, in the first study of its kind to be done in true mixed-grass prairie. The objectives of this study were to compare range management strategies on bird densities, habitat structure, composition, and heterogeneity. The study was conducted in North Dakota, USA in sampling plots with two different management

strategies. The bison pastures were ~9000 ha and ~18,500 ha on National Park Service lands, had been burned recently and were grazed lightly. The cattle plots were dispersed on land managed by the US Forest Service, had not been burned, and were grazed more heavily. More cattle plots (64 in 1999 and 168 in 2000) were sampled than bison plots (19 in 1999 and 32 in 2000). Bird surveys and habitat measurements were taken at each plot in both years. One conclusion of this study was that bison plots were used by a lower diversity of birds than cattle plots. This study did not differentiate ungrazed controls from grazed areas in either the bison-grazed pastures or the cattle-grazed pastures, which can preclude the ability to make robust conclusions from data analyses. This study did make an attempt to study the natural disturbance regime (bison + fire) and compared it to cattle production activities. However, the authors did not explain how they located their study plots in the bison pasture, making it difficult to draw conclusions from their work (Lueders et al. 2006).

Many of the studies that have focused on bison and cattle grazing have attempted to control for the different management strategies used for bison and cattle by managing bison more similarly to cattle (i.e. Towne et al. 2005). This may prevent bison from behaving naturally and therefore does not allow for a comparison to be made between effectively free-roaming bison grazing on songbirds and current impacts due to cattle grazing (Griebel et al. 1998). The study I conducted in the West Block and East Block of GNP to compare bison and cattle grazing has a number of advantages over previous work done. I included ungrazed controls in both blocks of the study, and both areas had pre-grazing data collected on bird abundance, although the data in the West Block were slightly less useful (see Introduction: Limitations). Although fire might be an important

component of the natural disturbance regime, it can be important to first understand the impacts of bison grazing alone, with the option of including fire at a later stage in the research. I also included a range of grazing intensities by counting fecal patties as an indicator of grazing intensity (i.e. Milchunas et al. 1989), allowing me to analyze bird abundance non-linearly. Finally, my study areas are very similar in their grazing history, climate, and vegetation types, making them highly suitable for a comparative study between bison and cattle.

My study helped to fulfill a number of research gaps existing in the literature. First, no bison/cattle comparison study used a continuous independent variable in order to detect ecological thresholds, whereas mine used number of patties per plot as a continuous indicator of grazing intensity. Second, I used ungrazed controls in both areas to attempt to control for variation between the West Block and East Block, whereas most of these studies did not incorporate controls. Finally, my study allowed for comparison of an effectively free-roaming bison herd with production herds of cattle because these are relevant differences that I was interested in. Other studies attempted to control for these differences between bison and cattle managing them similarly.

3.0 METHODS

3.1 STUDY DESIGN

The Biodiversity and Grazing Management Area study was designed by a group of experts prior to its implementation in 2006 to provide the park with information about cattle grazing impacts on the wildlife community (Parks Canada 2006). Beyond-BACI ("beyond-Before-After-Control-Impact") was chosen as the study design, because this type of study would provide information on the communities present in the park before grazing was initiated, which is crucial for understanding the relationships between grazing and the response of the communities of interest (Underwood 1994). Also, this design allowed for between-year variability to be monitored because ungrazed controls were included after grazing was initiated (Osenberg et al. 1994).

Because a range of grazing intensities was used in this study, I used grazing intensity (stocking rate) as a continuous variable, which allowed me to interpolate my results within the range of intensities sampled (Koper et al. 2008). Further, this design allowed me to analyze the data for non-linear and curvilinear responses of birds to grazing intensity, which would reveal any thresholds in the response of songbirds to grazing intensity.

Finally, because the pasture size chosen for this study was similar to neighboring ranch pastures at approximately 300 ha (Parks Canada 2006, Koper et al. 2008), the results of this study will not only be valuable to park management, but also to surrounding landowners who may have an interest in managing their land for the benefit of wildlife.

The bison/cattle portion of this study took advantage of steps taken by Grasslands National Park to fulfill its mandate of ecological integrity, and as such there are some issues with the study design that need consideration. Of primary importance is the dispersion of the study sites. All of the bison plots are located in the West Block, and all of the cattle plots are located in the East Block. Further, the bison have chosen to graze mostly in the northern part of the West Block, whereas the cattle grazing plots are dispersed from north to south. This can present a problem because of differing climatic conditions that exist on an east-west and north-south gradient, such as precipitation and temperature (Kantrud and Kologiski 1983, Askins et al. 2007), even over the 10-km spread of the grazing experiment. Further, there could be a difference in soil properties and vegetation characteristics between the East Block and West Block. Ideally, the bison and cattle plots would be interspersed to remove any possible bias or pre-existing differences on the gradient (Quinn and Keough 2002).

To partially account for this issue, bird surveys done prior to bison reintroduction by park staff as well as the 2006 pre-grazing data from BAGMA were used to check for any patterns in bird abundance that might exist in relation to the sampling plots and future grazing intensity. This allowed me to be confident that any patterns I detected were related to grazing and not due to spurious or pre-existing patterns (Underwood 1994). These baseline data provide information on "before impact" and allowed me the study to be categorized as a "before-after-control-impact" (BACI) design, although the "before" data in the West Block included only one round of point counts and thus the research methods are slightly different than those used in 2009 and 2010.

Another issue arises when trying to compare bison grazing pressure and cattle grazing pressure. In 2009 and 2010, grazing pressures were estimated by counting bison and cattle fecal pats along a 200-m × 2-m transect at each plot, and for analyses I assumed that each bison and cattle fecal pat represented the same grazing intensity (assumption based on similar defecation rates between bison and cattle, see Wagnon 1963, Belovsky and Slade 1986). Although this technique has been used in previous studies as an estimate of grazing pressure, ungulates may not defecate in the same place that they graze (Julander 1955, Hafez et al. 1969, Tate et al. 2003, E. Bork, personal communication), which may present a problem for using fecal pat counts as a representation of actual grazing pressure. Also, bison and cattle might spend the same amount of time in an area, but the grazing pressures might be different because bison spend less time grazing and more time on social activities (Hartnett et al. 1997). Nutritional requirements may be different because of the difference in digestion efficiencies between bison and cattle (Schaefer et al. 1978). However, because of the difficulty in assessing grazing pressure in the West Block, fecal patty counts were the best representation of grazing pressure available. Preliminary analyses of my data indicated that this method does result in expected correlations with bird species and habitat structure variables, and also that logged patties are highly correlated with stocking rates in the East Block ($r^2 = 0.82$). Further, I know from reviewing the literature that bison and cattle have innate differences in grazing preferences and capabilities, and because this was what I was interested in understanding, it did not represent a significant problem for the study design. Finally, by using a count of fecal pats, I was able to use

grazing intensity as a continuous variable in data analyses, which allowed me to analyze the data for non-linear and curvilinear responses to grazing intensity.

Controls are one of the most important components of a robust study design (Quinn and Keough 2002). However, in field experiments it is difficult to find true controls since the study is generally taking advantage of naturally occurring events. In this study, the control plots are the ungrazed plots and the community pastures, as they are representative of the prairie without grazing and with long-term grazing. In both the East Block and the West Block, grazing had been excluded since at least 1984 (Parks Canada 2009), and there were 17 ungrazed plots in the East Block and 30 ungrazed controls in the West Block. Further, pre-grazing data can be used as an indication of the variability already present in a pasture; therefore, the 2006-2008 data collected for songbirds in the East Block, the 2008 data collected for habitat in the East Block, and the 2004 data collected for songbirds in the West Block were all important pre-treatment controls for this study.

3.2 Study Area

This study was conducted in the East and West Blocks (EB and WB) of Grasslands National Park in southwestern Saskatchewan, Canada. The park consists of native mixed-grass prairie with rolling hills in the East Block and uplands with rolling hills and badlands in the West Block. The park falls completely within the Missouri River drainage basin (Coupland 1950, Parks Canada 2006). The soils are made of mostly glacial and postglacial deposits, and the prairie is predominantly a *Stipa-Bouteloua* community (Coupland 1950). The upland grasslands are dominated by the following vegetation species: grasses include *Stipa comata*, *Elymus lanceolatus*, *Bouteloua gracilis*,

Koeleria macrantha, *Pascopyrum smithii*; forbs include *Artimesia frigida*, *Phlox hoodii*, *Sphaeralcea coccinea*; *Selaginella densa* is the prevalent spikemoss (Coupland 1950, Parks Canada 2006).

A large-scale grazing experiment reintroduced cattle into the East Block of the park in May 2008, where grazing had been excluded for at least 15 years. In 2006, 12 pastures were designed including six pastures for cattle, three pastures as ungrazed controls, and three adjacent Mankota Community Pastures as long-term grazing controls; each pasture was ~300 ha and had similar amounts of upland, lowland, and riparian areas (Parks Canada 2006, Koper et al. 2008). In 2008, fencing for the cattle pastures was erected, and these pastures were supplemented with two water troughs, one located in the lowland and one in the upland, to encourage grazing distribution and to eliminate dependence on the natural water source (Koper et al. 2008). Each of these twelve pastures had ten point count stations, four in the lowlands and six in the uplands (Figure 1). For the purposes of this study, only the upland point count stations were used. The grazed pastures in the Park had a range of grazing intensities varying from below normal for the area (0.23 AUM/ha) to very high for the area (0.83 AUM/ha), and the community pastures had been managed at a moderate stocking rate (~0.5 AUM/ha) for at least fifteen years (Koper et al. 2008). The study was designed as a Before-After-Control-Impact manipulative experiment, and therefore baseline data were collected on songbirds in 2006, 2007, and 2008, and on habitat structure in 2008 prior to grazing reintroduction (Koper et al. 2008). A number of wildfires occurred in the East Block of the park and in the community pastures in late summer 2006; any plots that were impacted by the wildfires were removed from the dataset, resulting in 36 grazed plots and 17 ungrazed

control plots (n = 53) in the East Block, and 17 long-grazed controls in the community pastures. Each plot was at least 200 m from the nearest fence to ensure birds were not selecting for habitat in the adjacent pastures.

The West Block is approximately 18,500 ha and is home to over 150 minimally managed bison, which were reintroduced to the park in 2006 (Parks Canada 2004, Parks Canada 2009). Plots were chosen in the West Block to represent grazed and ungrazed areas in the uplands, with a variety of grazing pressures from low to high. The West Block consisted of 27 grazed plots and 17 ungrazed control plots (n = 44) in 2009, and 42 grazed plots and 30 ungrazed plots (n = 73) in 2010, each at least 150 m from the nearest fence (Figure 2).

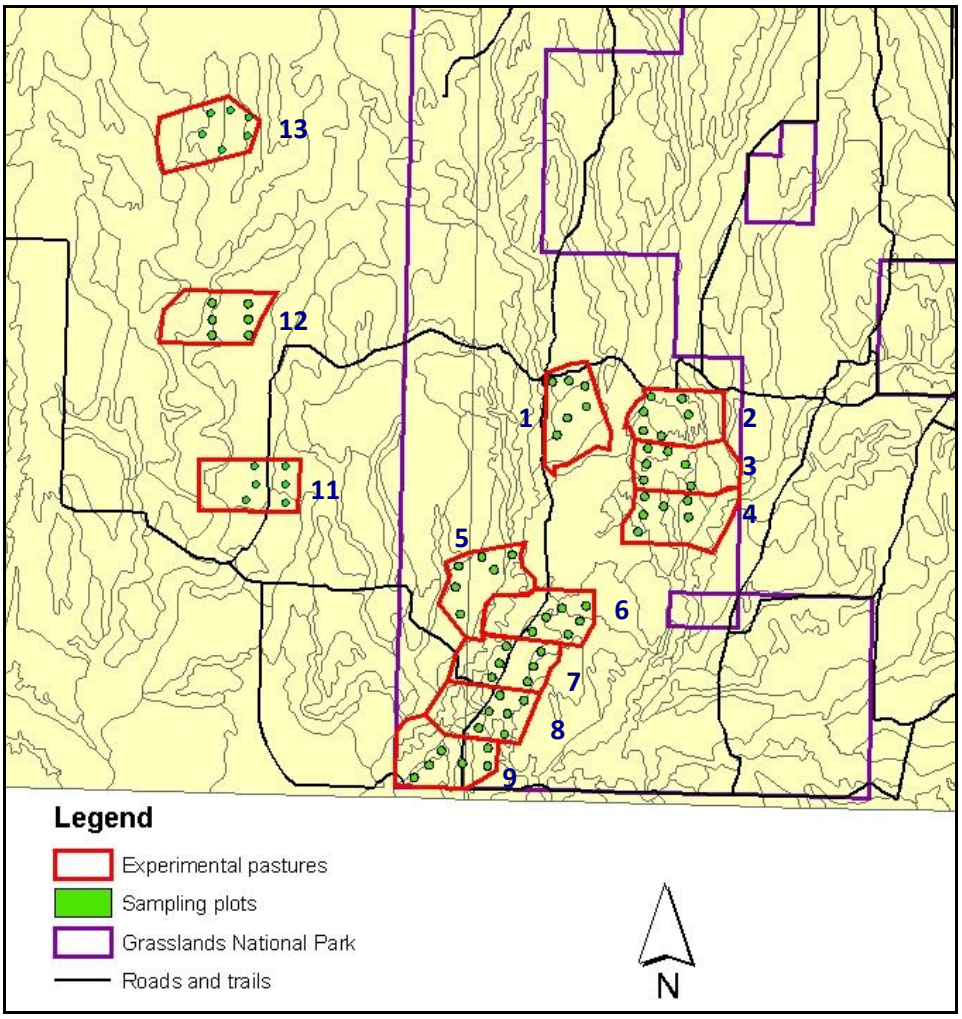


Figure 1. Map of the Biodiversity and Grazing Management Area in the East Block of Grasslands National Park and the adjacent Mankota Community Pastures, with pastures numbers in blue, southwestern Saskatchewan, Canada, 2006-2010.

Table 1. Stocking rates for the first two years of the Biodiversity and Grazing Management Area (BAGMA) and the Mankota Community Pastures (MCP), southwestern Saskatchewan, Canada, 2009-2010.

		2009	2010
Area	Pasture	AUM/ha	AUM/ha
BAGMA	1	0.00	0.00
BAGMA	2	0.23	0.25
BAGMA	3	0.66	0.71
BAGMA	4	0.74	0.82
BAGMA	5	0.00	0.00
BAGMA	6	0.36	0.39
BAGMA	7	0.54	0.57
BAGMA	8	0.81	0.83
BAGMA	9	0.00	0.00
MCP	11	0.47	0.53
MCP	12	0.51	0.38
MCP	13	0.56	0.42

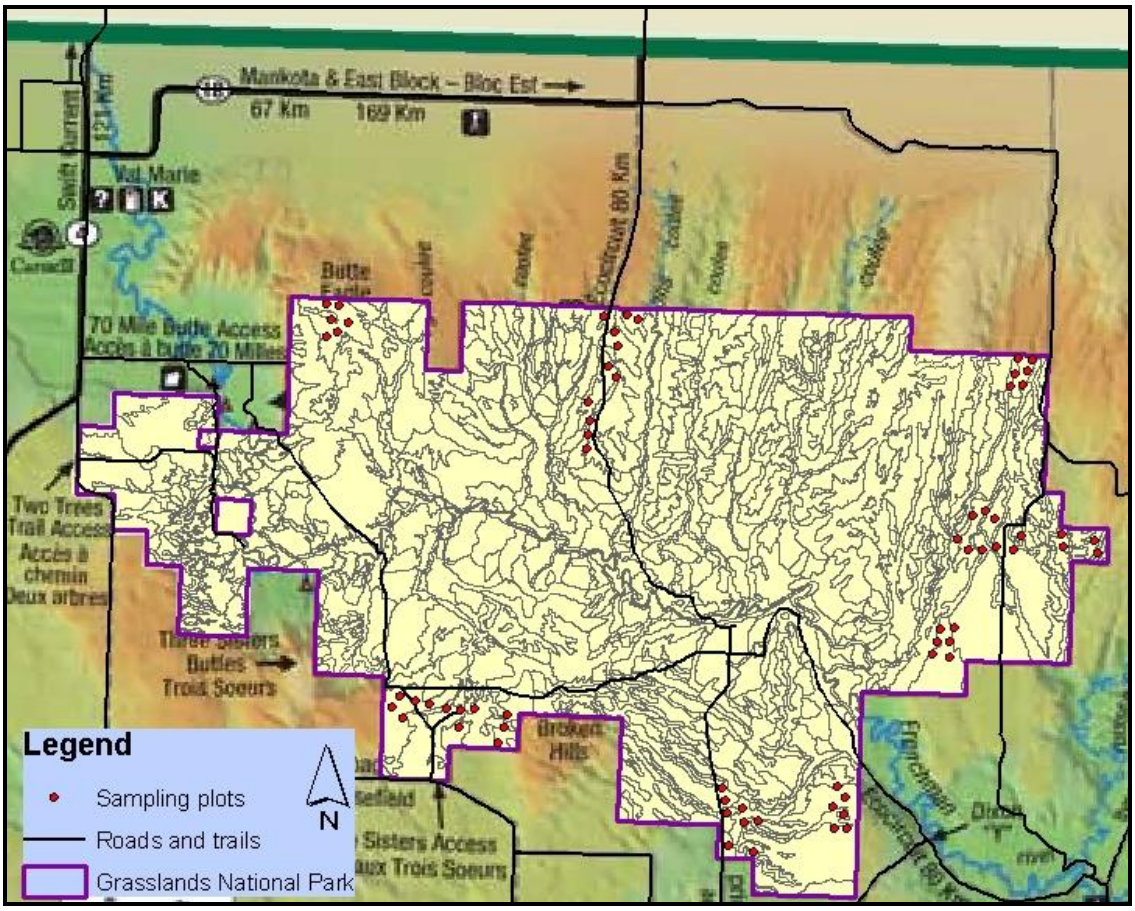


Figure 2. Map of the West Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010. Background map courtesy of Grasslands National Park, Canada.

3.3 FIELD METHODS

3.3.1 Bird Surveys

Three rounds of point counts were conducted in BAGMA from 2006 through 2010 between mid-May and 30 June, and three rounds of point counts were conducted in the West Block bison plots between mid-May and 30 June 2009 and 2010. All plot centers were located at least 250 m apart so that birds were not recorded twice at separate plots. The point counts were six minutes each, with birds recorded in intervals of two minutes, two minutes, one minute, and one minute. All birds detected by either sight or sound within a 100-m radius were recorded along with the direction and distance at which they were detected, the sex of the bird (if possible), and the bird's behavior. Protocols followed were adapted from Hutto et al. (1986). All point counts were conducted between sunrise and 1000 hours and each plot was surveyed by at least 2 different observers in all years to lessen effects of observer bias. No surveys were conducted on days with excessive wind (>15 km/h) or rain, which lessen detectability.

Unadjusted point counts were averaged over the three rounds within each year as a measure of relative abundance (see Koper and Schmiegelow 2006). Bird diversity (including richness, Shannon-Wiener diversity, and evenness) was calculated for each plot for songbirds. The Shannon-Wiener diversity index was chosen because it is sensitive to rare species (Wiens 1989), which are of management concern. Total abundance of all songbird species was calculated for each plot. Only songbird species occurring in each year in 10% or greater of plots were analyzed because lower sample sizes often do not converge. Unfortunately, McCown's longspurs, a species of

conservation concern, did not meet this requirement; however, a qualitative assessment was made concerning their occurrence.

3.3.2 Habitat structure

At each plot in BAGMA I surveyed the habitat structure once in May and once in July of 2008, 2009, and 2010, and at each West Block bison plot in May and July of 2009 and 2010. Each survey included eight 1.0-m × 0.5-m sampling frames at 50 m and 100 m from the center of the plot in the four cardinal directions. At each frame, measurements included height-density (using the Robel pole visual obstruction method, Robel et al. 1970), tallest vegetation (by meter stick and canopy height [Styrofoam method, see below]), litter depth in the center of the frame, and visual percent cover estimates of litter, dead standing vegetation, grass, forbs, cactus, sagebrush, western snowberry, greasewood, exposed moss/lichen, bare ground, animal waste, and other shrubs. Cover class estimates were: 0 (0%), 1 (>0 to 0.1%), 2 (0.1 to 1%), 3 (1 to 3%), 4 (3 to 10%), 5 (10 to 25%), 6 (25 to 50%), 7 (50 to 75%), 8 (75 to 95%), and 9 (95 to 100%). The Styrofoam method to measure canopy height used a 20 × 50 × 2.5 cm piece of Styrofoam with a hole in the middle, through which the meter stick was placed. The meter stick was then placed upright in the middle of the sampling frame, and the height at which the Styrofoam rested on the vegetation was recorded as canopy height. Prior to analysis, 2.5 cm was subtracted from the Styrofoam measurement to account for the width of the Styrofoam. All variables were averaged for each plot, and the standard deviations of vegetation height, canopy height, density, and litter depth were calculated as a measure of heterogeneity within each plot. Even though standard deviation (SD) is correlated with the mean (higher mean results in higher SD), and the coefficient of variation accounts for

this correlation by dividing SD by the mean, SD was chosen as the measure of heterogeneity. Coefficient of variation can over-correct for the correlation between mean and SD, which makes it less suitable to the species of interest in this study (Bleho 2009).

3.3.3 Grazing Intensity

For the BAGMA study, grazing intensity in the East Block was determined using stocking rates, otherwise known as Animal Unit Months (AUM), per hectare. This method takes into account the number of animals in a pasture, the size of the pasture, and the time spent there (Gillen et al. 2000, Pratt and Rasmussen 2001). At BAGMA, the stocking rate ranged from 0 AUM/ha (ungrazed), to 0.23 AUM/ha (low grazing intensity), up to 0.83 AUM/ha (very heavy grazing intensity for the area, Parks Canada 2006).

Bison and cattle patties were counted at each plot along a 200-m × 4-m transect in 2009 and 2010 and were used for data analyses in the bison/cattle study. One patty was either a well-formed individual patty or a set of closely located patties (see Figure 3). All patties detected within the transect were counted without distinction between old or new patties.



Figure 3. Photos of patties in Grasslands National Park, 2009. Both of the patties shown here were counted as one. Photo courtesy of Darcy Henderson.

3.4 STATISTICAL ANALYSIS

All analyses were done using SAS Statistical software (SAS Institute 2008). Data were analyzed on a per-plot basis using mixed-effects models with grazing intensity and years as independent variables. Because mixed-effects models allow inclusion of a random effect to account for spatial clustering of sampling points, data did not have to be averaged across sites, which is useful because averaging across sites results in the loss of data and lower statistical power (Quinn and Keough 2002).

Distributions of the residuals of all response variables were first determined using Generalized Linear Models (GLMs). Distributions used included normal, Poisson, and negative binomial.

Non-linear mixed-models were used to determine if a response to grazing intensity was non-linear. A set of models including the null, year or grazing duration, grazing intensity (AUM/ha or patties), polynomial factors of grazing intensity, interactions between intensity and year, exponential, and logistic (see Appendix 1) was compared using Akaike's Information Criterion (AIC). Because AIC has a tendency to select for more complicated models (Quinn and Keough 2002), only those models that were at least two AIC points lower than the null were selected. If models were not non-linear or did not converge using NLMMs, analyses using a similar set of models were done using generalized linear mixed-models (GLMMs). Parameters included in the selected model were considered highly important when their confidence intervals did not include 0 (Koper and Schmiegelow 2006).

3.4.1 Biodiversity and Grazing Management Area

At BAGMA, none of the songbird or habitat responses were non-linear (i.e. logistic or exponential), but NLMMs were used for all subsequent analyses. NLMMs use a maximum likelihood estimation technique to determine AIC values, which is more accurate than the estimation technique used by Proc Glimmix for GLMMs in SAS Software (SAS Institute 2008). AICs were used to compare the set of models tested and the model with the lowest AIC was selected, except where Δ AIC was ≤ 2, in which case the null model was selected.

Independent variables included in the models were stocking rate (AUM/ha) and grazing duration. Models included data from 2008-2010 for habitat structure analyses, while songbird analyses included data from 2006-2010; all pre-grazing years (2008 for habitat structure, 2006-2008 for songbirds) were labeled as "0" for grazing duration. Polynomials of stocking rate up to cubic (i.e. AUM/ha × AUM/ha × AUM/ha) were also included to allow the response to be curvilinear (Koper et al. 2008). An interaction between grazing duration and stocking rate was included in the set of test models to determine if grazing duration changed the effect of stocking rate (Table 2; see Appendix 1 for a sample code of the models tested in NLMMs). Because all of the non-null models except for horned lark included grazing duration as an influential parameter, the figures presented were divided into two sections each: one year with grazing (2009), and two years with grazing (2010).

Habitat structure variables were analyzed as dependent variables. Measures analyzed included the mean and standard deviation of litter depth, vegetation height, canopy height, vegetation density, and mean bare ground cover and mean litter cover.

Litter depth data were used from May 2008, July 2009, and July 2010 because litter depth data were collected incorrectly in May 2009, and because habitat structure data were not collected in the grazed sites (pastures 2-4, 6-8) in July 2008. May 2008, 2009, and 2010 data were used for the remainder of the habitat structure variables. An analysis using pre-grazing data was used to check for pre-existing patterns due to environmental conditions using measurements of litter depth, vegetation height, density, and litter cover with stocking rates overlaid on plots. To determine if climate was an important factor in the changes detected using stocking rates, the controls sites (ungrazed) were analyzed separately using year as the independent variable for litter depth, vegetation height, canopy height, and vegetation density.

Songbird species analyzed as dependent variables included Baird's sparrows, chestnut-collared longspurs, grasshopper sparrows, horned larks, Savannah sparrows, Sprague's pipits, vesper sparrows, and western meadowlarks on a per-plot basis. Richness, diversity (Shannon-Wiener index), evenness, and total abundance were also analyzed per plot. The dataset analyzed included all data from 2006 through 2010. A pre-grazing model was used to confirm that there were no underlying patterns in songbird abundance and diversity prior to grazing by analyzing 2006-2008 data with future stocking rates overlaid on the plots. Similarly to habitat structure, the ungrazed control sites were analyzed separately using year as the independent variable to determine any effects of climate on Baird's sparrow, chestnut-collared longspur, Sprague's pipit, and songbird richness.

Table 2. Dependent and independent variables used in the models for analyzing data collected in the East Block of Grasslands National Park, 2006-2010. All independent variables were included in the set of models used to analyze each dependent variable.

Songbird Data (2006-2010)		Habitat Data (2008-2010)	
Independent	Dependent	Independent	Dependent
Null	Baird's sparrow	Null	Vegetation height
AUM/ha	Chestnut-collared longspur	AUM/ha	SD vegetation height
Duration (0, 1, 2)	Grasshopper sparrow	Duration (0, 1, 2)	Litter depth
AUM/ha^2	Horned lark	AUM/ha^2	SD Litter depth
AUM/ha^3	Savannah sparrow	AUM/ha^3	Vegetation density
AUM/ha*Duration	Sprague's pipit	AUM/ha*Duration	SD Vegetation density
AUM/ha^2*Duration	Vesper sparrow	AUM/ha^2*Duration	Canopy height
AUM/ha^3*Duration	Western meadowlark	AUM/ha^3*Duration	SD Canopy height
	Richness		Litter cover
	Shannon-Wiener diversity		
	Evenness		
	Abundance		

Sorensen's quantitative index was calculated for comparing community similarity within BAGMA, and between BAGMA and the Mankota community pastures. Sorensen's quantitative index accounts for differences in community composition and species' abundances between two sites (Jongman et al. 1995). Sorensen's quantitative index is useful in this study because the variability in mixed-grass prairies supports a wide range of species within single pastures. Two-way comparisons were made between data that were grouped into ungrazed sites, medium grazed sites, heavily grazed sites, and the long-term grazed community pastures. Because this index is sensitive to sample size (Jongman et al. 1995), each group included 17 randomly selected plots, in which the individual species' abundances were summed.

3.4.2 West Block Bison Grazing

The 2004 dataset (pre-grazing) was analyzed using GLMMs to determine if songbird abundances had a pre-existing pattern in the West Block due to environmental

conditions. The 2004 plots were not the same as those in the present study; therefore, patty counts were not available for these data. The data were analyzed in two ways in lieu of patty count data: (1) with categorical designations of grazing intensity (none, low, medium, high); (2) with bison collar data (a continuous variable). The categorical designations were based on field observations, and the GPS collar data came from two collared female bison in the West Block, and was a sum of any GPS locations within 200 m of a plot. It was assumed that the majority of the herd stayed together during the season, and that collars from female bison would approximately indicate where the herd was located (Wes Olson, personal communication).

NLMMs did not converge properly for the 2009-2010 data and therefore all models were done using GLMMs. A set of models was developed to analyze the independent variables: models could include patties, year, polynomials of patties, and an interaction between patties and year (see Appendix 2 for SAS code of the set of models). AIC was used for model selection; the null model was chosen when Δ AIC ≤ 2.

The response of mean and standard deviation of litter depth, vegetation height, canopy height, vegetation density, and the percent cover of litter, grass, forbs, mosses and lichens, and bare ground as estimated in July of each year were analyzed separately for their relationship to bison grazing. The control plots (patties = 0) were also analyzed separately to detect any possible effect of climate on litter depth, vegetation height, canopy height, and vegetation density between 2009 and 2010.

Songbird species were analyzed individually for their response to bison grazing. Species analyzed included Baird's sparrows, chestnut-collared longspurs, grasshopper sparrows, horned larks, Savannah sparrows, Sprague's pipits, vesper sparrows, and

western meadowlarks. Songbird richness, diversity (Shannon-Wiener index), evenness, and abundance were also analyzed on a per-plot basis. Year was included in the models to account for variation between 2009 and 2010. The control plots (patties = 0) were also analyzed separately to determine if climate affected bird abundance differently in 2009 and 2010.

Sorensen's binary and quantitative indices were used to compare community similarity within the West Block. Data were grouped into ungrazed and heavily grazed plots for comparison purposes. Plots with medium grazing intensities were not analyzed because there were too few plots in this designation. Both groups had a total of fifteen plots, and songbird abundances for each species were summed over plots.

3.4.3 Bison/Cattle Comparisons

An analysis using 2006 point count data with patties overlaid on the plots from the East Block and 2004 data from the West Block (see above) was done to ensure that no pre-existing patterns were present in the cattle or bison data in relation to the selected plots due to environmental conditions. An analysis for habitat structure was done for the BAGMA study using 2008 pre-grazing data, but there were no data available to do the same in the West Block.

Bison grazing was compared to cattle grazing in 2009 and 2010 using fecal patty counts as an index of grazing intensity. Bison patties and cattle patties were considered at a 1:1 ratio for evidence of grazing intensity (i.e. patties were untransformed). All analyses were done using GLMMs, because models using NLMMs did not converge.

The set of test models used to analyze the dependent variables included patties, grazer species, and year, an interaction between grazer species and patties, and

polynomials of patties (to allow a curvilinear response). Additionally, an interaction between grazer, intensity, and year was included in the set of models because bison were reintroduced to the West Block in 2006, whereas cattle were introduced to the East Block in 2008. The difference in cumulative effects of grazing was an important potential limitation of this study that needed to be accounted for in the data analysis. This interaction was insignificant and was removed for all models except two because it did not improve model fit.

Habitat structure variables analyzed individually included mean and standard deviation of vegetation height, canopy height, litter depth, and vegetation density, and mean percent cover of litter, bare ground, grass, forbs, and mosses and lichen. Cover estimates were analyzed for July 2009 and 2010 because there were more observers in July, which lessened observer bias for this slightly subjective measurement.

Songbird species analyzed individually included Baird's sparrows, chestnut-collared longspurs, grasshopper sparrows, horned larks, Savannah sparrows, Sprague's pipits, vesper sparrows, and western meadowlarks. Diversity measures analyzed included richness, diversity (Shannon-Wiener index), evenness, and total songbird abundance.

4.0 EFFECTS OF CATTLE STOCKING RATE ON SONGBIRDS AND HABITAT STRUCTURE OF THE MIXED-GRASS PRAIRIE

4.1 ABSTRACT

Information on the effects of cattle stocking rates on mixed-grass prairies and wildlife is scarce, even though most remaining native prairie is used for cattle operations. In Grasslands National Park, Canada, a large-scale manipulative experiment has been initiated to study impacts of cattle stocking rates on wildlife. I conducted songbird surveys from 2006-2010 and collected habitat structure measurements from 2008-2010 in twelve 300-ha pastures. From 2006-2008, all sites within the park were ungrazed. In 2009-2010, 6 sites were grazed at a range of stocking rates, from very low to very high, and 3 sites were ungrazed controls. In addition, 3 adjacent community pastures, which were grazed at moderate intensities for at least fifteen years, were sampled from 2006-2010. I used non-linear mixed models to determine effects of stocking rate, grazing duration, and the interaction between stocking rate and grazing duration on ten habitat structure variables, nine songbirds, and four diversity measures. Vegetation and canopy height decreased with stocking rate starting at 0.4 AUM/ha in 2010, while litter depth decreased with all stocking rates in 2009. Chestnut-collared longspurs increased in relative abundance starting at a threshold of about 0.4 AUM/ha, while grasshopper and Savannah sparrows decreased in abundance starting at 0.4 AUM/ha in both 2009 and 2010. Sprague's pipits and Baird's sparrows decreased with any increase in stocking rate. Brown-headed cowbird occurrence increased dramatically with the introduction of cattle to the landscape. 0.4 AUM/ha was an important threshold for habitat and songbirds in this region; stocking rates above this can be used for species that prefer sparser

vegetation, while stocking rates below this can be used for species that prefer taller and denser vegetation. Baird's sparrows and Sprague's pipits would benefit from grazing exclusion. Stocking rates can be used to modify habitat for the benefit of threatened songbird populations, but the risk of increased brown-headed cowbird populations associated with the construction of fences for managing the cattle are important risks that must be considered.

4.2 INTRODUCTION

One third of the listed threatened or endangered species in Canada are grassland species (Samson and Knopf 1994), and most grassland bird species have experienced population declines over the past forty years (Knopf 1994). This has been attributed to habitat loss and degradation of the prairies (Samson and Knopf 1994, Askins et al. 2007), but also to more subtle changes caused by grazing regimes that differ from historical grazing patterns (Vickery et al. 1999, Coppedge et al. 2008). Prior to European settlement, grazing by bison was spatially and temporally heterogeneous at large scales: the return interval for bison may have been between eight and thirty-five years (Malainey and Sherriff 1996), and some areas would have been heavily grazed, while others were left ungrazed for longer time periods (Towne et al. 2005).

Although it would seem intuitive that native ungulates would be most effective for managing prairies for native biodiversity, studies have shown that cattle are an economically and ecologically viable alternative to bison (Plumb and Dodd 1993, Pieper 1994, Steuter et al. 1995). However, current management of commercial livestock operations on mixed-grass prairies is aimed at homogenous use of the landscape (Biondini et al. 1999, Coppedge et al. 2008). Further homogenizing of the landscape has

occurred because management on federal lands included a policy of grazing and fire exclusion, and provincial lands management was similar to private ranchland management (Parks Canada 2006). Thus, habitat conditions on both private and public lands do not support all endemic songbird species because many grassland birds require habitats other than those created by the common management practices (Wiens 1985, Temple et al. 1999, Vickery et al. 1999); specifically, relatively intensely disturbed or relatively undisturbed. Because of the lack of habitat created by other types of grazing regimes, it is important to introduce a grazing management plan that will help to restore those habitats required by all mixed-grass prairie species (Fuhlendorf and Engle 2001). Future management plans should foster a landscape that includes habitats with sparsely vegetated areas, heavily vegetated areas, and a range of vegetation characteristics in between. Through this study, I evaluated the effects of a range of stocking rates on habitat structure, songbird abundance, and songbird diversity in the northern mixed-grass prairie.

Two models proposed in the 1980s are widely used to describe the impact of disturbances on rangelands. The first was the range model (also known as the Milchunas-Sala-Lauenroth (MSL) range model), proposed by Milchunas and colleagues (1988), and the second was the state-and-transition model, proposed by Westoby and colleagues (1989). The MSL model, on the other hand, uses two site characteristics to predict the site's response to grazing by generalist herbivore: site productivity (mainly precipitation), and evolutionary history of grazing (Milchunas et al. 1988, Cingolani et al. 2005). In the arid mixed-grass prairie with a long history of grazing, the MSL model predicts that plant diversity will be highest at low to moderate grazing intensities, and will begin to decrease

at higher grazing intensities (Milchunas et al. 1988). In wet years in the mixed-grass prairie, such as in 2009 and 2010, the model predicts that highest diversity will be at moderate grazing intensities (Milchunas et al. 1988). The state-and-transition model proposes that grazing or other disturbances to grasslands can result in an irreversible change to a state different than the one initially present (Westoby et al. 1989). For example, a vegetation change caused by grazing that results in high levels of erosion may result in irreversible alteration of the community structure (Westoby et al. 1989). The main strength of the state-and-transition model was that it challenged range managers to develop a model that was suitable for their specific location (Cingolani et al. 2005). It is now understood that the MSL range model is actually a special case of the state-and-transition model (Briske et al. 2003) and that the two can be used together to inform an understanding of the dynamics present on rangelands. Cingolani and colleagues (2005) modified the MSL model to include non-equilibrium dynamics and irreversible changes in plant communities that allowed it to be better suited to a variety of situations present on rangelands.

Stocking rates are a typical tool used for maintaining constant utilization on ranchland, and were used by range managers to predict the effects of grazing on range condition using the MSL range model (Westoby et al. 1989, Anderies et al. 2002). Cattle can be managed to create a range of vegetation characteristics by subjecting a group of pastures to a range of stocking rates (Wiens 1985, Severson and Urness 1994). This should help to restore a given group of pastures to a more heterogeneous state at a variety of scales, which will be attractive to a variety of songbird species (Bork and Werner 1999). Further, low or moderate stocking rates should promote within-pasture

heterogeneity due to selective foraging of cattle (Hart et al. 1993), which should create habitat for different species that require a range of different habitats for nesting and feeding. Moderate and high stocking rates in other pastures can be used to reduce canopy height, vegetation height, and litter depth (Milchunas et al. 1989). Finally, sustained grazing at moderate and high stocking rates can increase the effects of grazing (Hartnett et al. 1996).

A number of studies have been conducted to understand the effects of cattle grazing on wildlife in mixed-grass prairies (Collins and Barber 1985, Davis et al. 1999) but only one study has been done in the mixed-grass prairies to understand the impacts of various stocking rates (Gillen et al. 2000). The small spatial scale of this study made it less relevant to managing wildlife at the scale typical of ranchland or the vast tracts of prairie remaining in Grasslands National Park (Koper et al. 2008). Further, no previous studies on cattle and songbirds incorporated before-treatment controls, which are important for controlling for background variation in ecological parameters while allowing me to detect relationships between the community response and grazing (Koper et al. 2008, Underwood 1994).

Because of the importance of ranching in the Great Plains and its ability to help protect the remaining mixed-grass prairie (Lauenroth et al. 1994, Askins et al. 2007), it is crucial that managers develop management strategies that are both effective at preserving wildlife, and are relevant to commercial livestock operations. With these goals in mind, a large-scale, long-term grazing experiment was developed to understand the effects of a range of stocking rates on the wildlife of the mixed-grass prairie in southwestern Saskatchewan, at scales that are relevant to the ranching community and managers of

government-owned land at Grasslands National Park in Canada (Koper et al. 2008). I collected data from 2006-2010 to determine initial effects of stocking rate and grazing duration on habitat structure and songbird abundance and diversity. I predicted that the range of stocking rates applied would result in a variety of responses from songbirds based on their habitat preferences, and that changes in the habitat structure due to grazing would explain some of these responses. For example, because Baird's sparrows and Sprague's pipits prefer taller and denser grass cover (Owens and Myres 1973, Wilson and Belcher 1989, Davis et al. 1996), I predicted that their abundances would decline with grazing. Alternately, because chestnut-collared longspurs prefer sparser grass and the presence of dung pats (Davis et al. 1999, Davis 2005), I predicted that their abundance would increase with grazing intensity. The MSL range model predicts that there will be few changes to arid, mixed-grass prairies with the introduction of grazing; however, because my study took place during a period of time with excess rainfall, it is likely that grazing will have a number of effects on the songbird population and habitat structure.

4.3 METHODS

4.3.1 Study Site

This study was conducted in the East Block of Grasslands National Park in southwestern Saskatchewan, Canada. The park consists of rolling hills of native mixed-grass prairie, and falls within the Missouri River drainage basin (Coupland 1950, Parks Canada 2006). The soils are made of mostly glacial and postglacial deposits, and the prairie is predominantly of the *Stipa-Bouteloua* association (Coupland 1950). The upland grasslands were dominated by grasses including *Stipa comata, Elymus lanceolatus, Bouteloua gracilis, Koeleria macrantha, Pascopyrum smithii,* and forbs including

Artimesia frigida, *Phlox hoodii*, *Sphaeralcea coccinea*; *Selaginella densa* was the prevalent spikemoss (Coupland 1950, Parks Canada 2006).

A large-scale grazing experiment reintroduced cattle into the East Block of the park in May 2008, where grazing had been excluded for at least 15 years. In 2006, 12, ~300-ha pastures were designed, with six pastures for cattle, three pastures as ungrazed controls, and three, 300-ha units (within larger pastures) as long-term grazing controls; these latter pastures were in the Mankota Community Pastures immediately adjacent to the East Block. Each pasture had similar amounts of upland, lowland, and riparian habitats (Parks Canada 2006). In 2008, fencing for the six new cattle pastures was erected, and each pasture was supplemented with two water troughs, one located in the lowland and one in the upland, to encourage grazing distribution (Bailey et al. 1996, Koper et al. 2008). The present study focused on effects of grazing in upland habitats, and each pasture contained six, 100-m radius permanent upland sampling plots (Figure 1).

The grazed pastures in the Park had a range of grazing intensities varying from below normal for the area (0.23 AUM/ha; estimated to result in approximately 20% biomass removal annually) to very high for the area (0.83 AUM/ha; estimated to result in approximately 70% biomass removal annually), while the community pastures had been managed at a low - moderate stocking rate (0.2 - 0.5 AUM/ha) for at least fifteen years (Table 1, Abouguendia 1990, Koper et al. 2008).

The study was designed as a Before-After-Control-Impact manipulative experiment, and therefore baseline data were collected on songbirds in 2006, 2007, and 2008, and on habitat structure in 2008 prior to grazing reintroduction (Koper et al. 2008).

It is crucial to collect pre-treatment data in ecological field experiments to detect patterns that exist naturally due to environmental conditions prior to application of the treatment, and to be able to relate the results to the effects of the treatment (Underwood 1994). Following reintroduction of grazing, songbirds and habitat structure were surveyed in 2009 and 2010. There were 36 grazed plots and 17 ungrazed control plots (n = 53) inside the East Block, and an additional 17 long-term grazed controls in the community pastures.

4.3.2 Field Methods

Two rounds of point counts were conducted each year from 2006 through 2010 between mid-May and 30 June. All plot centers were located at least 250 m apart so that birds were not recorded twice at separate plots. The point counts were five minutes each and all birds detected by either sight or sound within a 100-m radius were recorded; protocols followed were adapted from Hutto et al. (1986). All point counts were conducted between sunrise and 1000 hours and each plot was surveyed by at least 2 different observers in all years to lessen effects of observer bias. No surveys were conducted on days with excessive wind (>15km/h) or rain, which lessen detectability.

Unadjusted point counts were averaged over the two rounds as a measure of relative abundance (Koper and Schmiegelow 2006, Johnson 2008). Unadjusted point counts were used because distance sampling assumptions are difficult to meet in the field, and detectability of mixed-grass prairie birds is relatively high (Lueders et al. 2006, Efford and Dawson 2009). Bird diversity (including richness, Shannon-Wiener diversity, and evenness) and total abundance was calculated for each plot for songbirds. The Shannon-Wiener diversity index was chosen because it is sensitive to rare species (Wiens

1989), which are of management concern. Only songbird species occurring in each year in 10% or greater of plots were analyzed individually. Unfortunately, McCown's longspur, a species of conservation concern, did not meet this requirement; however, a qualitative assessment was made concerning their occurrence.

At each plot I surveyed the habitat structure once in May and once in July of 2008, 2009, and 2010. Each survey included eight 1.0-m × 0.5-m sampling frames at 50 m and 100 m from the center of the plot in the four cardinal directions. At each frame, I measured vegetation density (using the Robel pole visual obstruction method, Robel et al. 1970), tallest vegetation (hereafter called vegetation height), canopy height, litter depth, and visual percent cover estimates of litter and bare ground. All variables were averaged for each plot, and the standard deviations of vegetation height, canopy height, density, and litter depth were calculated as a measure of heterogeneity within each plot.

4.3.3 Statistical Analysis

All analyses were done using SAS Statistical software (SAS Institute 2008). Habitat structure, songbird relative abundance, and diversity were analyzed to evaluate their response to stocking rate and grazing duration, using nonlinear mixed-effects models (NLMMs). Plots were my units of replication, and NLMMs were chosen because it allowed inclusion of a random effect to account for the spatial clustering of plots within sites. Site (group of 6 plots within a pasture) was used as the random effect in all models because it explained more random variation than did plot, and including two random effects usually caused the models to fail to converge. Biologically, site is appropriate as the random effect because season-long grazing at a single stocking rate applied to each pasture may result in plots that are more similar to each other than to those plots in other

pastures. The benefit of using a non-linear approach to data analyses was that it allowed for the detection of curvilinear responses (Koper et al. 2008); for example, I was able to detect if a species' abundance increased at moderate grazing intensities and decreased at high grazing intensities.

Distributions of the residuals of all response variables were determined using Generalized Linear Models (GLMs) and associated diagnostic graphs and the deviance/df ratio; following these preliminary analyses, we concluded that distributions of the error terms were best described as normal or Poisson, depending on the response variable. A set of models (see Appendix 1) was tested to determine the effects of stocking rate on habitat structure and songbirds using Akaike's Information Criterion (AIC) model selection to determine which model best explained the variation in the data. Songbirds were analyzed using stocking rates instead of habitat structure in order to make a direct link between grazing and songbirds to simplify making management decisions, while habitat structure was also analyzed to ensure that grazing was causing the expected changes and make links between structure and songbird habitat selection. The model set included a null model, a model that included only grazing duration, a model that included only stocking rate, a model that included polynomial factors of grazing intensity (to allow a curvilinear response [Koper et al. 2008]), and a model that included main effects and interactions between grazing duration and stocking rate. Interactions between grazing duration and stocking rate were included to determine whether one or two years of grazing had a different effect on the dependent variables (vegetation and songbirds). Because AIC has a tendency to select for more complicated models (Quinn and Keough 2002), only those models that were at least two AIC points lower than the null model

were selected. Parameters included in the selected model were considered more influential when the confidence interval for that parameter did not include 0 (Koper and Schmiegelow 2006).

Mean and standard deviation (a measure of heterogeneity) of litter depth, vegetation height, canopy height, vegetation density, and mean litter cover were analyzed individually to determine their relationships to stocking rate and grazing duration. Standard deviation was chosen as a measure of habitat heterogeneity because it does not over-correct for correlation with the mean as is common with coefficient of variation in mixed-grass prairie (Bleho 2009). Litter depth data were analyzed from May 2008, July 2009, and July 2010 due to some field errors in measuring these variables in May of 2009; May 2008-2010 data were used for the remainder of the habitat structure variables. A model using the 2008 pre-grazing data with future stocking rates overlaid on plots was used to check for pre-existing patterns due to environmental conditions. This allowed me to be confident that the patterns I detected were due to grazing and were not spurious or related to environmental conditions within the pastures (Underwood 1994). Finally, I analyzed the ungrazed control sites separately for litter depth, vegetation height, canopy height, and vegetation density, to determine how climate affected the habitat structure between 2008 and 2010. Three models were tested using AIC including null, linear (year), and quadratic (year*year) to allow the response to curve.

Songbird species analyzed individually included Baird's sparrow, chestnut-collared longspur, grasshopper sparrow, horned lark, Savannah sparrow, Sprague's pipit, vesper sparrow, and western meadowlark. To confirm there were no underlying patterns in songbird abundance and diversity prior to reintroduction of cattle, I analyzed 2006-

2008 data with future stocking rates overlaid on the plots as above. The dataset used for the final analysis included all data from 2006-2010, with grazing duration for 2006-2008 set as 0, 2009 duration set as 1, and 2010 duration set as 2.

The ungrazed control sites were also analyzed separately for 2006-2010 to evaluate effects of interannual climatic variability on Baird's sparrow, chestnut-collared longspur, Sprague's pipit, and songbird richness. Four models were tested including null, linear (year), quadratic (year*year), and cubic (year*year*year). Finally, because brown-headed cowbirds only occurred in 3% of plots between 2006 and 2008, a simple linear regression was used to determine the relationship between grazing duration and percent of plots in which brown-headed cowbirds were detected.

Sorensen's quantitative index was calculated for comparing community similarity within BAGMA, and between BAGMA and the Mankota community pastures. Sorensen's quantitative index accounts for differences in species' abundances between two sites and is a measure of similarity in species diversity and relative abundance (Jongman et al. 1995). Comparisons were made between data that were grouped into ungrazed, moderately grazed (0.23-0.57 AUM/ha), heavily grazed (0.66-0.83 AUM/ha), and long-term grazed community pastures (0.38-0.56 AUM/ha). Because this index is sensitive to sample size (Jongman et al. 1995), each grouping included 17 randomly selected plots for 2006 (pre-grazing), 2009, and 2010. The indices for 2006 (using future grazing), 2009, and 2010 were then ordered based on expected similarity (i.e. the heavily grazed/long-term grazed index was expected to be most similar, while the heavily grazed/ungrazed index was expected to be least similar). A simple linear regression was then used to determine if the expected ranking I assigned was correlated with the actual

values of the index. Finally, an ANOVA was used to determine if the slope of the 2009 or 2010 indices was significantly different from the 2006 indices. The 2006 indices were all expected to be similar (i.e. no correlation with ranking order), whereas the 2009 and 2010 indices were expected to have a strongly correlated relationship with the ranking order and be different from 2006.

4.4 RESULTS

4.4.1 Habitat structure

The analysis using pre-grazing data from 2008 revealed that prior to grazing reintroduction, percent litter cover had a quadratic pattern in the pastures that was correlated with the 2009 and 2010 stocking rates ($\beta = -1.15$, SE = 0.375, $p = 0.015$, Figure 4d); all other models showed no significant patterns (Δ AIC < 2 from null model). Analysis of the control sites revealed that vegetation density did not change between years (Δ AIC < 2 from null model), while litter depth increased between years ($\beta = 2.16$, SE = 0.691, $p = 0.003$), and vegetation height ($\beta = 4.29$, SE = 0.999, $p < 0.001$) and canopy height ($\beta = 3.17$, SE = 0.596, $p < 0.0001$) decreased from 2008 to 2009, then increased from 2009 to 2010.

The null model fit best for mean vegetation density and bare ground cover both prior to grazing reintroduction and after reintroduction. Mean vegetation height decreased with moderate grazing in 2009 but increased with moderate grazing in 2010, and declined by 10 cm and 5 cm from ungrazed controls to highest stocking rate in 2009 and 2010, respectively. Canopy height declined from approximately 12 cm to 9 cm in both years from ungrazed controls to highest stocking rate. Litter depth declined from approximately 4.5 cm to 1 cm in both years from ungrazed controls to highest stocking rate, and

increased slightly at moderate to high stocking rates in 2009. Litter cover decreased by 12% and 5% cover with stocking rate in 2009 and 2010, respectively, but showed inverted curvilinear patterns in 2009 and 2010 (Table 4, Figure 4).

Heterogeneity of vegetation height responded to an interaction between duration and stocking rate, which showed that height decreased with stocking rate in 2009 but increased with stocking rate in 2010 (Figure 4a). Heterogeneity of litter depth increased at moderate stocking rates in 2009 and at low-moderate stocking rates in 2010, and decreased at higher stocking rates (Figure 4b). Heterogeneity of vegetation density increased very slightly but significantly at moderate stocking rates in both years (Figure 4c).

Eight variables varied between years, including vegetation and canopy height, vegetation density, litter depth, litter cover, and heterogeneity of canopy height, litter depth, and vegetation density (Table 3).

Six variables responded to an interaction between stocking rate and grazing duration, including vegetation and canopy height, litter depth, litter cover, and heterogeneity of vegetation height and litter depth (Table 4); most interactions indicated a slight change in the shape of the response curve, and therefore did not change the interpretation of the overall response (Figure 4).

Table 3. Mean and standard deviation (as a measure of heterogeneity) of habitat structure variables per plot that varied by year in the East Block of Grasslands National Park, southwestern Saskatchewan, 2006-2010. Mean and SD shown include data from both ungrazed plots and grazed plots. Mean vegetation height was the average of tallest vegetation measured within eight frames at each plot. Mean canopy height was the measure of average vegetation height within eight frames at each plot.

	pre-grazing		2009		2010	
Variable	Mean	SD	Mean	SD	Mean	SD
Mean vegetation height (cm)	41.69	5.119	30.39	8.218	38.06	6.891
Heterogeneity of vegetation height (cm)	9.88	3.038	9.06	3.444	11.00	3.036
Mean canopy height (cm)	15.10	2.929	10.81	2.543	12.37	2.439
Heterogeneity of canopy height (cm)	5.20	2.942	4.27	3.287	3.78	2.641
Mean litter depth (cm)	5.09	2.939	2.65	1.450	4.09	1.621
Heterogeneity of litter depth (cm)	3.78	1.977	2.59	1.301	2.46	1.494
Heterogeneity of vegetation density (cm)	4.23	1.765	3.28	2.702	2.43	1.101
Mean litter cover (% cover)	0.62	0.159	0.47	0.166	0.51	0.221

Table 4. Non-linear mixed-effects models and parameter estimates for AIC-selected models for habitat structure variables in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2006-2010.[a]

Variable	Model selected	Confidence Intervals that did not include 0	β	SE	*p-value*
Mean vegetation height	A + A2 + y + A*y + A*A*y	A	-139.300	19.555	<0.001
		A2	150.460	28.258	<0.001
		y	-2.009	0.864	0.048
		A*y	82.726	11.520	<.001
		A*A*y	-93.926	15.691	<.001
Heterogeneity of height	A + y + A*y	A	-0.602	0.220	0.026
		A*y	0.344	0.137	0.037
Mean canopy height	A + A2 + y + A*y + A*A*y	A	-28.571	7.422	0.005
		A2	29.439	10.713	0.025
		Y	-0.985	0.353	0.023
		A*y	13.187	4.381	0.017
		A*A*y	-14.482	5.947	0.041
Heterogeneity of canopy height	y	y	-0.193	0.062	0.015
Mean litter depth	A + A2 + A3 + y + A*y + A*A*y + A*A*A*y	y	-0.990	0.316	0.014
		A*y	22.337	11.157	0.080
Heterogeneity litter depth	A + A2 + A3 + y + A*y + A*A*y + A*A*A*y	y	-0.868	0.240	0.007
		A*y	21.829	7.687	0.022
		A*A*y	-69.840	26.466	0.029
		A*A*A*y	54.659	21.939	0.037
Mean vegetation density	Null	N/A			
Heterogeneity of vegetation density	A + A2 + y	A2	-1.975	0.977	0.078
		y	-0.286	0.072	0.004
Bare ground cover	Null	N/A			
Litter cover	A + y + A*y	A	-0.346	0.107	0.012
		y	-0.048	0.023	0.069
		A*y	0.153	0.069	0.057

[a] Abbreviations: A = AUM, A2 = AUM*AUM, A3 = AUM*AUM*AUM, y = grazing duration, A*y = AUM*duration, A*A*y = AUM*AUM*duration, A*A*A*y = AUM*AUM*AUM*duration

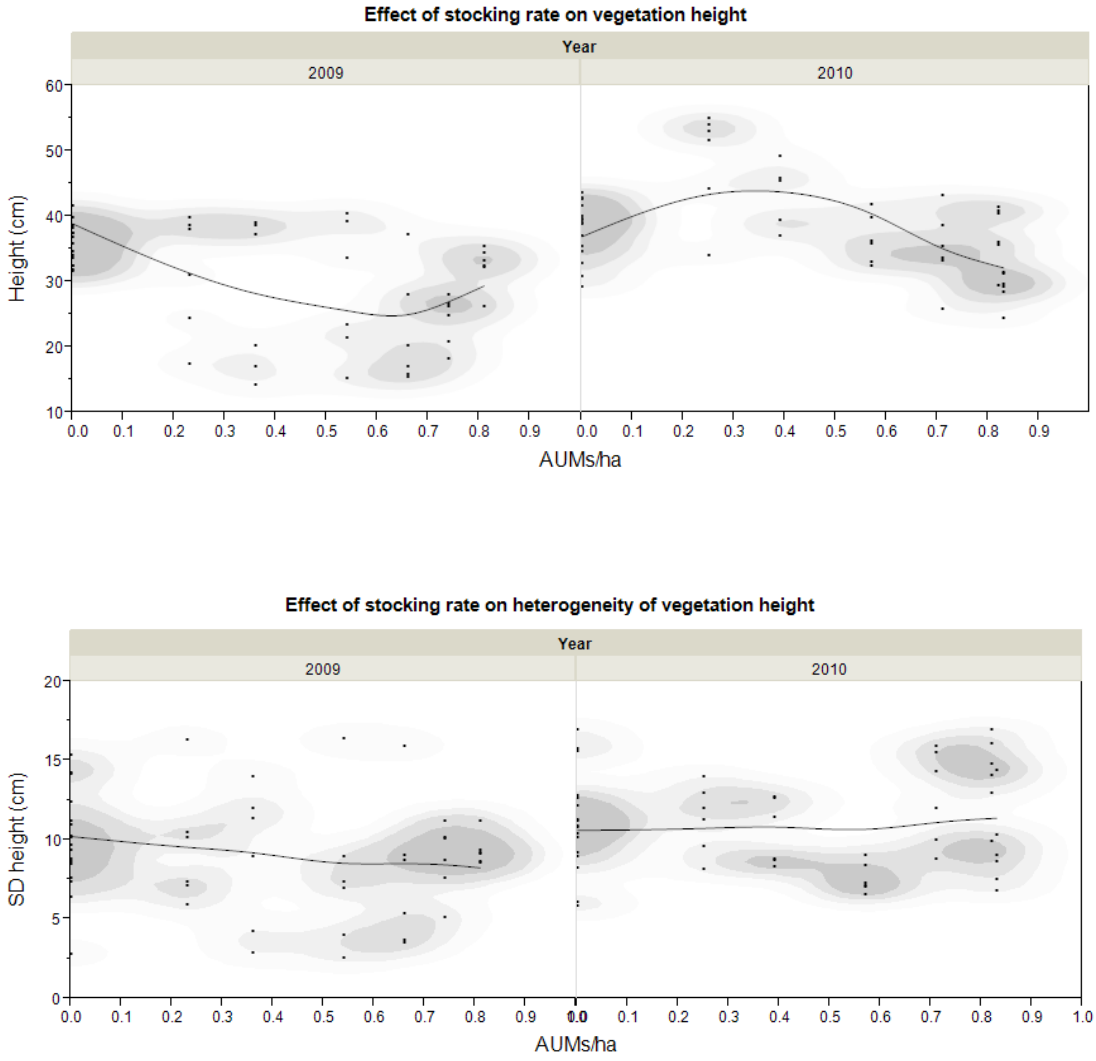


Figure 4a. Effects of stocking rate and grazing duration on vegetation height and heterogeneity of vegetation height per plot in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010. Figures show the actual data and the predicted response curve for 2009 and 2010. The shaded areas indicate the density of the raw data points, with darker areas indicating more points and lighter areas indicating fewer points.

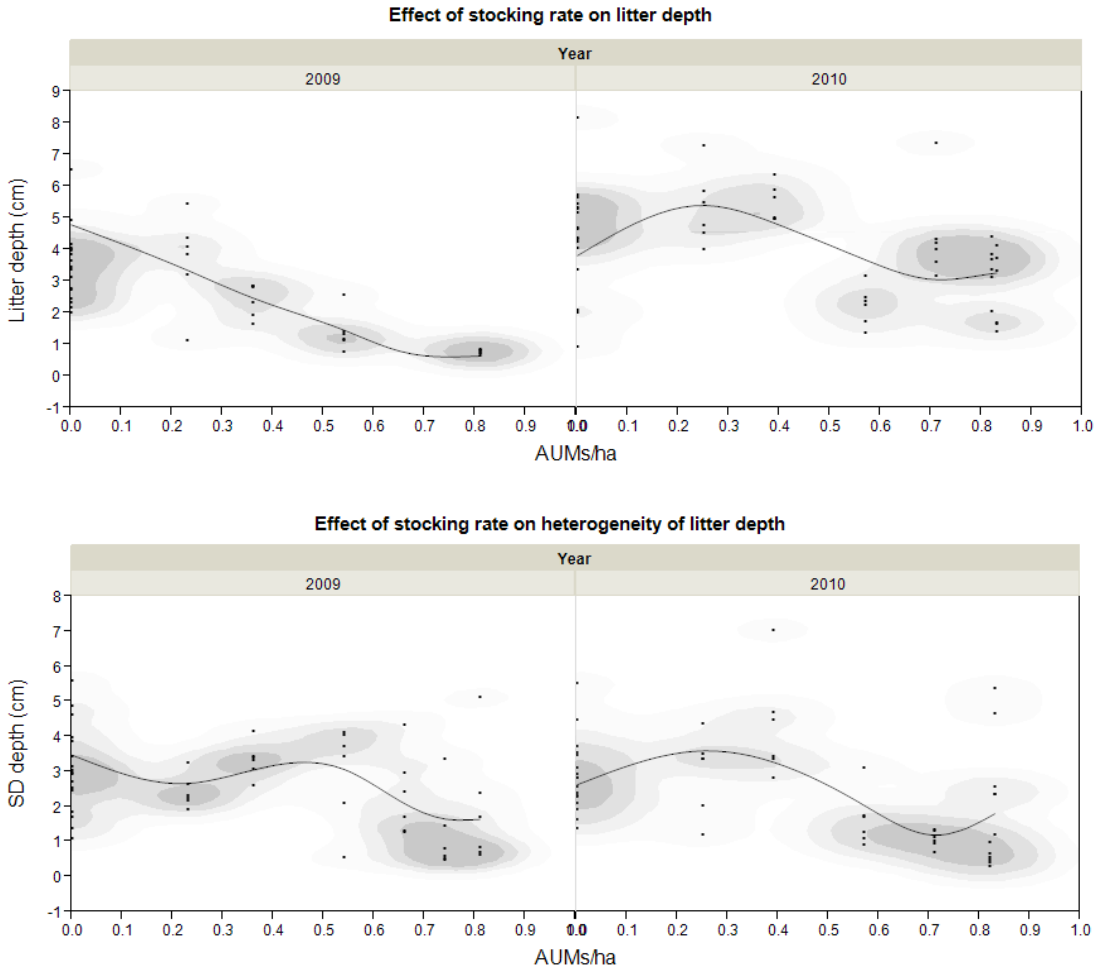


Figure 4b. Effects of stocking rate and grazing duration on litter depth and heterogeneity of litter depth per plot in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010. Figures show the actual data and the predicted response curve for 2009 and 2010. The shaded areas indicate the density of the raw data points, with darker areas indicating more points and lighter areas indicating fewer points.

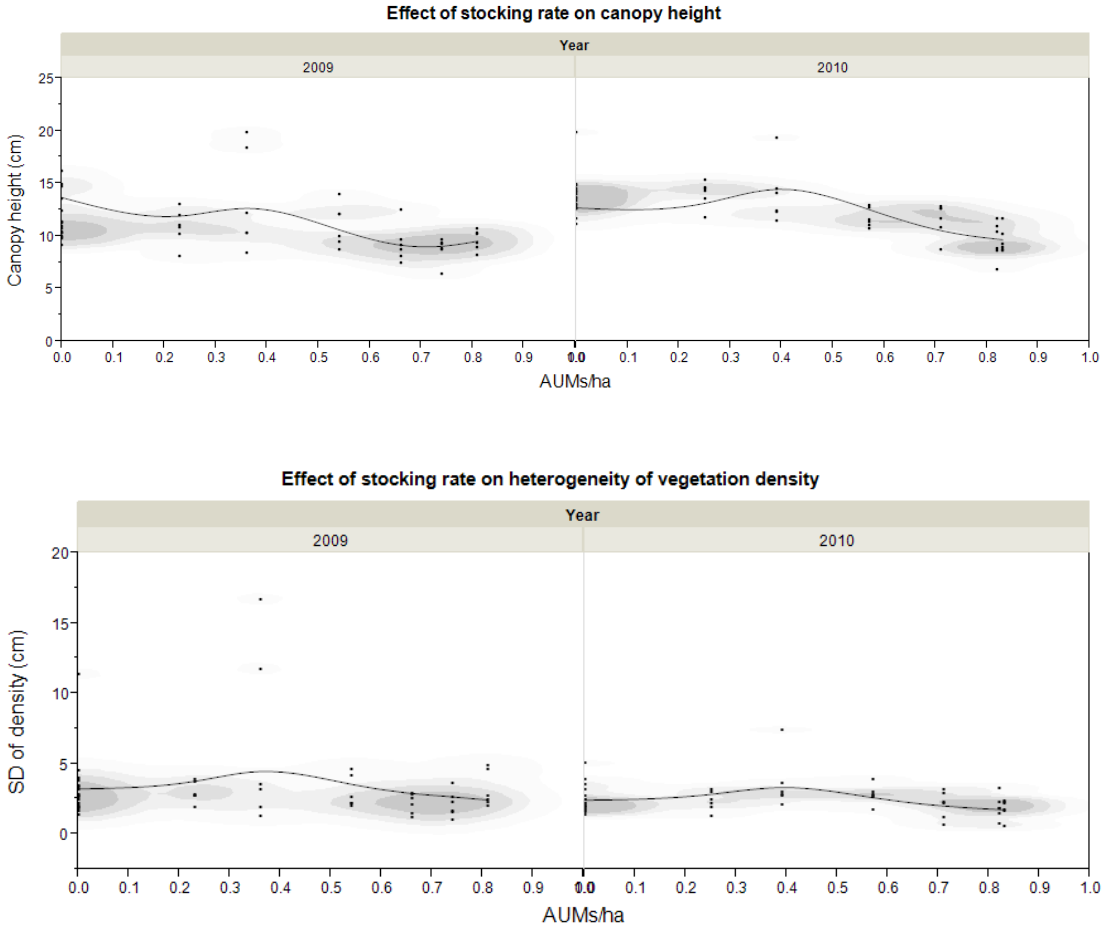


Figure 4c. Effects of stocking rate and grazing duration on canopy height and heterogeneity of vegetation density per plot in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010. Figures show the actual data and the predicted response curve for 2009 and 2010. The shaded areas indicate the density of the raw data points, with darker areas indicating more points and lighter areas indicating fewer points.

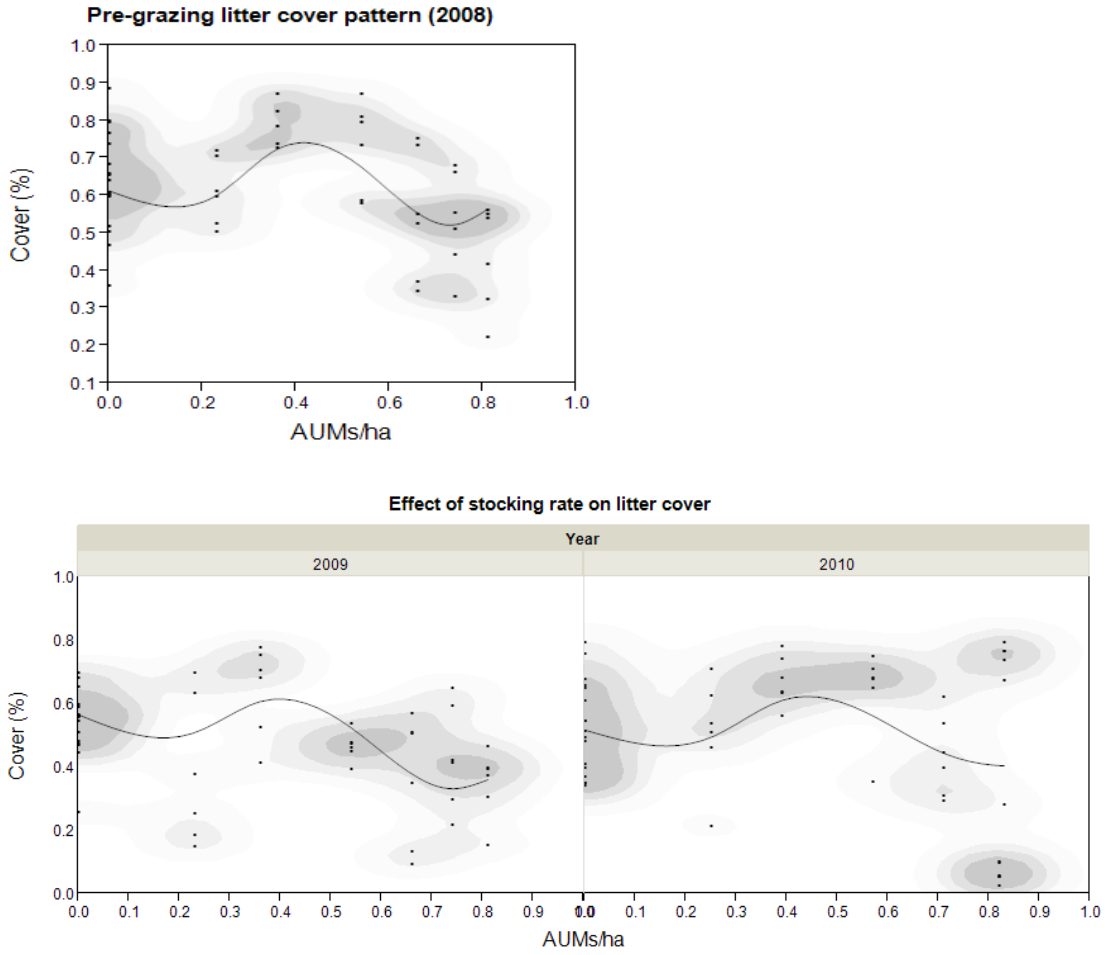


Figure 4d. Effects of stocking rate and grazing duration on percent litter cover per plot in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2008-2010. Figures show the actual data and the predicted response curve for 2008 (pre-grazing), 2009 and 2010. The shaded areas indicate the density of the raw data points, with darker areas indicating more points and lighter areas indicating fewer points. Also shown is the 2008 pre-grazing data, because this variable had a pre-existing pattern in the experimental plots.

4.4.2 Songbird Abundance and Diversity

The analysis using 2006-2008 data revealed that there were no pre-existing patterns in relation to future stocking rates (Δ AIC from null < 2). Analysis of the ungrazed control sites showed increased Baird's sparrow (β = 0.12, SE = 0.040, p = 0.003) and Sprague's pipit (β = 0.24, SE = 0.046, $p < 0.0001$) relative abundance from 2006 to 2010 by approximately 1 bird per plot. Chestnut-collared longspur relative abundance decreased from about 1.5 birds per plot in 2006 to 0.5 birds per plot in 2008, but then increased again to over 1.5 birds per plot in 2010 (β = 0.24, SE = 0.050, $p <$ 0.0001). Songbird richness decreased from 4.2 species in 2006 to 3.5 species in 2007 and 2008, but then increased 5.2 species per plot in 2010 (β = 0.29, SE = 0.047, $p < 0.0001$).

All songbirds and diversity indices responded to some of the grazing variables (Table 6). Baird's sparrow relative abundance declined from ungrazed to highest stocking rate by about 1.3 and 0.7 birds per plot in 2009 and 2010, respectively, while Sprague's pipit relative abundance declined with stocking rate by 0.7 birds per plot in both years. Horned lark relative abundance increased by 0.1 birds per plot with stocking rate. Chestnut-collared longspur relative abundance was fairly stable up to 0.4 AUM/ha, at which point abundance increased from approximately 1 bird in ungrazed plots to 2.5 birds in heavily grazed plots (Figure 5). Grasshopper sparrow and Savannah sparrow both increased very slightly at moderate stocking rates and began to decline at 0.4 AUM/ha, declining by about 0.5 bird per plot as grazing intensity increased (Figure 5).

Baird's sparrow and chestnut-collared longspur were the only two species that responded significantly to an interaction between stocking rate and grazing duration;

however, the difference between the 2009 and 2010 was slight and did not change the interpretation of the results.

Brown-headed cowbird occurrence increased significantly with grazing duration from 0% occurrence in upland plots in 2006 to 27% occurrence in upland plots in 2010 ($R^2 = 0.87$, $p = 0.02$).

Richness decreased slightly with stocking rate in 2009 and increased by about 1 species per plot with stocking rate in 2010. Shannon-Wiener diversity responded significantly only to grazing duration, and was 15% greater in 2010 than 2009, and 31% greater in 2010, compared with pre-grazing diversity. Evenness decreased slightly at moderate stocking rates in 2009, and increased then decreased at moderate stocking rates in 2010. All species' abundances increased with grazing duration (Table 5).

Table 5. Mean and standard deviation of relative songbird abundances (birds/3.2-ha plot) and diversity measures per plot that varied by year in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2006-2010.

	pre-grazing		2009		2010	
Variable	Mean	SD	Mean	SD	Mean	SD
Baird's sparrow	2.342	0.69	1.830	0.78	2.623	0.69
Chestnut-collared longspur	0.795	0.79	1.255	1.20	1.868	1.02
Grasshopper sparrow	0.168	0.32	0.330	0.47	0.415	0.46
Horned lark	0.264	0.43	0.349	0.48	0.406	0.48
Sprague's pipit	1.568	0.63	1.764	0.68	2.245	0.68
Vesper sparrow	0.065	0.20	0.085	0.21	0.425	0.47
Western meadowlark	0.196	0.36	0.226	0.35	0.518	0.44
Richness	3.606	0.87	4.104	0.76	5.566	1.08
Shannon-Wiener diversity	1.942	0.40	2.179	0.28	2.546	0.31
Evenness	0.121	0.03	0.139	0.03	0.177	0.04
Total abundance	6.202	1.35	6.896	1.51	10.208	1.37

Table 6. Non-linear mixed-effects models and parameter estimates for AIC-selected models for relative songbird abundance and diversity measures in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2006-2010.[a]

Variable	Model selected	Confidence intervals that did not include 0	β	SE	*p-value*
Baird's sparrow	A + y + A*y	A	-2.112	0.442	0.001
		y	0.249	0.076	0.011
		A*y	0.704	0.289	0.041
Chestnut-collared longspur	A + A2 + A3 + y + A*y + A*A*y + A*A*A*y	A	-24.825	9.046	0.025
		A2	69.269	27.900	0.038
		A3	-45.145	21.362	0.068
		y	0.262	0.085	0.015
		A*y	11.596	4.951	0.047
		i2	-31.379	15.289	0.074
Grasshopper sparrow	A + A2 + y	A2	-4.109	2.127	0.089
		y	0.568	0.128	0.002
Horned lark	A	A	0.337	0.270	0.038
Savannah sparrow	A + A2 + y	y	0.345	0.091	0.005
Sprague's pipit	A + y	A	-0.705	0.194	0.007
		y	0.479	0.065	<0.001
Vesper sparrow	A + A2 + A3 + y + A*y + A*A*y + A*A*A*y	y	0.579	0.172	0.009
Western meadowlark	y	y	0.483	0.095	0.001
Richness	A + y + A*y	A	-1.265	0.562	0.055
		y	0.768	0.099	<0.001
		A*y	1.087	0.368	0.018
Shannon-Wiener diversity	y	y	0.294	0.028	<0.001
Evenness	A + A2 + A3 + y + A*y + A*A*y + A*A*A*y	y	0.019	0.004	0.001
		A*y	0.421	0.162	0.032
		A*A*y	-1.151	0.562	0.075
Total abundance	A + A2 + y + A*y + A*A*y	A	-17.922	4.267	0.003
		A2	21.150	6.064	0.008
		y	1.681	0.170	<0.001
		A*y	11.437	2.694	0.003
		A*A*y	-13.284	3.694	0.007

[a] Abbreviations: A = AUM, A2 = AUM*AUM, A3 = AUM*AUM*AUM, y = grazing duration, A*y = AUM*duration, A*A*y = AUM*AUM*duration, A*A*A*y = AUM*AUM*AUM*duration

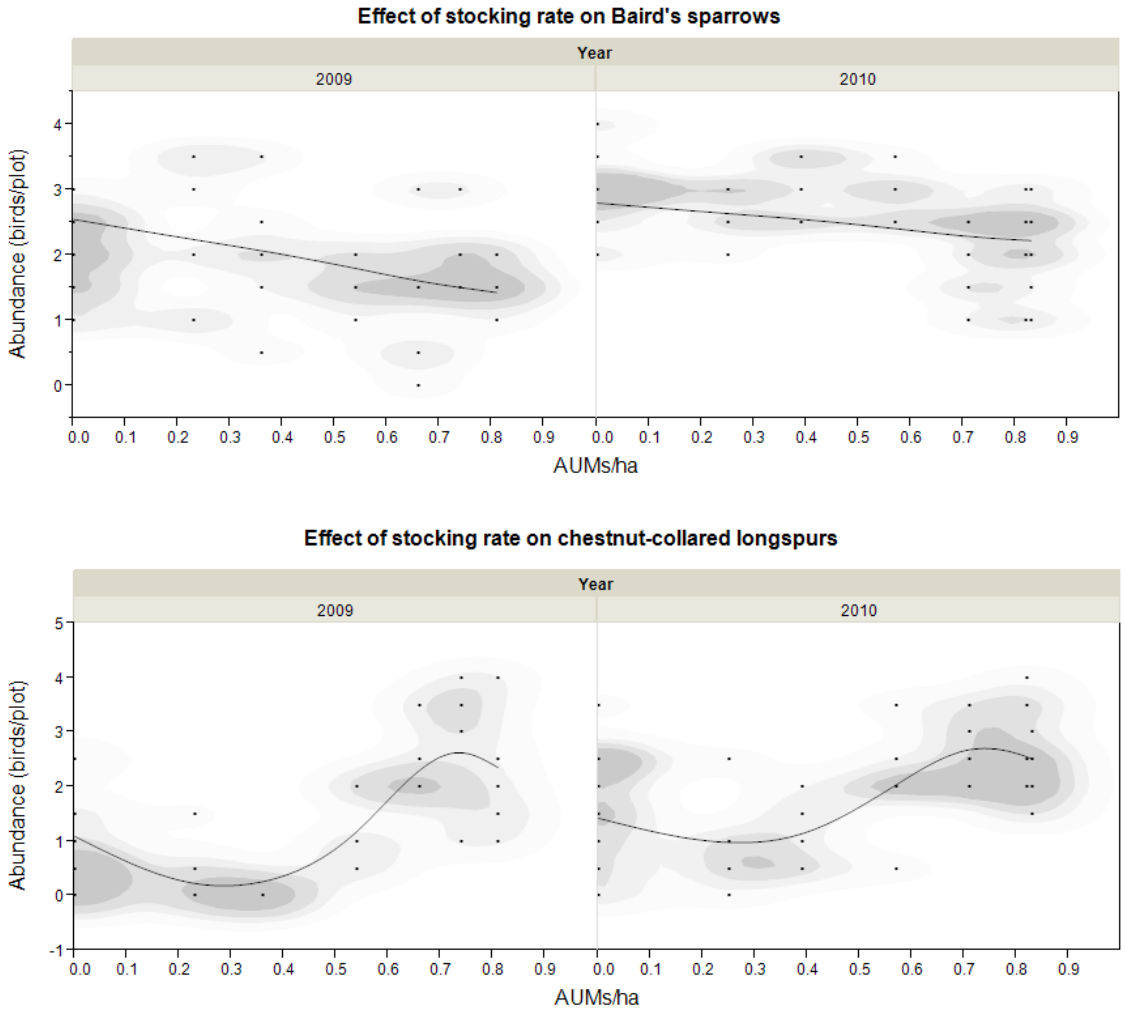


Figure 5a. Effect of stocking rate and grazing duration on Baird's sparrow and chestnut-collared longspur relative abundances per 3.2-ha plot in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2006-2010. Figures show the actual data and the predicted response curve for one year with grazing (2009), and two years with grazing (2010). The shaded areas indicate the density of the raw data points, with darker areas indicating more points and lighter areas indicating fewer points.

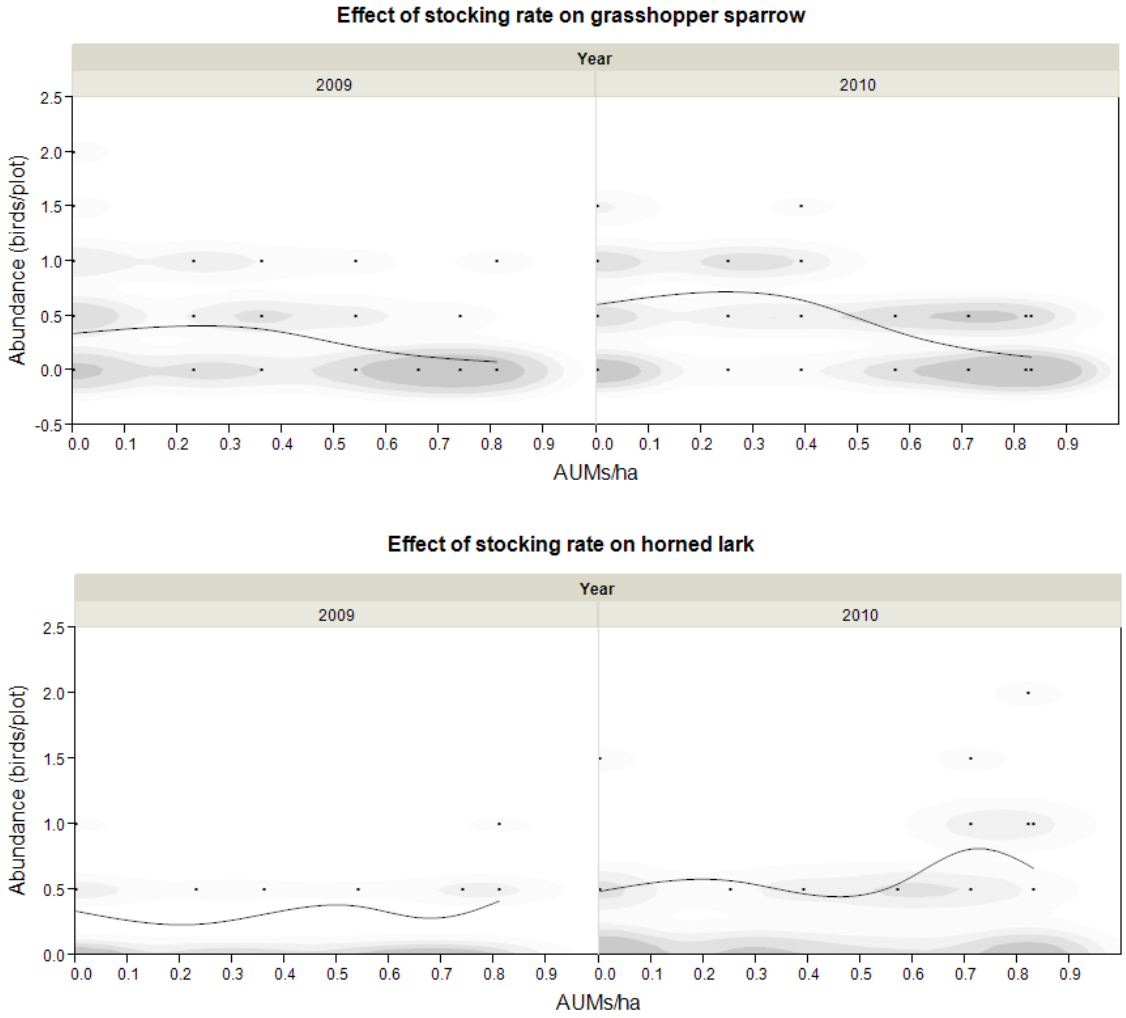


Figure 5b. Effect of stocking rate and grazing duration on grasshopper sparrow and horned lark relative abundances per 3.2-ha plot in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2006-2010. Figures show the actual data and the predicted response curve for one year with grazing (2009), and two years with grazing (2010). The shaded areas indicate the density of the raw data points, with darker areas indicating more points and lighter areas indicating fewer points.

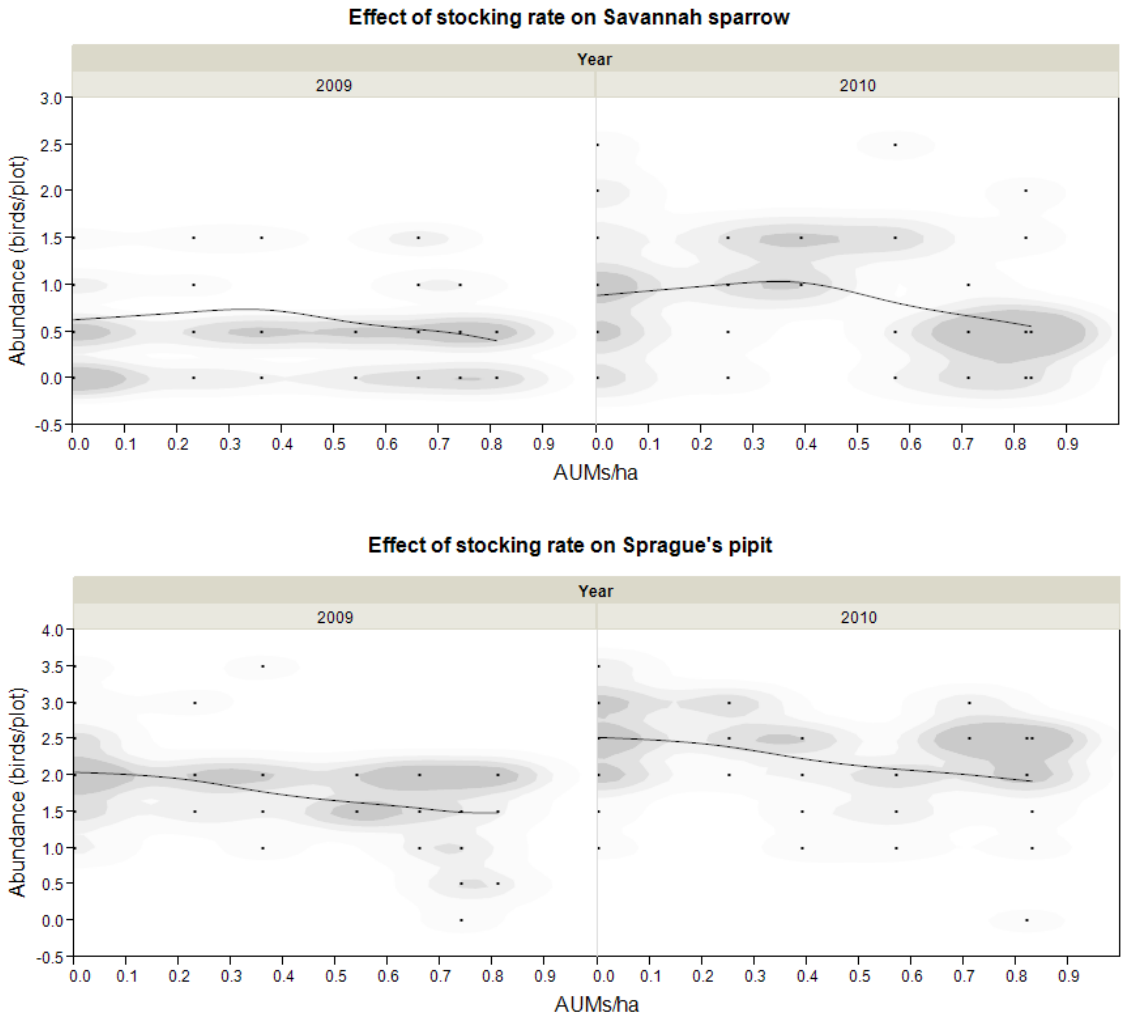


Figure 5c. Effect of stocking rate and grazing duration on Savannah sparrow and Sprague's pipit relative abundances per 3.2-ha plot in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2006-2010. Figures show the actual data and the predicted response curve for one year with grazing (2009), and two years with grazing (2010). The shaded areas indicate the density of the raw data points, with darker areas indicating more points and lighter areas indicating fewer points.

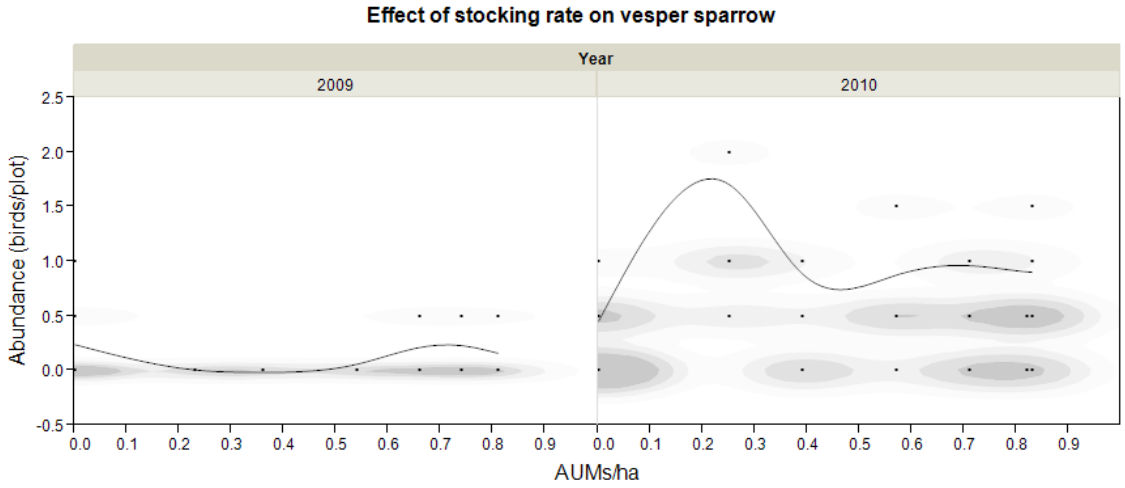


Figure 5d. Effect of stocking rate and grazing duration on vesper sparrow relative abundance per 3.2-ha plot in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2006-2010. The figure shows the actual data and the predicted response curve for one year with grazing (2009), and two years with grazing (2010). The shaded areas indicate the density of the raw data points, with darker areas indicating more points and lighter areas indicating fewer points.

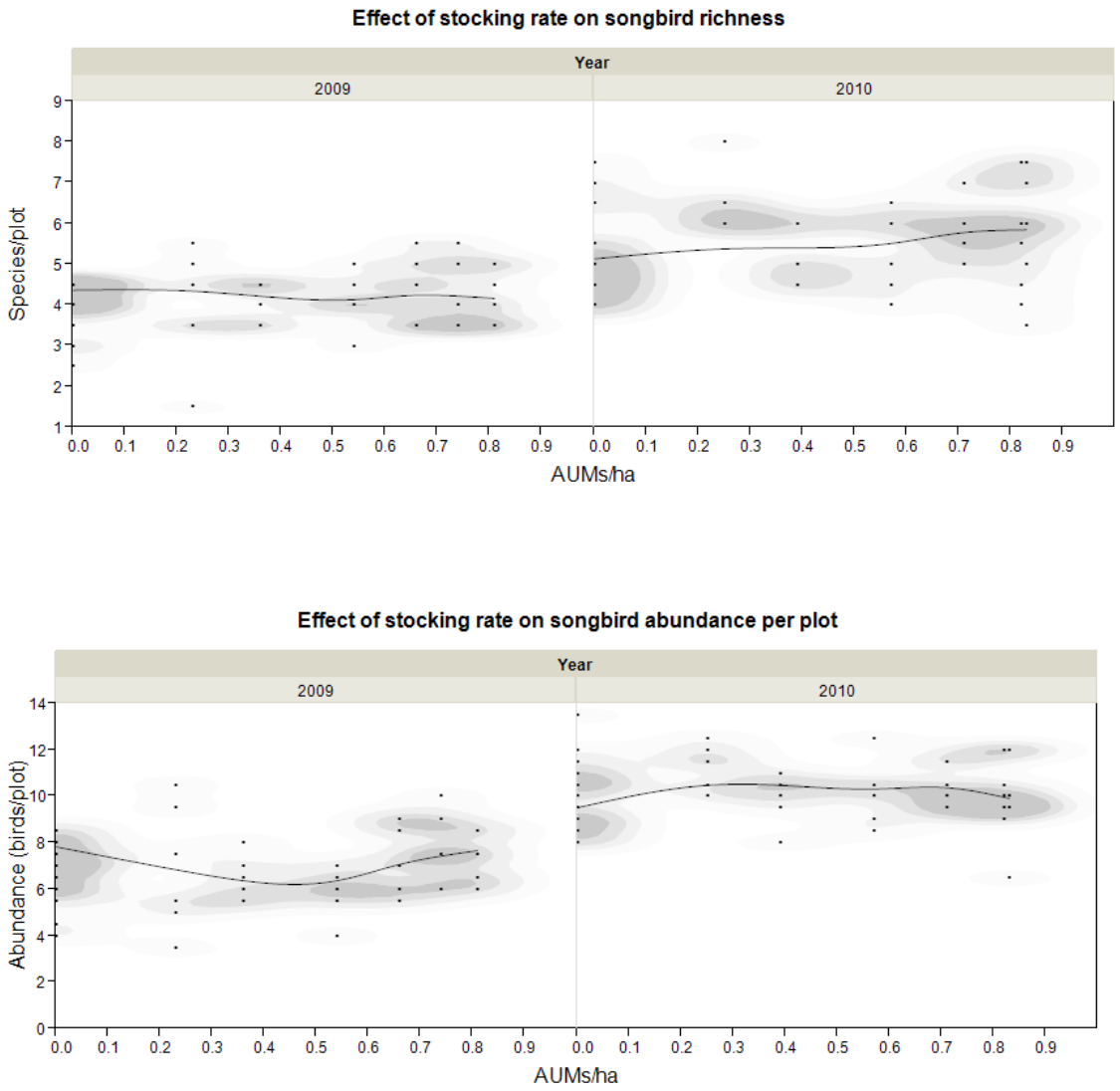


Figure 6a. Effect of stocking rate and grazing duration on songbird richness and average abundance per 3.2-ha plot in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2006-2010. Figures show the actual data and the predicted response curve one year with grazing (2009), and two years with grazing (2010). The shaded areas indicate the density of the raw data points, with darker areas indicating more points and lighter areas indicating fewer points.

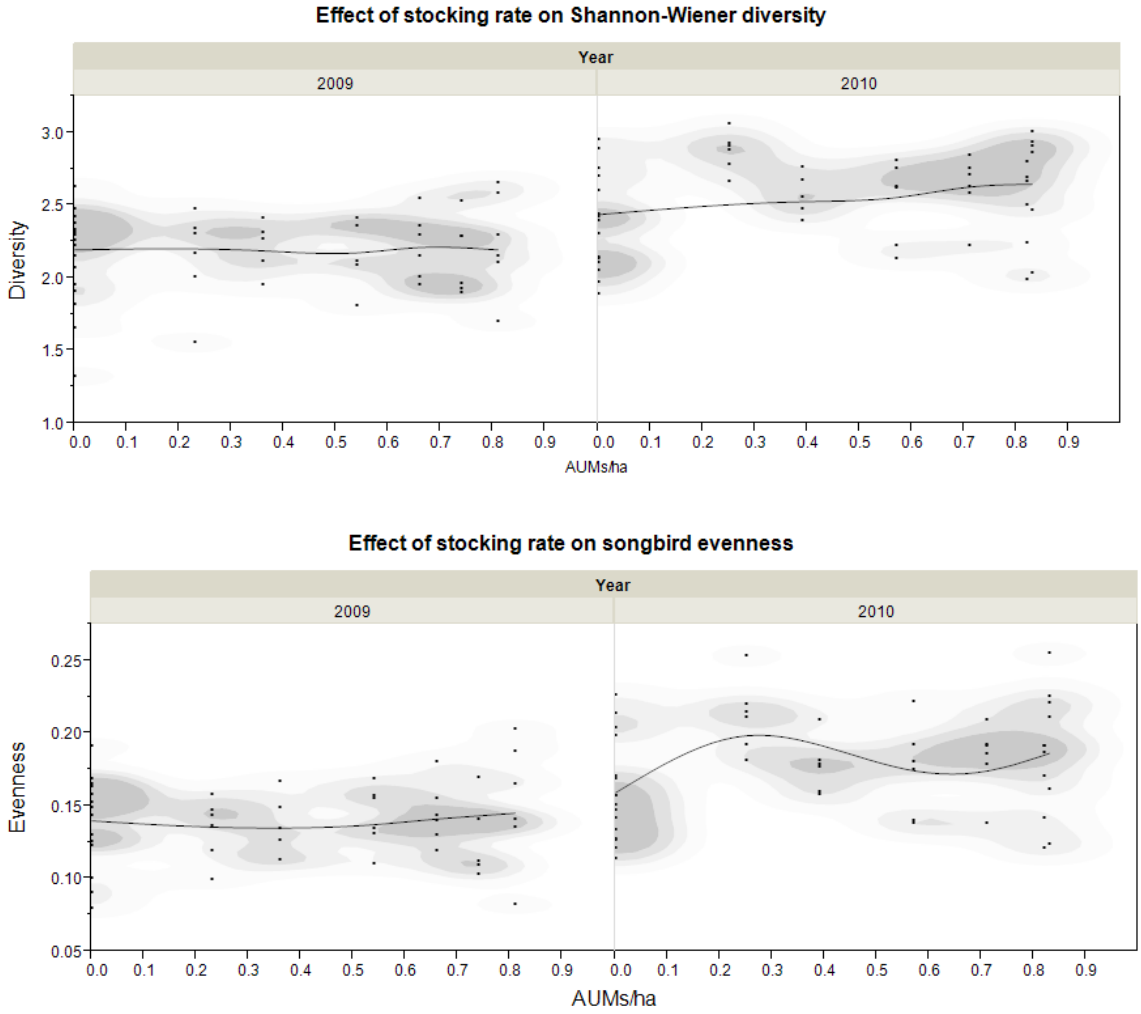


Figure 6b. Effect of stocking rate and grazing duration on Shannon-Wiener diversity and evenness per 3.2-ha plot in the East Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2006-2010. Figures show the actual data and the predicted response curve for one year with grazing (2009), and two years with grazing (2010). The shaded areas indicate the density of the raw data points, with darker areas indicating more points and lighter areas indicating fewer points.

4.4.3 Songbird Community

Sorensen's quantitative index showed a high degree of similarity (> 79%) among all sites in the grazing experiment and the long-term grazed areas of the Mankota community pastures in 2006 (Table 7). In 2009, the songbird communities in the grazed areas of the park (both medium and high) diverged slightly from the ungrazed areas (quantitative index < 70%). The heavily grazed areas increased in similarity to the community pastures after one year of grazing (83% similar in 2006-2008, to 89% similar in 2009). I predicted a negative correlation between the ranking order and the index in 2009 and 2010 because of decreasing similarity with increasing rank, and this is what I found (Table 8). I predicted no correlation between the ranking order and the index in 2006, but the slope was positive, this suggests that pre-existing conditions did not drive the observed pattern of decreasing similarity with increasing rank after grazing was introduced. The 2009 index was significantly different from the 2006 index, but the 2010 index was not (Table 8), indicating that the communities may have become slightly more similar again in 2010.

Table 7. Sorensen's quantitative index for songbird communities in the East Block of Grasslands National Park, southwestern Saskatchewan, 2006-2010. Pre-grazing indices are included as an indicator of what was present in the park prior to grazing reintroduction. "Long" indicates the Mankota community pastures, which had been consistently grazed for at least 15 years. Comparisons are listed in order of expected least similarity to greatest similarity.

		2006 (pre-grazing)	2009	2010
Comparison	Expected Similarity	Quantitative index	Quantitative index	Quantitative index
None-high	6	0.886	0.667	0.781
None-long	5	0.849	0.697	0.802
Med.-long	4	0.811	0.694	0.796
Med.-high	3	0.863	0.674	0.802
None-med.	2	0.796	0.834	0.901
High-long	1	0.801	0.893	0.901

Table 8. Results from regression analysis and ANOVA for 2006, 2009, and 2010 used to determine if Sorensen's quantitative index differed with grazing pressure in the East Block of Grasslands National Park and the Mankota Community Pastures, southwestern Saskatchewan, Canada, 2006, 2009-2010.

Year	R^2	slope	*p*-value	Different from 2006?	*p*-value
2006	0.562	+	0.074		
2009	0.721	-	0.032	Yes	0.054
2010	0.766	-	0.022	No	0.890

4.5 DISCUSSION

Above 0.4 AUM/ha, the range of each of the habitat structure measurements shifted below the range that was present prior to grazing within each pasture, indicating an important ecological threshold at this stocking rate. This also indicates that grazing management was successful at altering habitat structure beyond intrinsic diversity, which is high in mixed-grass prairie habitats (Bork and Werner 1999, Fuhlendorf and Smiens 1999). Further, the effects of stocking rate on all vegetation variables was consistent with other research: averaged measurements decreased with stocking rate (Milchunas et al. 1988), although to a greater degree in 2009 than 2010, and most of the heterogeneity measures, including vegetation density, litter depth, and canopy height, increased at moderate stocking rates (Hart et al. 1993). Although the decreases seem relatively small with only a 3 cm difference between ungrazed pastures and heavily grazed pastures for litter depth, this difference is substantial (13%) because the litter depth in our study area reached a maximum of 22.2 cm. Additionally, mean vegetation height and canopy height increased slightly up to a moderate stocking rate (0.4 AUM/ha) and then declined at higher stocking rates in 2010 but not in 2009, which is consistent with research showing

that plant growth can be optimized at low and moderate grazing intensities and reduced at high grazing intensities (Biondini et al. 1998).

The increase of most heterogeneity indices at low and moderate stocking rates (0.2-0.6 AUM/ha) was consistent with theories suggesting that in dry mixed-grass prairies with long histories of grazing, heterogeneity will increase with moderate levels of grazing (Hart et al. 1993, Milchunas et al. 1988, Biondini et al. 1998). Some songbirds, such as western meadowlark and horned lark, may increase in abundance with habitat heterogeneity because it is a habitat selection cue since different activities require different habitats (i.e. nesting and foraging) (Wiens 1974, Derner et al. 2009); therefore, heterogeneity may be an important management goal. Grazing regimes that increase multi-scale heterogeneity are also likely to be more similar to the historical grazing patterns exhibited by bison, which will presumably benefit many grassland birds (Coppedge et al. 2008). Finally, heterogeneity may be important for increasing species diversity because a wider range of habitats is available to support more species (MacArthur and MacArthur 1961).

Relative abundance, richness, Shannon-Wiener index, and evenness increased over time after grazing was reintroduced, even though some species tend to prefer ungrazed or lightly grazed areas. This could be partly due to increased rainfall in 2010, which would be good for species that prefer taller and denser vegetation, while the two years of grazing might still have provided increased habitat for those species that prefer sparser vegetation (Lueders et al. 2006). Some species, such as chestnut-collared longspurs and Savannah sparrows, may also be directly attracted to the presence of grazers or indicators of recent presence (such as patties) (Davis 2005). Alternatively,

because grassland songbirds evolved with nomadic herds of bison and are therefore partially nomadic themselves (Johnson and Grier 1988, Jones et al. 2007), individuals of different species may have found the high-quality prairie in the East Block by chance in 2010, causing richness, diversity, and evenness to increase overall. Even with increased abundance of all species, there were still detectable responses of individual species to stocking rate.

The shift in habitat structure caused by grazing presumably explains some of the shifts in songbird abundance that were generally consistent with other studies (Bakker et al. 2002, Askins et al. 2007). However, Sprague's pipits and Baird's sparrows occurred at highest relative abundances in the ungrazed pastures in both 2009 and 2010 and declined approximately linearly with increased stocking rates. This contradicts studies that suggest both of these species are relatively insensitive to low and moderate levels of grazing (Davis et al. 1999, Koper and Schmiegelow 2006). Further, a decline of approximately 1 bird per plot is quite large when accounting for the fact that each 3.2-ha plot could hold at most 2 to 4 territories (Robbins and Dale 1999, Green et al. 2002).

The McCown's longspur, also a species of conservation concern (COSEWIC 2010), occurred at highest relative abundance in the long-term grazed community pastures in all years: the species was recorded only once in the ungrazed pastures inside the park between 2006 and 2008, while there were thirteen observations in the community pastures during the same years. Unfortunately McCown's longspur abundance was too low to analyze statistically, but the evidence is consistent with other studies that found McCown's longspurs to prefer very sparsely vegetated areas that are provided by heavy grazing (With 1994a, b).

I also detected a number of curvilinear responses that allowed me to detect thresholds in the response to grazing at which the slope of the response changed directions, indicating an important ecological response. For instance, the chestnut-collared longspur, also a species of conservation concern (COSEWIC 2010), remained at relatively level abundances at ungrazed and low-moderate stocking rates (0.2-0.4 AUM/ha), and began to increase in abundance above 0.4 AUM/ha, indicating that 0.4 AUM/ha was an important threshold stocking rate for this species. The slightly lower abundance at 0.4 AUM/ha is consistent also with the tallest vegetation height at that stocking rate in 2010, and a relatively tall vegetation height in 2009. Two years of grazing at low and moderate stocking rates did not provide improved habitat to longspurs because there were lower abundances at those stocking rates, but grazing at higher stocking rates improved habitat considerably after only one year of grazing. This finding contrasts with one study that found that chestnut-collared longspurs were not influenced by grazing intensity (Davis et al. 1999), although this study did not distinguish areas further than idle, lightly, moderately, and heavily grazed pastures. My findings are, however, consistent with another study that found that chestnut-collared longspurs were at higher abundances in early seral stages of grasslands (Fritcher et al. 2004), which can be created by grazing in mixed-grass prairies. Low stocking rates will likely continue to fail to provide more suitable habitat for chestnut-collared longspurs because the vegetation height and litter depth will not be sufficiently reduced. However, moderate stocking rates might help to provide more suitable habitat when sustained for a number of years, because the cumulative grazing pressure should reduce vegetation height and litter depth (Hartnett et al. 1996).

The decline of grasshopper sparrow abundance at stocking rates above 0.3-0.4 AUM/ha was another curvilinear response that was consistent with two studies that showed this species to be relatively insensitive to low grazing intensities and more sensitive to higher grazing intensities (Walk and Warner 2000, Fritcher et al. 2004). Further, Savannah sparrows also declined only above 0.4 AUM/ha, which is consistent with the species' habitat preference for tall and dense vegetation (Wheelright and Rising 2008). The increase of these two species at moderate stocking rate is also consistent with the slight increase in vegetation height at moderate stocking rates due to their preference for taller vegetation.

The brown-headed cowbird is a brood parasite and thus can pose a threat to the productivity of grassland songbirds (Davis 2003, Shaffer et al. 2003). The increase in cowbird abundance in upland plots from 0% prior to grazing introduction to 26% after grazing introduction is consistent with a number of other studies that have shown increased cowbird abundance near livestock operations (Goguen and Mathews 2000, 2001, reviewed in Shaffer et al. 2003). The introduction of cattle and establishment of perch sites (fencing) may have provided suitable habitat for cowbirds that had not been present in the upland portions of the park prior to 2008. Although brown-headed cowbirds rely directly on grazing cattle for foraging sites (Goguen and Mathews 1999, Goguen and Mathews 2001), cowbirds did not increase in abundance with increased stocking rate. This was likely because cowbirds' home range varies between 160 and 4344 ha, and their commute between foraging and breeding areas can be as long as 10 km (Goguen and Mathews 2000, 2001). Therefore, with the introduction of cattle to the area, cowbirds were not restricted to the grazed pastures or to fencelines, but were able to

extend into a large portion of the study area. Fortunately, the Sprague's pipit and chestnut-collared longspur are parasitized less than other prairie birds, although the Baird's sparrow is often parasitized (Davis 2003). The risk of increased cowbird abundance with the introduction of cattle requires continued examination to ensure that grazing management does not result in lower nesting success of species of conservation concern.

Sorensen's quantitative index showed the greatest difference among songbird communities between the ungrazed and heaviest grazed areas of the park, and the medium grazed areas of the park and long-term grazed community pastures. These values still suggest relatively high levels of similarity (Ratliff 1993). The difference between the slopes of the 2006 and 2009 ranked data suggests that the range of stocking rates significantly altered the songbird community within the East Block in 2009, and is also evidence that there are a variety of habitats now available across the landscape of the East Block.

I predicted a number of additional responses to stocking rate that I did not detect. For example, western meadowlarks, Shannon-Wiener diversity, and vegetation density did not respond to stocking rate, while some curvilinear responses, such as that of the vesper sparrow, species richness, and evenness, were unexplainable. Interestingly, the lack of response of Shannon-Wiener diversity may actually be desirable from a management perspective; increasing diversity at the plot level, or even the pasture level, should not be a management goal in mixed-grass habitats because an increase at this scale often entails increased abundance or occurrence of generalist species rather than endemics (Knopf 1994). It would, however, be preferable to increase diversity at a larger

scale, such as in a group of pastures that has been managed to support a variety of species that have different habitat preferences, such as McCown's longspurs and Sprague's pipits.

One reason that we may not have detected some predicted responses is that the second year of grazing in this study, 2010, had the highest amount of rainfall for April and May in the five years of this study, at 173 mm; this was 30% higher than the second wettest year, which occurred during the study in 2006, at 132 mm. Normal rainfall for the area during April and May is ~42 mm (Environment Canada 2011). This abnormally high rainfall might explain the lack of response for some species and diversity measures, and the slight response of most of the habitat structure variables, because there was likely sufficient growth to overcome the effects of grazing even in the heaviest grazed pastures (Biondini and Manske 1996). Even though the ungrazed control sites had increased litter depth, vegetation height, and canopy height from 2008 to 2010, and an increased abundance of Baird's sparrows and Sprague's pipits, likely due to increased precipitation, cattle grazing still resulted in the predicted decreased vegetation variables and changes in songbird abundances in the grazed pastures, indicating that grazing outweighed the effects of climate.

To determine if any of the responses I detected or did not detect were spurious will require additional years of data collection. Furthermore, the impacts of sustained heavy grazing may include increased degradation of the land due to damage to the soil crust layer from trampling or grazing (Anderson et al. 1982, Brennan and Kuvlesky 2005), or increased shrub invasion (Campbell et al. 1994, Anderies et al. 2002). These

impacts will need to be monitored if heavy grazing is to be used for promoting conservation and management of species that prefer heavily grazed areas.

Although my study showed that 0.4 AUM/ha was an important threshold for grazing effects on vegetation height, heterogeneity of habitat structure, chestnut-collared longspurs, and grasshopper sparrows, the pastures in the study have only been grazed for two years. Grazing at 0.4 AUM/ha over a longer time period will cause a cumulative increase in grazing intensity (Milchunas et al. 1988, Hartnett et al. 1996), which will in turn change the effects of grazing on habitat and songbirds. The temporal effects of grazing is one component that has been studied very little (Biondini et al. 1998), and requires further study to understand how the effects of a range of stocking rates accumulate and affect wildlife over longer periods of time.

4.6 Management Implications

0.4 AUM/ha was an important threshold for both habitat structure and songbirds. Although this is the typical stocking rate for the area (Parks Canada 2006), it is not the optimum stocking rate for most species because abundance and habitat structure began to change at this stocking rate; maximum abundances for individual species were generally above or below, but not at, about 0.4 AUM/ha. This may mean that many mixed-grass prairie songbirds experience reduced or sub-optimal abundances on most commercial ranchland today, which is managed at moderate stocking rates (Temple et al. 1999, Fuhlendorf and Engle 2001, Derner et al. 2009). It is, therefore, important to encourage landowners to manage their land for a variety of species, which will entail using a range of stocking rates on a group of pastures. Studies have shown that management for heterogeneity, including grazing at high stocking rates, did not cause a decline in

economic well-being (Fuhlendorf and Engle 2004, Derner et al. 2008), which may help promote the idea of managing ranchland for heterogeneity in the ranching community. To further promote beneficial management practices, goals can be simplified to focus on multi-species management, because management for Sprague's pipit and Baird's sparrow will also favor the Savannah sparrow and grasshopper sparrow, while management for the chestnut-collared longspur will also favor McCown's longspur and horned lark.

In the short term, high stocking rates are required in some pastures to improve the habitat for chestnut-collared longspurs and other species that prefer sparser habitat, but in the long term it is possible that a constantly applied moderate stocking rate will result in similarly suitable habitat. Grasslands National Park has an opportunity to help fill this knowledge gap by continuing to study the effects of cattle grazing on the wildlife in the park, while at the same time managing for mixed-grass obligate species. Also, because climate is both highly variable and highly influential in mixed-grass prairies, long-term monitoring will help the park evaluate effects of climate on grazing management.

5.0 IMPACTS OF BISON GRAZING ON SONGBIRDS AND HABITAT OF THE MIXED-GRASS PRAIRIE

Note to reader: this chapter is not intended for publication and therefore only presents results, discussion, and management implications for the benefit of the Park's management plan. For methods, see section 3.4.2.

5.1 RESULTS

5.1.1 Habitat structure

There were no data available similar to mine to conduct an analysis on habitat structure data prior to the 2006 reintroduction of bison into the West Block. Therefore some patterns might result from environmental conditions present in the area prior to grazing. The analysis of ungrazed control sites revealed that canopy height and vegetation density did not change between 2009 and 2010, while litter depth ($\beta = 2.91$, SE = 0.527, $p < 0.0001$) and vegetation height ($\beta = 8.37$, SE = 1.231, $p < 0.0001$) increased from 2009 to 2010.

Vegetation height decreased by 4 cm from ungrazed controls to the heaviest grazed plots (Figure 7). Canopy height also decreased by approximately 4 cm from ungrazed controls to the heaviest grazed plots (Figure 7). Vegetation density decreased by 3.5 cm from ungrazed controls to the heaviest grazed plots (Figure 7). Mean litter depth and percent bare ground cover varied curvilinearly with grazing intensity (Figure 7, Table 9). Eight variables were higher in 2010 than in 2009, while mean canopy height was slightly lower in 2010 than 2009 (Tables 8, 9). Mean litter depth was the only variable that had a significant interaction between intensity and year, indicating a slight change in the curve of the response as number of years grazed increased. The interaction between year and intensity also influenced bare ground cover (Table 9, Figure 7),

indicating that measurements in 2010 had bare ground cover greater than zero percent, while the majority of measurements from 2009 had zero bare ground cover.

Table 9. Generalized-linear mixed-effects models and parameter estimates for AIC-selected models looking at change in habitat structure variables with bison grazing in the West Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010. [a]

Variable	Model selected	Parameters with $p < 0.1$	β	SE	*p*-value
Mean vegetation height	P + Y	P	-0.048	0.023	0.042
		Y	-7.999	0.839	<0.001
Variability of vegetation height	Y	Y	-0.406	0.076	0.006
Mean canopy height	P + Y	P	-0.029	0.011	0.012
		Y	0.998	0.323	0.037
Variability of canopy height	Null	N/A			
Mean litter depth	P + P2 + Y + i1 + i2				
		P	-0.133	0.038	0.002
		P2	0.001	0.001	0.016
		Y	-2.383	0.335	0.002
		i1	0.105	0.048	0.031
Variability of litter depth	P + Y	P	-0.022	0.009	0.032
		Y	-0.730	0.276	0.057
Mean vegetation density	P + Y	P	-0.042	0.009	<0.001
		Y	-0.751	0.312	0.074
Variability of vegetation density	Null	N/A			
Grass cover	Y	Y	11.455	2.859	0.016
Forb cover	Y	Y	-4.330	0.498	0.001
Exposed mosses and lichens	Y	Y	-15.291	2.767	0.005
Bare ground cover	P + P2 + Y + i1 + i2				
		P	0.105	0.037	0.006
		P2	0.001	0.001	0.015
Litter cover	Null	N/A			

[a] Abbreviations: P = patties, P2 = patties*patties, Y = year, i1 = patties*year, i2 = patties*patties*year

Table 10. Mean and standard deviation (as a measure of heterogeneity) of habitat structure variables per plot that varied significantly by year in the West Block of Grasslands National Park, southwestern Saskatchewan, 2009-2010. Mean vegetation height was the average of tallest vegetation measured within eight frames at each plot. Mean canopy height was the measure of average vegetation height within eight frames at each plot.

	2009		2010	
Variable	Mean	SD	Mean	SD
Mean vegetation height (cm)	23.388	4.24	31.353	4.50
Variability of vegetation height (cm)	6.202	2.32	9.375	4.71
Mean Styrofoam height (cm)	12.963	1.88	11.945	1.75
Mean litter depth (cm)	2.048	1.50	3.747	1.97
Variability of litter depth (cm)	1.883	1.38	2.586	1.49
Mean vegetation density (cm)	4.452	1.63	5.146	1.79
Grass cover (% cover)	25.014	9.46	31.350	12.26
Forb cover (% cover)	2.517	1.91	6.983	2.99
Exposed mosses and lichens (% cover)	30.520	16.19	47.277	17.24

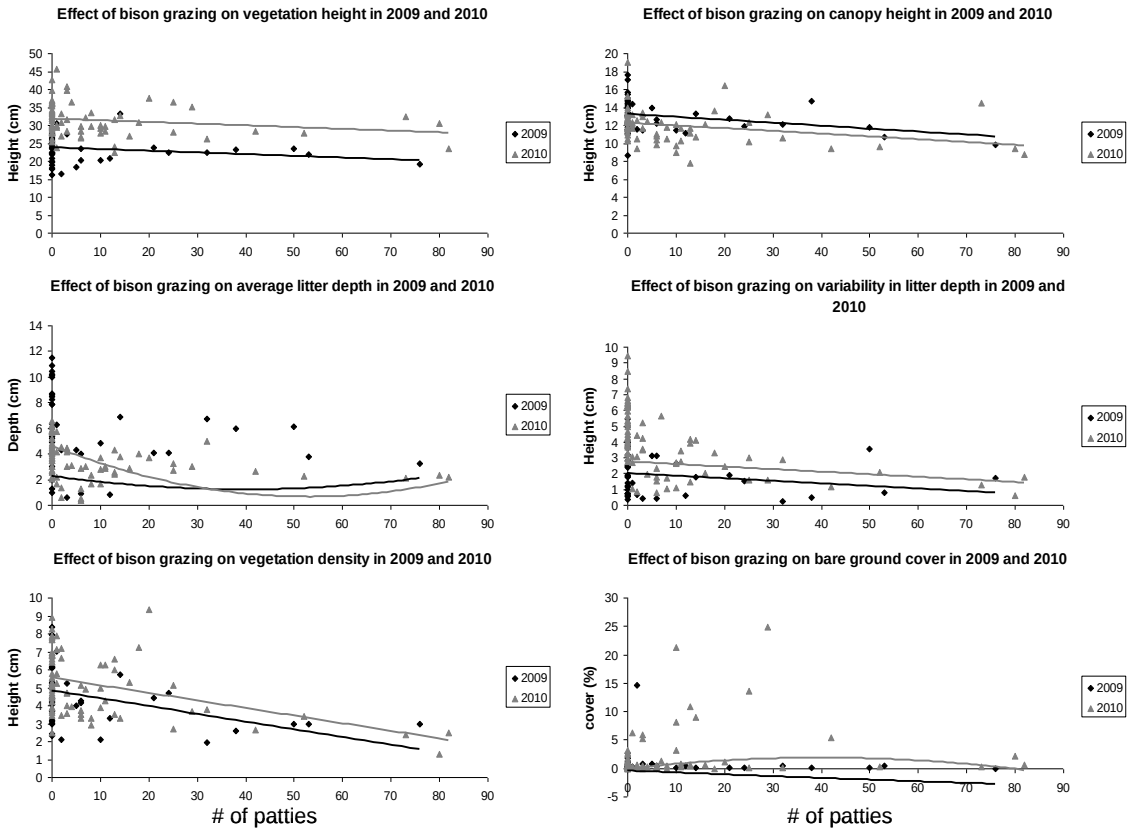


Figure 7. Effect of bison grazing intensity on vegetation height, canopy height, litter depth, variability of litter depth, vegetation density, and bare ground cover in the West Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010.

5.1.2 Songbird Abundance and Diversity

The analysis using pre-grazing data from 2004 showed that none of the songbirds had pre-existing patterns within the West Block based on the categorical grazing intensity index or on continuous grazing data from GPS collars. Analysis of the ungrazed control sites revealed that abundances of Baird's sparrow, chestnut-collared longspur, and Sprague's pipit did not change between 2009 and 2010 (Δ AIC < 2 from null), while songbird richness increased by 0.58 species per plot between 2009 and 2010 ($\beta = 0.58$, SE = 0.243, $p = 0.22$).

Chestnut-collared longspurs and horned larks did not respond to grazing duration or grazing intensity in 2009 and 2010. Baird's sparrow, grasshopper sparrow, Savannah sparrow, and Sprague's pipits all decreased in abundance with increased grazing intensity, while vesper sparrow, songbird richness, Shannon-Wiener diversity, and evenness all increased with increased grazing intensity (Table 11, Figure 8). All non-null models included year as an influential parameter, and all except Baird's sparrow and grasshopper sparrow were significantly different in the two years of the study (Tables 10, 11). Western meadowlark and total songbird abundance had year as the only significant variable in the model (Table 11), indicating that their abundances were greater in 2010 than 2009. Finally, Sprague's pipits decreased more in 2010 than 2009 with bison grazing, and evenness responded to an interaction between grazing intensity and year (the response was curvilinear). The interaction between intensity and year was an influential parameter for richness and Shannon-Wiener diversity, indicating changes in the slope of the curve in 2009 and 2010.

Table 11. Generalized-linear mixed-effects models and parameter estimates for AIC-selected models looking at songbird relative abundance and diversity per 3.2-ha plot in response to bison grazing in the West Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010.[a]

Variable	Model selected	Parameters with $p < 0.1$	β	SE	p-value
Baird's sparrow	P + Y	P	-0.016	0.005	<0.001
Chestnut-collared longspur	Null	N/A			
Grasshopper sparrow	P + Y	P	-0.007	0.004	0.080
Horned lark	Null	N/A			
Savannah sparrow	P + Y	P	-0.008	0.003	0.021
		Y	-0.253	0.094	0.055
Sprague's pipit	P + Y + i1	P	-0.014	0.004	0.002
		Y	-0.359	0.118	0.038
		i1	0.013	0.006	0.030
Vesper sparrow	P + Y	P	0.009	0.004	0.018
		Y	-0.328	0.096	0.027
Western meadowlark	Y	Y	-0.214	0.070	0.004
Richness	P + P2 + P3 + Y + i1 + i2 + i3	Y	-0.602	0.204	0.042
Shannon-Wiener diversity	P + P2 + Y + i1 + i2	P	0.017	0.006	0.008
		P2	<-0.001	<.0001	0.099
		Y	-0.189	0.061	0.036
Evenness	P + P2 + P3 + Y + i1 + i2 + i3	P3	<-0.001	0.000	<0.001
		Y	-0.027	0.009	0.036
		i1	0.005	0.002	0.062
		i2	0.000	<.0001	0.041
		i3	<-0.001	0.000	<0.001
Total abundance	Y	Y	-1.283	0.263	0.008

[a] Abbreviations: P = patties, P2 = patties*patties, P3 = patties*patties*patties, Y = year, i1 = patties*year, i2 = patties*patties*year, i3 = patties*patties*patties*year

Table 12. Mean and standard deviation of songbird relative abundances (birds/3.2-ha plot) and diversity measures per plot that varied significantly by year in the West Block of Grasslands National Park, southwestern Saskatchewan, 2009-2010.

	2009		2010	
Variable	Mean	SD	Mean	SD
Savannah sparrow	0.789	0.54	0.998	0.60
Sprague's pipit	2.219	0.65	2.486	0.78
Vesper sparrow	0.293	0.40	0.542	0.69
Western meadowlark	0.211	0.31	0.419	0.41
Richness	4.398	0.98	4.965	0.91
Shannon-Wiener diversity	2.292	0.38	2.482	0.28
Evenness	0.191	0.05	0.217	0.05
Total abundance	8.000	1.98	9.423	1.50

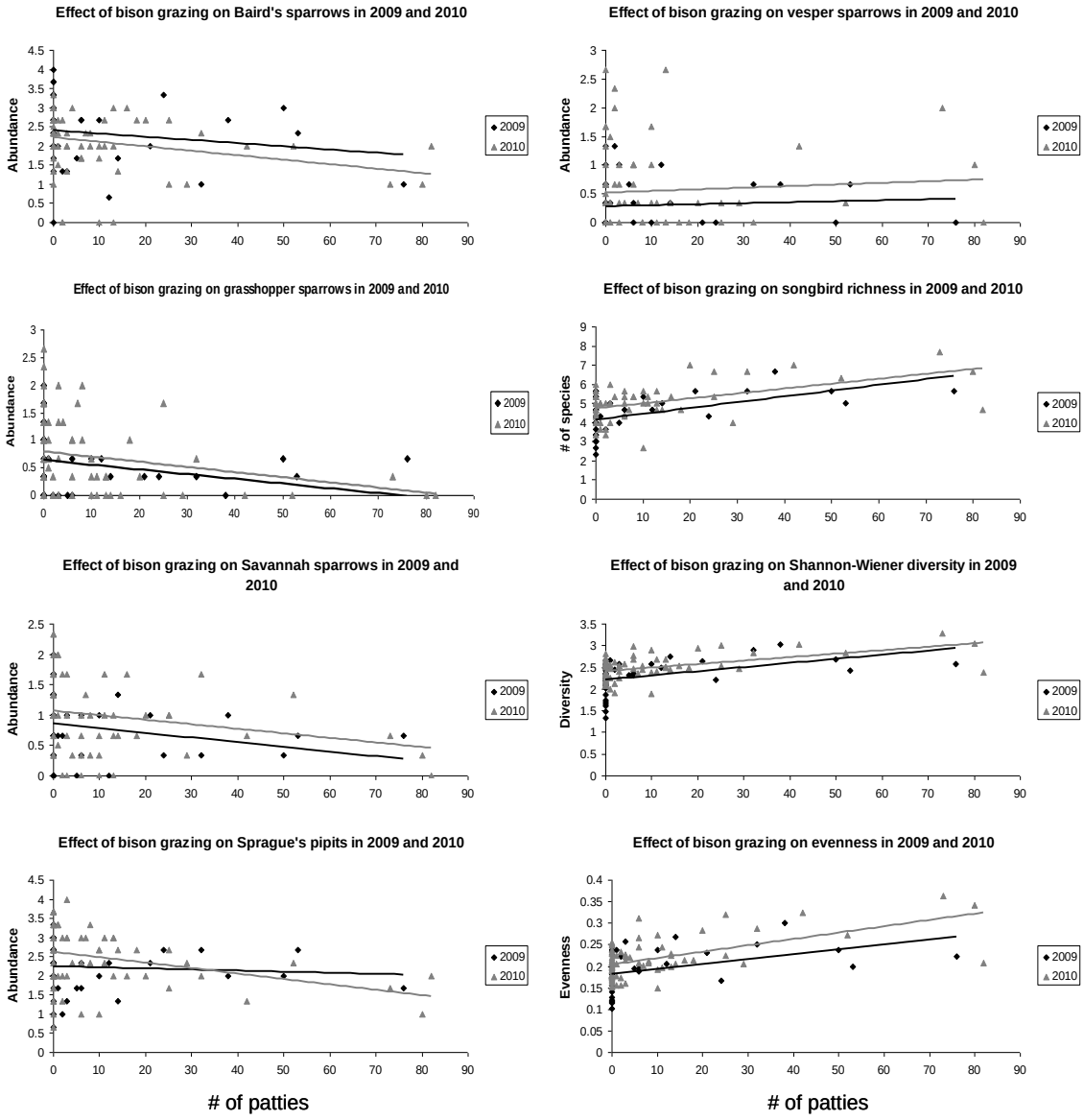


Figure 8. Effect of bison grazing on Baird's sparrow, grasshopper sparrow, Savannah sparrow, Sprague's pipit, and vesper sparrow relative abundances per 3.2-ha plot, and richness, Shannon-Wiener diversity, and evenness in the West Block of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010.

5.1.3 Songbird Community

The binary index shows a high amount of similarity between ungrazed areas and heavily grazed areas in the West Block in both years of this study (~80%, Table 13). The quantitative index shows that the two areas are less similar when species abundance is accounted for: in 2009, similarity between ungrazed areas and heavily grazed areas was 68%, and in 2010 it was 76% (Table 13). Prior to grazing reintroduction in 2004, similarity in the ungrazed and grazed areas of the park were quite alike (> 77%).

Table 13. Sorensen's binary and quantitative similarity indices for songbirds in southwestern Saskatchewan, 2009-2010, comparing ungrazed sites and sites grazed heavily by bison.

	2004	2009	2010
Binary Index	0.778	0.818	0.800
Quantitative index	0.839	0.687	0.761

5.2 DISCUSSION

Both years of grazing resulted in decreased vegetation height, canopy height, litter depth, and vegetation density as I expected (Biondini et al. 1998). Forb cover was expected to increase and grass cover was expected to decrease with increasing bison grazing (Collins 1987, Damhoureyeh and Hartnett 1997), but these varied only by year. However, from a grassland bird management perspective, this might not be important; cover of forbs and grasses are less important to grassland birds that select territories based on the structure of the habitat (Cody 1985). It is important to note that there were no pre-grazing data available for habitat structure, and that some differences detected here may have existed prior to grazing reintroduction (Underwood 1994); however, the results were consistent with predictions for the impact of grazing on habitat structure.

Baird's sparrows, grasshopper sparrows, Savannah sparrows, and Sprague's pipits decreased linearly with bison grazing, while vesper sparrows increased linearly with bison grazing. Because the pre-grazing data showed that all areas of the park were similar prior to grazing, these results indicate that bison probably had an effect on the abundances of each of these songbirds. Other authors have suggested that bison in large enclosures will have high conservation value because of their ability to behave as if they were free-roaming (Knapp et al. 1999, Boyd and Gates 2006), and the results presented here suggest that the bison within the park are having an ecologically meaningful impact on their landscape and that bison can be an effective habitat management tool for these songbird species. The interaction between grazing intensity and year for Sprague's pipits showed that bison grazing caused greater declines of Sprague's pipit abundances in 2010 than in 2009, which could have been due to a cumulative effect of bison grazing on habitat structure (Hartnett et al. 1996).

Because the bison herd is at low densities, their grazing is probably reaching only moderate intensities. Therefore, the peak in songbird richness, Shannon-Wiener diversity, and evenness at the highest level of bison grazing present in the bison paddock is consistent with theories of range models indicating that diversity will be highest at a moderate level of grazing (e.g., Milchunas et al. 1989). This is because at moderate levels of grazing, heterogeneity is increased, which provides habitat for a greater number of species (Hart et al. 1993). The interaction between year and grazing in relation to each of these variables indicates a slight change in the slope of the response curve, but does not change the interpretation.

Species richness was higher in the heavily grazed areas than in the ungrazed areas after bison were reintroduced, whereas it remained approximately the same in the ungrazed areas prior to and after grazing reintroduction. This likely indicates that bison grazing increased landscape heterogeneity of the West Block, which allowed more species to inhabit the area. This is consistent with other studies that have shown that bison increased habitat heterogeneity on a large scale (Griebel et al. 1998, Knapp et al. 1999, Lueders et al. 2006), and heterogeneous habitat can support a wider range of species (MacArthur and MacArthur 1961).

Sorensen's binary and quantitative indices show a high degree of similarity between the ungrazed regions and the grazed regions prior to bison reintroduction. The quantitative index is higher than the binary index, which shows that there were a number of species present in both sites, but that abundances varied between sites. In this case, there were single individuals of four different species observed in the ungrazed areas (Brewer's blackbird, clay-colored sparrow, grasshopper sparrow, and lark bunting). Sorensen's binary index showed that there were similar species present in the communities in the ungrazed and grazed areas of the West Block, but the lower quantitative index showed that there were differences in species abundance. The McCown's longspur, a species of conservation concern, was only observed once in the ungrazed areas of the West Block in both years of this study, while there were thirteen observations of the species in the heavily grazed areas of the West Block (data not shown). Chestnut-collared longspurs, an additional species of conservation concern, had abundances three times higher in the heavily grazed areas in both years of this study (data not shown). Baird's sparrows and Sprague's pipits had higher total abundances in the

ungrazed areas of the West Block. These indices show that the West Block supported similar species in different areas prior to grazing, but that these areas have diverged as a result of the reintroduction of bison.

Val Marie, SK, the town nearest to the West Block of Grasslands National Park, experienced rainfall three times higher in April and May of 2010, at 115 mm, than in April and May of 2009, 36 mm, while 64 mm is normal (Environment Canada 2011). Because of this, the effects of bison grazing on habitat and songbirds may have been smaller in 2010 than they might have been with normal levels of precipitation (Biondini and Manske 1996, Knopf et al. 2007). Even though there was an increase in vegetation height and litter depth from 2009 to 2010 in the ungrazed controls, I still detected a decrease in these two variables with bison grazing, which showed that bison grazing likely overcame the effects of increased precipitation.

5.3 Management Implications

The fact that the effects of bison grazing on habitat and songbirds were linear is important to consider when making management decisions, because it shows that there were not any thresholds associated with bison grazing. This is important to management because it suggests that the positive and negative ecological effects of bison grazing will increase with stocking density. Over time, there may be an accumulation of impacts of bison over different portions of the landscape, and this will be important to monitor to ensure that bison are having the desired impact on the habitat and songbirds of interest.

Bison are an alternative to cattle when grazing is used for habitat modification and may be preferred by the park because there is less need for management of the herd, fewer fencing requirements (Plumb and Dodd 1993), and bison provide teaching and

interpretive opportunities and visitor experiences that are not possible with cattle. Further, my research (see Ch. 6), as well others (Peden et al. 1974, Damhoureyeh and Hartnett 1997, Coppedge and Shaw 2000), suggest that bison and cattle may not serve identical ecological roles; therefore, selecting bison for management purposes may result in an ecosystem that better represents pre-settlement conditions. If bison are selected to restore the prairie's former natural disturbance regime, then it is important to understand how bison are affecting the landscape. Bison do appear to be changing the habitat for the benefit of certain species, such as chestnut-collared and McCown's longspurs, in the West Block of Grasslands National Park. Sprague's pipits and Baird's sparrows decline with increased bison grazing, but there are many regions of the West Block that have yet to be grazed by bison, suggesting that habitat for these species is still abundant. Ongoing assessment of the impact of bison on the prairie landscape is important to understanding how their continued presence changes the landscape (Hartnett et al. 1996), and whether the herd will require management via fencing or water supplements for further benefit to the grassland community. If the bison herd in the West Block is indeed acting as a free-roaming herd, there will likely be no need for further management, such as moving the bison from one area of the park to another. However, if natural growth of the bison population is allowed to occur, culling might be required at some point in the future to prevent degradation of the vegetation.

6.0 ARE IMPACTS ON MIXED-GRASS PRAIRIE SONGBIRDS AND HABITAT DIFFERENT BETWEEN BISON GRAZING AND CATTLE GRAZING?

6.1 ABSTRACT

Grassland songbirds are experiencing population declines due to both habitat loss and changes in disturbance regimes resulting from the exchange of free-roaming bison for cattle ranching. Behavioral, physiological, and management differences between bison and cattle may lead to differing effects on the mixed-grass prairie habitat structure and songbird community. I compared an effectively free-roaming bison herd with cattle stocked at a range of grazing intensities consistent with typical ranching practices. I conducted habitat structure and songbird surveys in 2009 (n = 95) and 2010 (n = 125) in 100-m radius upland plots. Data were analyzed using Generalized Linear Mixed Models with site as a random effect to account for spatial clustering of plots. Information theory was used to determine which of a set of eleven models best explained the response of habitat structure and songbirds to bison and cattle grazing. Bison caused a greater decrease in litter depth and vegetation density than did cattle, indicating that these two species did affect habitat structure differently. Further, Baird's sparrows and Sprague's pipits decreased more with bison grazing than cattle grazing, while chestnut-collared longspurs increased more with bison grazing, results that are consistent with the hypothesis that bison might have a greater impact on prairies than cattle. Both of these grazer species are capable of altering habitat structure for the benefit of certain songbird species. Selecting which grazer is appropriate for management purposes will require consideration of the different economic, ecological, and societal benefits that come with

both of these species, and which bird species are of greatest conservation concern in a region.

6.2 INTRODUCTION

Prior to European settlement, bison roamed the prairies in large herds and created a complex landscape mosaic ranging from ungrazed to heavily and frequently grazed patches (Brennan and Kuvlesky 2005, Askins et al. 2007). Today, only 24% of native mixed-grass prairie remains in Saskatchewan, Canada (Askins et al. 2007), and most of this remaining native prairie is grazed by non-native livestock for commercial purposes on privately and publicly owned ranchland (Fuhlendorf et al. 2010). Some researchers have stated that bison and cattle are ecologically interchangeable (Plumb and Dodd 1993, Derner et al. 2009), while others have stated that the differences between bison and cattle may make substituting cattle for bison ecologically detrimental (Hartnett et al. 1997, Towne et al. 2005, Fuhlendorf et al. 2010). These differences stem from divergent evolutionary histories that have resulted in a number of physiological and behavioral differences (Hartnett et al. 1997, Towne et al. 2005, Fuhlendorf et al. 2010). Further, bison herds tend to be managed on large landscapes typically for conservation purposes, while cattle herds are managed for production purposes. These management strategies are likely to result in further differences in the ecological effects of bison and cattle. The purpose of this study was to determine if bison and cattle affected habitat and songbirds similarly or differently, and to make recommendations as to which species may be more relevant for conservation purposes in mixed-grass prairies.

One behavioral difference between bison and cattle that may cause divergent impacts on habitat and songbirds is wallowing, a behavior exhibited by bison and not by

cattle (Coppedge and Shaw 2000). Wallowing can increase patch diversity and change the structure of a site (Polley and Collins 1984). Another difference is that cattle exhibit greater selectivity at the individual plant level, while bison exhibit greater selectivity at the landscape scale (Peden et al. 1974, Schwartz and Ellis 1981). Variable selection pressures on different plant species due to these differences in preference (Peden et al. 1974, Damhoureyeh and Hartnett 1997) can be a mechanism resulting in divergent habitat structure, because of the competitive advantage to ungrazed species (Ellis et al. 1976, Anderson and Briske 1995). Physiologically, bison and cattle also have different digestive capabilities that may result in greater forage intake by bison (Peden et al. 1974, Schaefer et al. 1978), and the structure of the jawbone of bison is such that they can graze closer to the ground than cattle (Hartnett et al. 1997). Cumulatively, these differences between bison and cattle may result in different effects on the habitat structure at either a local or landscape level, which may translate into different effects on songbirds.

Strategies typically used to manage bison and cattle are also different and may result in different effects on habitat and songbirds. Bison in conservation herds are effectively free-roaming, with the ability to choose grazing sites within large home ranges (Bailey et al. 1996, K. Ellison, personal communication), while cattle are strictly managed with cross fencing, water and feed supplements to encourage grazing uniformly in their pastures (Bailey et al. 1996). This periodic and highly selective grazing of sites by bison results in less uniform habitat structure across the landscape than that caused by annual grazing of smaller pastures by cattle (Askins et al. 2007).

It is exceedingly difficult to design a robust study for understanding ecological differences between bison and cattle (Fuhlendorf et al. 2010) for at least two reasons: (1)

there are only fourteen conservation bison herds in existence in the northern mixed-grass prairie, a small number of which inhabit landscapes larger than 15,000 ha (Boyd and Gates 2006, Gates et al. 2010); (2) finding a suitable study site with a bison herd near a ranching operation of a size applicable to landscape-scale questions is difficult, but comparing bison and cattle in wholly different landscapes provides little useful information (Fuhlendorf et al. 2010). Because of these difficulties, there is little information available that compares bison and cattle effects on songbirds and habitat structure in the literature. In response to these literature gaps, I designed a study that compared a conservation herd of bison that is effectively free-roaming with a nearby large-scale cattle grazing experiment that mimics typical cattle ranching operations in southwestern Saskatchewan. This study compared the impacts of bison and cattle on vegetation and songbirds when the evolutionarily relevant management strategies are used for both bison and cattle, instead of attempting to account for differences in evolution by managing both for production. My objectives were to determine whether bison and cattle affect habitat and songbirds differently in the mixed-grass prairies, and how each grazer may be useful in the conservation of threatened prairie species.

6.3 METHODS

6.3.1 Study site

This study was conducted in the East and West Blocks of Grasslands National Park in southwestern Saskatchewan, Canada. The park consists of native northern mixed-grass prairie with rolling hills in the East Block and uplands with rolling hills and steep coulees in the West Block (Coupland 1950, Parks Canada 2006). The soils are made of mostly glacial and postglacial deposits, and the prairie is predominantly a *Stipa*-

Bouteloua community (Coupland 1950). The upland grasslands are dominated by grasses such as *Stipa comata*, *Elymus lanceolatus*, *Bouteloua gracilis*, *Koeleria macrantha*, *Pascopyrum smithii*, and forbs such as *Artimesia frigida*, *Phlox hoodii*, *Sphaeralcea coccinea*, and *Selaginella densa* is the prevalent spikemoss (Coupland 1950, Parks Canada 2006).

A large-scale grazing experiment reintroduced cattle into the East Block of the park in May 2008, where grazing had been excluded for at least 15 years. In 2008, 9 pastures were created including six pastures for cattle and three pastures as ungrazed controls; each pasture was ~300 ha and had similar amounts of upland, lowland, and riparian areas (Parks Canada 2006, Koper et al. 2008). The grazed pastures in the Park had a range of grazing intensities varying from below normal for the area (0.23 AUM/ha, predicted to remove about 20% of the above-ground biomass annually; Abouguendia 1990) to very high for the area (0.83 AUM/ha, predicted to remove about 70% of the above-ground biomass annually; Abouguendia 1990, Koper et al. 2008). There were 36 grazed plots and 17 ungrazed control plots (n = 53) in the East Block.

The West Block, 50 km west of the East Block, contains an approximately 18,500-ha fenced paddock that is home to over 150 effectively free-roaming bison, which were reintroduced to the park in 2006 (Parks Canada 2004, 2009). Plots were chosen in the uplands of the West Block to represent a variety of grazing pressures from none to low to high. The West Block consisted of 27 grazed plots and 17 ungrazed control plots (n = 44) in 2009, and 42 grazed plots and 30 ungrazed plots (n = 72) in 2010.

6.3.2 Field methods

Three rounds of point counts were conducted in 2009 and 2010 between mid-May and 30 June. All plot centers were located at least 250 m apart so that birds were not recorded twice at separate plots. The point counts were five minutes each and all birds detected by either sight or sound within a 100-m radius (3.2 ha) were recorded; protocols followed were adapted from Hutto et al. (1986). All point counts were conducted between sunrise and 1000 hours and each plot was surveyed by at least 2 different observers in all years to minimize effects of observer bias. No surveys were conducted on days with excessive wind (>15km/h) or rain, which lessen detectability. At each plot in both blocks, fecal patties were counted along a 200-m × 4-m transect to provide an index of grazing intensity. Bison grazing reached only moderate intensities compared to cattle grazing: the maximum number of bison patties counted was only 50% of the maximum number of cattle patties counted. Additionally, one round of avian point count surveys was conducted in a similar manner in the West Block in 2004, two years prior to bison reintroduction and in the East Block in 2006, two years prior to cattle reintroduction.

Unadjusted point counts were averaged over the two rounds as a measure of relative abundance (Koper and Schmiegelow 2006, Johnson 2008). Unadjusted point counts were used because distance sampling assumptions are difficult to meet in the field, and detectability of mixed-grass prairie birds is relatively high (Lueders et al. 2006, Efford and Dawson 2009). Bird diversity (richness, Shannon-Wiener diversity, and evenness) and total abundance was calculated for each plot for songbirds. The Shannon-Wiener diversity index was chosen because it is sensitive to rare species (Wiens 1989), which are of management concern. Only songbird species occurring in each year in 10%

or greater of plots were analyzed individually. McCown's longspur, a species of conservation concern, did not meet this requirement; however, a qualitative assessment was made concerning their occurrence.

At each plot I surveyed the habitat structure once each in May and July of 2009 and 2010. Each survey included eight 1.0-m × 0.5-m sampling frames at 50 m and 100 m from the center of the plot in the four cardinal directions. At each frame, measurements included vegetation density (using the Robel pole visual obstruction method, Robel et al. 1970), tallest vegetation (hereafter called vegetation height), canopy height, litter depth, and visual percent cover estimates of litter, bare ground, grass, forbs, and mosses/lichens. All variables were averaged for each plot, and the standard deviations of vegetation height, canopy height, density, and litter depth were calculated as a measure of plot-scale heterogeneity.

6.3.3 Statistical methods

Bison grazing was compared to cattle grazing in 2009 and 2010 using Generalized Linear Mixed-effects Models (GLMMs) in SAS Statistical Software (SAS Institute 2008) with fecal patty counts as an index of grazing intensity. Bison patties and cattle patties were considered as equal evidence of grazing (i.e. 10 bison patties = 10 cattle patties) because observational studies have shown that bison and cattle defecate at approximately equal rates per day (Wagnon 1963, Belovsky and Slade 1986). Site was the only random effect included in the models because preliminary analyses demonstrated that it accounted for the spatial clustering of plots in the two study areas, while adding plot as a random effect explained little additional variation and often caused the models to fail to

converge. A preliminary analysis was conducted using generalized linear models were used to determine the distribution of the error term prior to analyses.

Dependent variables analyzed individually included thirteen habitat structure variables (including means and standard deviations [as a measure of variability]), and relative abundances of eight songbird species. Ten candidate models (Appendix 3) were compared to determine the response of the dependent variables to combinations three independent variables: patties (hereafter called grazing intensity), grazer species, and year. Songbirds were analyzed using grazing intensity instead of habitat structure variables because I wanted to make a link between grazing and songbird responses. Year was included in the models to account for differences that may have occurred between 2009 and 2010 due to climate or other interannual variation. An interaction between grazer species and grazing intensity was included to determine if birds responded differently to grazing by cattle and bison. Polynomial models were used to allow the effect of grazing intensity to be curvilinear (Koper et al. 2008). Polynomials can be useful because they allow detection of curvilinear patterns (Koper et al. 2008), but they also can result in spurious patterns being detected in the data. Because bison were reintroduced in 2006, while cattle were introduced in 2008, the cumulative effects of grazing resulting from different years of reintroduction was an important potential limitation of this study; therefore, the need for a three-term interaction between grazer, intensity, and year was explored prior to the final analyses. This three-term interaction was subsequently removed from the analysis, except for vesper sparrow, Shannon-Wiener diversity, and total abundance, because it did not change the interpretation of the results for other dependent variables and added unnecessary complexity to the models. Parameters

included in the selected models were considered influential when their confidence intervals did not include 0 (Koper and Schmiegelow 2006).

Models were compared using Akaike's Information Criterion (AIC); because AIC has a tendency to favor more complex models (Quinn and Keough 2002), the null model was chosen when Δ AIC ≤ 2 from the null model. An analysis using 2006 point count data from the cattle paddocks and 2004 data from the bison paddocks was conducted to ensure that no pre-existing patterns were present in the songbird data two years prior to the introduction of each grazer. 2008 habitat structure data from the cattle paddocks was analyzed to ensure that there were no pre-existing patterns as well, but no such data were available for the bison paddocks.

6.4 RESULTS

6.4.1 Habitat structure

Analysis of the habitat data from 2008 from the cattle paddocks showed that there were no pre-existing patterns prior to reintroduction of grazers. Forbs, exposed moss and lichen, and bare ground were slightly lower in 2009 than 2010, and litter cover had 11% greater cover in 2009 than 2010 (Tables 13, 14).

All habitat variables with grazing intensity included in the selected model decreased with increasing grazing intensity, except for grass cover, which had a curvilinear relationship with intensity (Figure 9). Vegetation height decreased by ~10 cm in the cattle paddocks in both years from ungrazed to heavily grazed sites, while height decreased by ~3 cm in the bison paddock in both years from ungrazed to moderately grazed sites. Variability of vegetation height and litter depth had similar results. Mean litter depth decreased more with bison grazing than cattle grazing in both years,

decreasing on average 3.36 cm with moderate bison grazing, and 2.71 cm with heavy cattle grazing (Figure 9a). Similarly, mean vegetation density decreased more with bison grazing than with cattle grazing in both years (Figure 9b).

Mean vegetation height, variability of vegetation height, and variability of litter depth were slightly lower on average in the bison paddock (Table 16).

Table 14. Generalized-linear mixed-effects models and parameter estimates for AIC-selected models for habitat structure variables in the bison paddocks and cattle paddocks of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010.[a]

Variable	Model selected	Confidence Intervals that did not include 0	β	SE	*p*-value
Mean vegetation height	I + G + Y	I	-0.052	0.017	0.002
		G	-7.721	1.030	<0.001
		Y	-7.353	0.815	<0.001
Variability of vegetation height	I + G + Y	I	0.003	0.000	<0.001
		G	-2.087	0.545	0.002
		Y	2.579	0.508	<0.001
Mean canopy height	I	I	-0.025	0.006	<0.001
Variability of canopy height	Null	Null			
Mean litter depth	I + G + Y + I*G	Y	-1.775	0.201	<0.001
		I*G	-0.025	0.011	0.034
Variability of litter depth	I + G + Y	I	-0.017	0.000	<0.001
		G	-0.484	0.228	0.050
		Y	0.501	0.183	0.007
Mean vegetation density	I + G + Y + I*G	I*G	-0.039	0.015	0.009
Variability vegetation density	Null	Null			
Grass cover	I + I2 + I3 + G + Y + I*G + I*I*G + I*I*I*G	I	0.831	0.280	0.003
		I2	-0.013	0.005	0.016
		I3	<0.001	0.000	<0.001
		Y	-5.094	1.636	0.009
		I*G	-1.252	0.462	0.007
		I*I*G	0.026	0.015	0.096
		I*I*I*G	<-0.001	0.000	<0.001
Forb cover	Y	Y	-0.552	0.073	<0.001
Exposed mosses and lichens	Y	Y	-5.215	2.075	0.029
Bare ground cover	Y	Y	-0.544	0.233	0.039
Litter cover	Y	Y	9.042	2.246	0.002

[a] Abbreviations: I = patties, I2 = patties*patties, I3 = patties*patties*patties, G = grazer (bison and cattle), Y = year, I*G = patties*grazer, I*I*G = patties*patties*grazer, I*I*I*G = patties*patties*patties*grazer

Table 15. Mean and standard deviation (as a measure of heterogeneity) of habitat structure variables per plot that varied significantly by year in all plots of the East and West Blocks of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010. Mean vegetation height was the average of tallest vegetation measured within eight frames at each plot. Mean canopy height was the measure of average vegetation height within eight frames at each plot.

	2009		2010	
Variable	Mean	SD	Mean	SD
Mean vegetation height (cm)	27.333	7.594	34.197	6.524
Variability of vegetation height (cm)	7.813	3.313	10.066	4.15
Mean litter depth (cm)	5.743	2.791	3.586	1.846
Variability of litter depth (cm)	2.726	1.438	2.383	1.319
Grass cover (% cover)	27.187	10.098	32.636	13.117
Forb cover (% cover)	3.435	2.54	6.286	3.02
Exposed mosses and lichens (% cover)	33.899	15.35	40.316	18.25
Bare ground cover (% cover)	0.896	2.33	1.935	3.82
Litter cover (% cover)	39.752	16.86	28.929	16.16

Table 16. Mean and standard deviation of habitat structure variables per plot that significantly between the bison paddock and cattle paddocks in both grazed and ungrazed plots in the East and West Blocks of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010.

	Bison		Cattle	
Variable	Mean	SD	Mean	SD
Mean vegetation height (cm)	28.463	5.833	34.223	8.476
Variability of vegetation height (cm)	8.224	4.282	10.031	3.375
Variability of litter depth (cm)	2.537	1.369	2.523	1.396

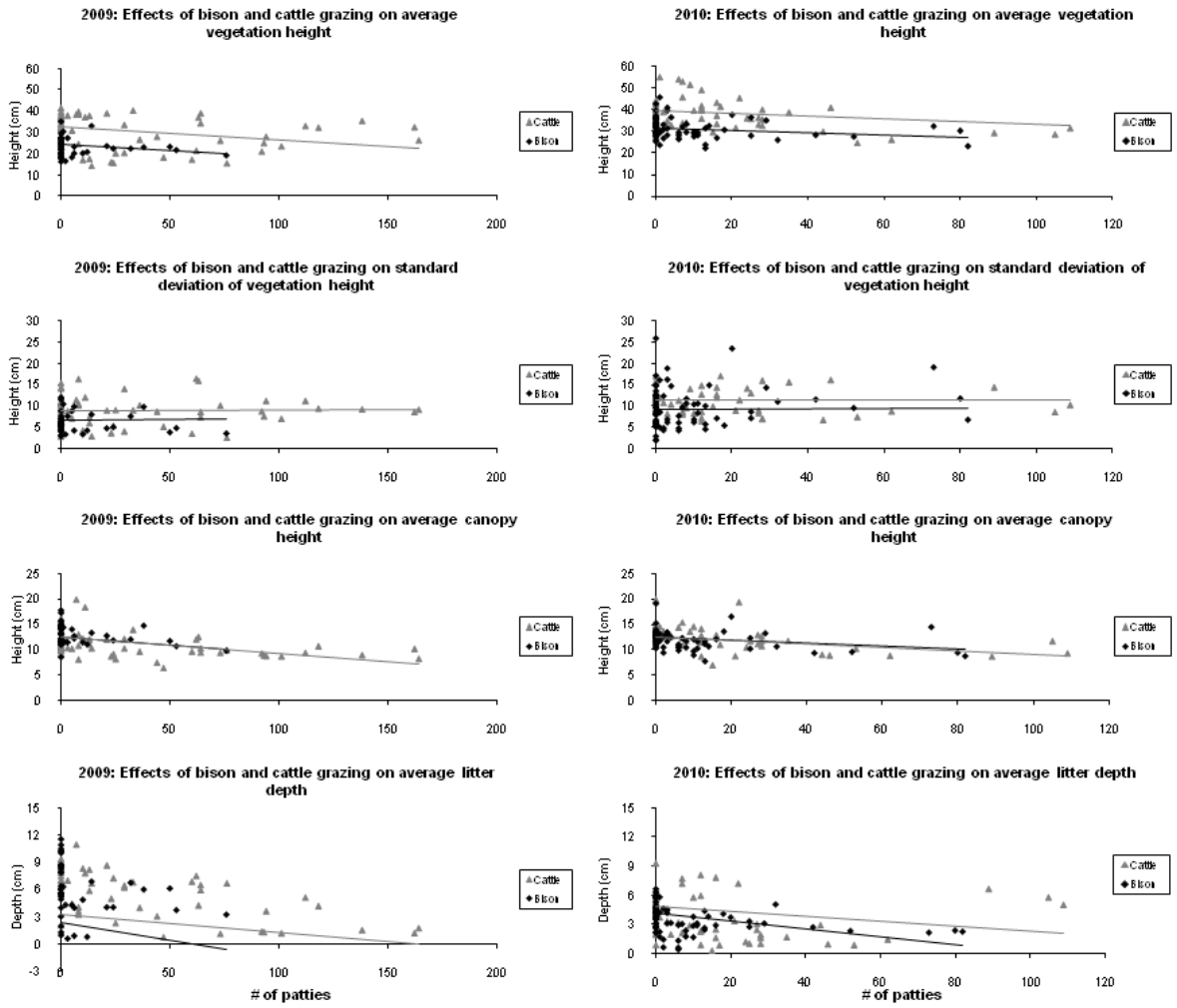


Figure 9a. Effects of bison and cattle grazing on vegetation height, variability of vegetation height, canopy height, and litter depth in the East and West Blocks of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010. Graphs are split into years (2009 and 2010), and each shows the actual data and the predicted response curve for bison grazing (black line) and cattle grazing (grey line) as measured using patty counts.

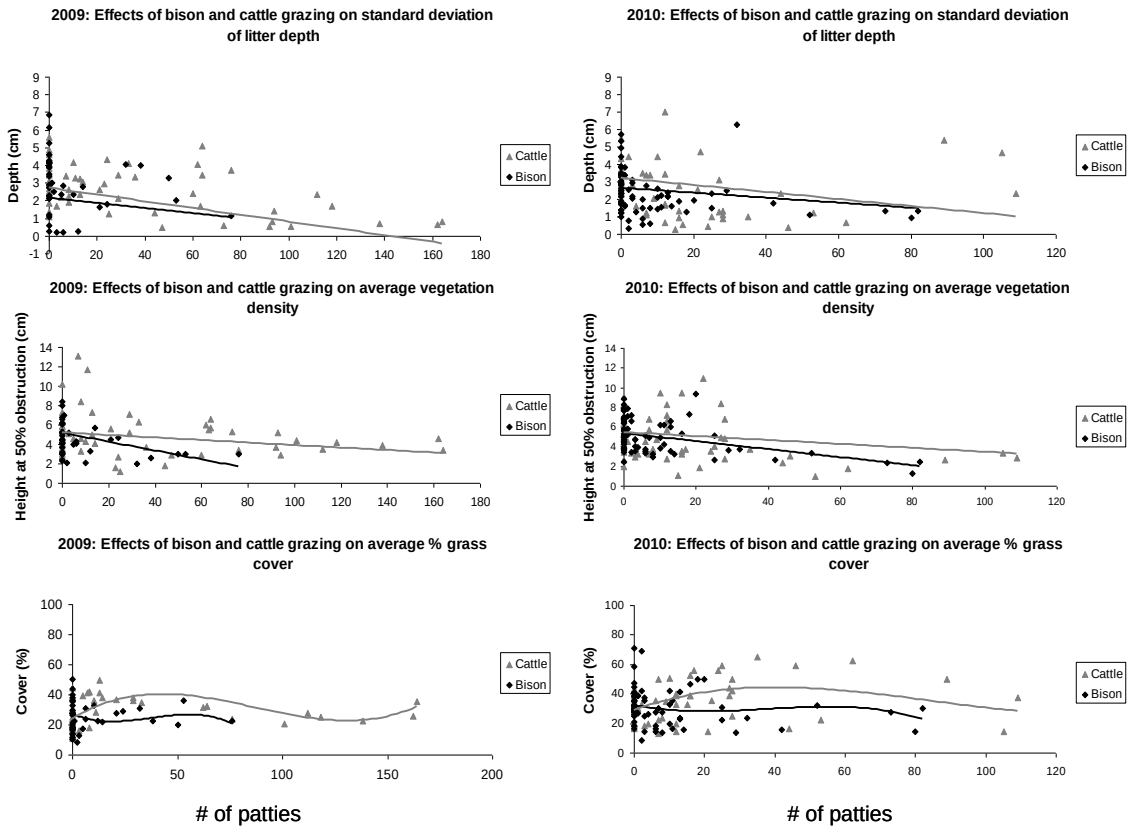


Figure 9b. Effects of bison and cattle grazing on variability of litter depth, variability of vegetation density, and percent grass cover in the East and West Blocks of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010. Graphs are split into years (2009 and 2010), and each shows the actual data and the predicted response curve for bison grazing (black line) and cattle grazing (grey line) as measured using patty counts.

6.4.2 Songbird Abundance and Diversity

Analysis of songbird abundance and diversity from 2006 data from the cattle paddocks showed that there were no pre-existing patterns in the distribution of abundance and diversity in relation to grazing intensity. Similarly, 2004 data from the bison paddock showed no pre-existing patterns in relation to grazing intensity; therefore, I am confident that the results are due to grazing by bison and cattle.

Each of the songbirds and avian community measures responded to at least one of the independent variables in 2009 and 2010. All dependent variables that varied by year increased in the second year of the study (Table 18). Baird's sparrow abundance increased on average 0.31 birds per plot, while Sprague's pipit abundance increased 0.5 birds per plot. Species richness increased by 1 additional species per plot from 2009 to 2010.

Chestnut-collared longspurs increased from ~0 birds to ~2 birds per plot in the cattle paddocks in both years, and from ~0.5 birds to ~3.25 birds per plot in the bison paddocks in both years. Although it appears that bison caused a greater increase in abundance of chestnut-collared longspurs than cattle did (Figure 10a), the interaction term was not included in the AIC-selected model, indicating that bison and cattle affected the species similarly.

Baird's sparrow decreased an average of 0.5 bird per plot more with bison grazing than with cattle grazing, even with the presumably lower grazing intensity of bison (maximum 82 patties in bison paddock versus maximum 164 patties in the cattle paddocks; Figure 10a). Sprague's pipit also declined more steeply with bison grazing than with cattle grazing (Figure 10a).

The model selected for vesper sparrow included the three-term interaction, and showed that abundance decreased with grazing intensity in 2009, but increased with grazing intensity in 2010. Vesper sparrows only increased with grazing intensity in the second year and their response to grazing did not differ between bison and cattle (Figure 10a). Horned lark had twice the relative abundance in the bison paddocks, but did not respond to grazing intensity (Table 19). McCown's longspur was observed most frequently in the heavily grazed areas in both the bison and cattle paddocks, although their sample size was too low to statistically analyze.

All of the songbird diversity measures increased with increased grazing intensity, and increased more with bison grazing than cattle grazing (Figure 10b). Richness and Shannon-Wiener diversity had a curvilinear response to grazing intensity, in which richness peaked at approximately 60 patties, or a moderate grazing intensity. The selected model describing effects of grazing on total abundance included the three-term interaction between grazing intensity, grazer species, and year, in which the direction of the response to grazing intensity was opposite between years (Table 17). Finally, Shannon-Wiener diversity also included the three-term interaction, but the Figure suggests little difference between years.

Table 17. Generalized-linear mixed-effects models and parameter estimates for AIC-selected models for relative songbird abundance and diversity measures in the bison paddock and cattle paddocks in the East and West Blocks of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010.[a]

Variable	Model selected	Confidence intervals that did not include 0	β	SE	*p*-value
Baird's sparrow	I + G + Y + I*G	Y	-0.299	0.096	0.008
		I*G	-0.014	0.006	0.015
Chestnut-collared longspur	I + G + Y	Y	-0.324	0.090	0.003
Grasshopper sparrow	Y	Y	-0.223	0.064	0.004
Horned lark	G	G	0.397	0.155	0.021
Savannah sparrow	Y	Y	-0.323	0.066	<0.001
Sprague's pipit	I + G + Y + I*G	Y	-0.459	0.076	<0.001
		I*G	-0.009	0.005	0.051
Vesper sparrow	I + G + Y + I*G + B	I	-14.487	4.721	0.003
		Y	0.218	0.066	0.001
		B	0.004	0.000	<0.001
Western meadowlark	Y	Y	0.264	0.048	<0.001
Richness	I + I2 + G + Y + I*G + I*I*G	I	0.000	0.000	<0.001
		I2	<-0.001	0.000	<0.001
		G	-0.551	0.179	0.007
		Y	1.027	0.115	<0.001
		I*G	0.059	0.000	<0.001
		I*I*G	-0.001	0.000	<0.001
Shannon-Wiener diversity	I + I2 + G + Y + I*G + B	G	-0.182	0.065	0.013
		Y	0.244	0.048	<0.001
		I*G	39.452	17.686	0.027
		B	-0.014	0.000	<0.001
Evenness	I + G + Y + I*G	I	<0.001	0.000	<0.001
		G	-0.016	0.008	0.079
		Y	0.035	0.005	<0.001
		I*G	0.001	0.000	<0.001
Total abundance	I + G + Y + I*G + B	I	-27.313	16.081	0.091
		Y	2.574	0.225	<0.001
		I*G	106.530	31.428	<0.001
		B	-0.039	0.000	<0.001

[a] Abbreviations: I = patties, I2 = patties*patties, G = grazer species, Y = year, I*G = patties*grazer, I*I*G = patties*patties*grazer, B = patties*grazer*year

Table 18. Mean and standard deviation of relative songbird abundances (birds/3.2-ha plot) and songbird diversity measures per plot that varied significantly by year in the East and West Blocks of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010.

	2009		2010	
Variable	Mean	SD	Mean	SD
Baird's sparrow	1.939	0.862	2.245	0.752
Chestnut-collared longspur	1.067	1.007	1.412	1.147
Grasshopper sparrow	0.422	0.46	0.639	0.62
Savannah sparrow	0.681	0.49	0.991	0.61
Sprague's pipit	1.938	0.661	2.443	0.727
Vesper sparrow	0.174	0.319	0.493	0.585
Western meadowlark	0.188	0.279	0.452	0.410
Richness	4.200	0.833	5.217	0.965
Shannon-Wiener diversity	2.306	0.327	2.544	0.285
Evenness	0.189	0.040	0.223	0.045
Total abundance	7.261	1.80	9.820	1.45

Table 19. Mean and standard deviation of relative songbird abundances (birds/3.2-ha plot) and songbird diversity measures per plot that varied significantly by grazer species in the East and West Blocks of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010.

	Bison		Cattle	
Variable	Mean	SD	Mean	SD
Horned lark	0.683	0.58	0.365	0.43
Richness	4.759	0.971	4.803	1.113
Shannon-Wiener diversity	2.413	0.331	2.473	0.318
Evenness	0.208	0.05	0.209	0.05

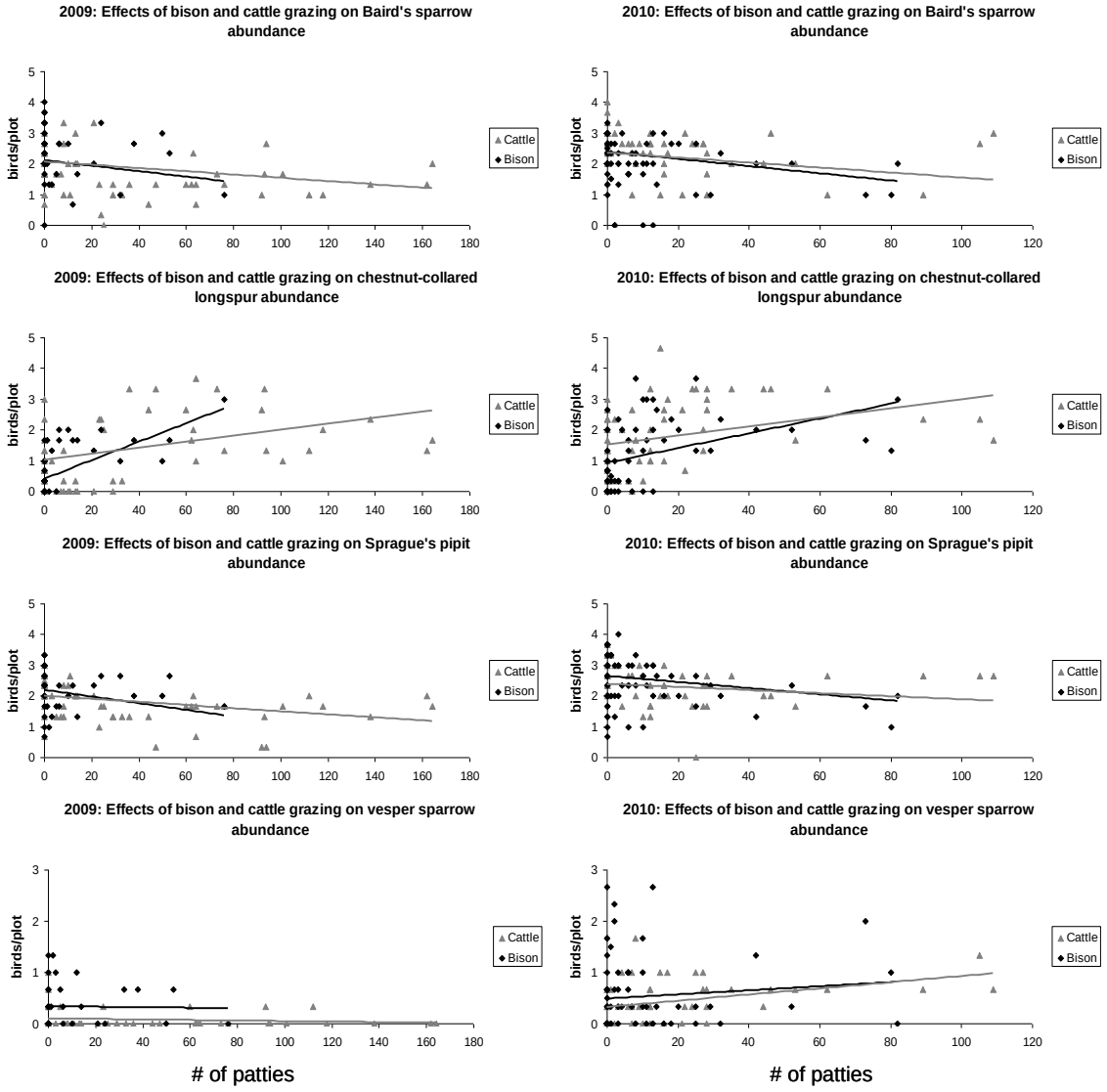


Figure 10a. Effects of bison and cattle grazing on Baird's sparrow, chestnut-collared longspur, Sprague's pipit, and vesper sparrow relative abundances per 3.2-ha plot in the East and West Blocks of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010. Graphs are split into years (2009 and 2010), and each shows the actual data and the predicted response curve for bison grazing and cattle grazing as measured using patty counts.

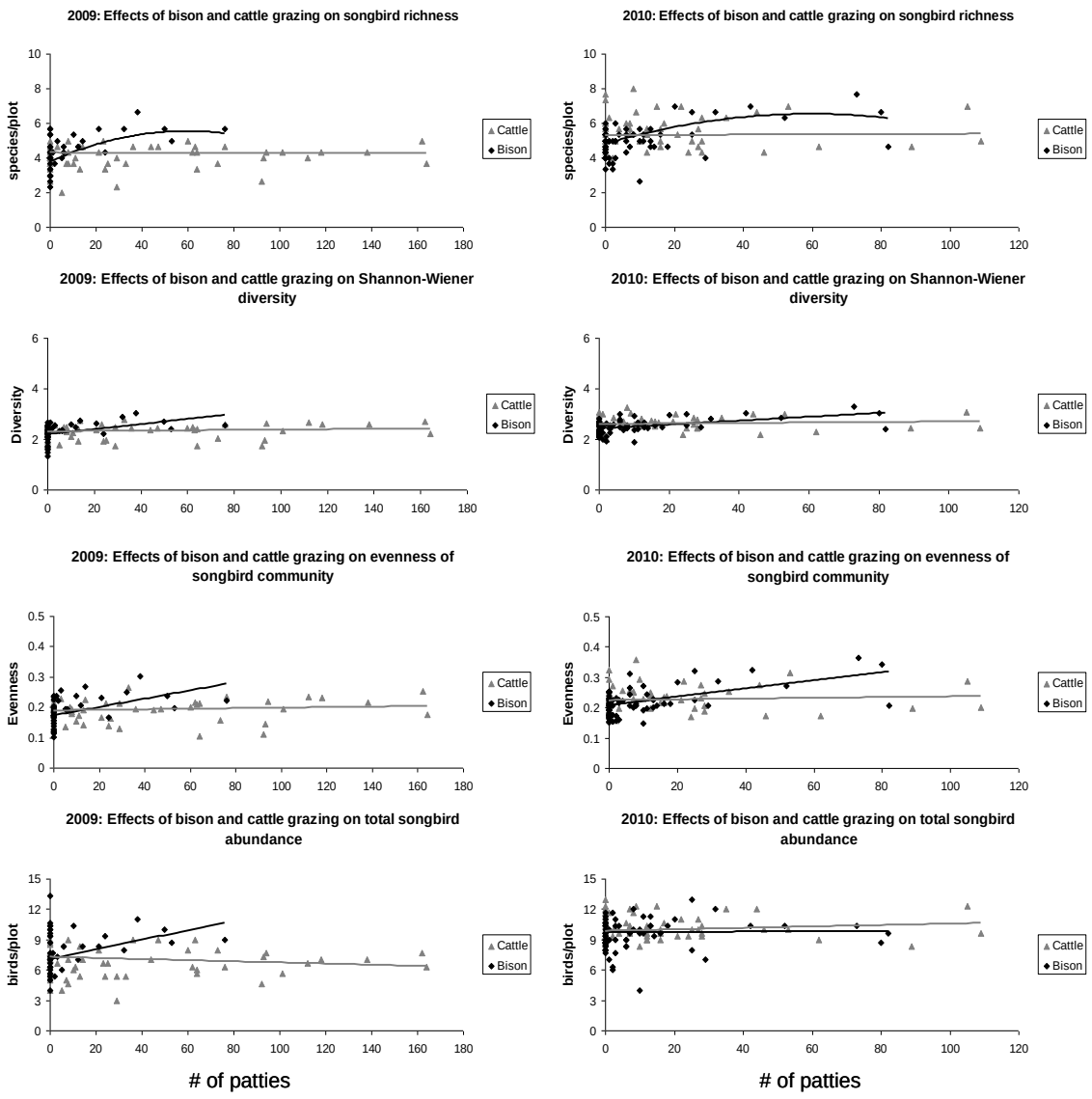


Figure 10b. Effects of bison and cattle grazing on songbird richness, Shannon-Wiener diversity, evenness, and total abundance per 3.2-ha plot in the East and West Blocks of Grasslands National Park, southwestern Saskatchewan, Canada, 2009-2010. Graphs are split into years (2009 and 2010), and each shows the actual data and the predicted response curve for bison grazing and cattle grazing as measured using patty counts.

6.5 DISCUSSION

I detected a number of differences in the effects of bison and cattle on habitat structure, suggesting that there are ecologically relevant differences between these two species. Litter depth and vegetation density declined more steeply with bison grazing than with cattle grazing, which is consistent with the fact that bison can graze closer to the ground (Hartnett et al. 1997). Even though some of the measurements in the ungrazed areas were lower in the bison paddock than the cattle paddock, the inclusion of a significant interaction between bison and cattle in the selected model indicates that the rate of decrease was still greater with bison grazing. Grass cover also decreased more with bison grazing than with cattle grazing, which is consistent with the findings of Collins and Barber (1985) and Collins (1987) that bison selected more strongly for grasses than did cattle. Although bison were reintroduced two years prior to cattle, which might have allowed for some effects of grazing to accumulate, the introduced herd was only 71 animals on 18,500 ha. It is reasonable to assume that the impacts of such a small bison herd were minimal in the first two years of grazing, and that comparing years 3 and 4 of bison grazing, when the herd had doubled, with years 1 and 2 of cattle grazing is ecologically meaningful. Litter depth, vegetation density, and grass cover are habitat structure components that strongly influence habitat selection by grassland birds (Wiens 1974, Lueders et al. 2006), and the different effects of bison and cattle grazing on these structure variables were likely some of the mechanisms that drove songbird responses to bison and cattle grazing.

Both Baird's sparrows and Sprague's pipits were more strongly impacted by bison than cattle grazing, presumably because bison had a stronger influence on some of

the habitat structure variables. Although the lowest abundances of these two species were similar in the bison and cattle paddocks, grazing reached a much higher intensity in the cattle paddocks due to their high stocking density (164 patties in cattle paddocks, versus 82 patties in bison paddock). Further, because each 3.2-ha plot only holds between 2 and 4 territories of most songbird species, the effect of both bison and cattle grazing is quite large, suggesting a decrease in population density of these species of as much as 25%. If the bison herd is allowed to grow naturally, then the herd's influence on both Baird's sparrows and Sprague's pipits will likely become more pronounced, resulting in abundances lower than I recorded in this study at either bison or cattle paddocks.

I am not aware of other bison and cattle comparison studies that compared effects of grazing intensity of each grazer species; other studies were restricted to comparing abundances relative to the presence or absence of bison and cattle (i.e. Griebel et al. 1998, Lueders et al. 2006), which makes it difficult to place my results in the context of the literature. However, there were some notable differences in songbird abundance between my study and some others. Sprague's pipits and chestnut-collared longspurs were not detected at all on bison plots in one study (Lueders et al. 2006), while in mine they were detected at both sites. In this study, a non-native grass (*Agropyron cristatum*) was common on the study site, and the stocking rate was much higher in the bison paddocks (Lueders et al. 2006), which may be why no Sprague's pipits or chestnut-collared longspurs were detected there. My finding that horned larks were more abundant on the bison grazed areas is consistent with at least one study (Griebel et al. 1998), but contradicts another (Lueders et al. 2006). The above contradictions among studies may be

due to varying sampling effort, quality of the prairies, regional variability, or other environmental conditions.

Habitat heterogeneity is an important factor that influences habitat selection of some bird species in mixed-grass prairies (Wiens 1974, Patterson and Best 1996). Habitat heterogeneity increases the number of microhabitats available on the landscape, and thus can make a given grassland suitable for supporting a large number of species (Fuhlendorf et al. 2006), making heterogeneity an important management goal. Lueders and colleagues (2006) found that habitat heterogeneity was greater in bison plots than it was in cattle plots, which was consistent with other studies (Knopf 1996, Askins et al. 2007). In contrast, my results suggest that heterogeneity was generally the same in the bison and cattle paddocks. Griebel and colleagues (1998) also found no difference in habitat heterogeneity between bison and cattle plots. Although I predicted that heterogeneity would increase at moderate levels of grazing, as suggested by a number of prominent rangeland theories (e.g. Hart et al. 1993, Biondini et al. 1998), it did not. The contradictions between my study and the others can likely be attributed to differences in management regimes, history of grazing, pre-existing environmental patterns, or climate, indicating the importance of conducting studies on the impacts of bison and cattle grazing across a variety of ecologically diverse regions.

Species diversity often increases with habitat heterogeneity (Roth 1976, Walk and Warner 2000). However, my study showed higher species richness in the cattle plots, even though there were no differences in heterogeneity between bison and cattle paddocks. In contrast, Griebel et al. (1998) found that there was higher species richness in the bison plots, although they also found that heterogeneity was the same in the bison

and cattle paddocks. One additional study found that species richness was higher in the more homogeneous cattle paddocks (Lueders et al. 2006). These studies show that effects of grazing on species richness varies regionally, and is influenced by a number of ecological factors other than habitat structure or habitat heterogeneity. Therefore, it is difficult to predict effects of either bison or cattle grazing on avian species richness, and management for higher species diversity at the plot or pasture level may not be a relevant management goal because generalist species may be selected for instead of specialist and threatened species (Van Horne 1983, Vickery et al. 1999).

Although there were negative impacts of bison grazing on certain songbirds, it is likely that most pastures will contain ungrazed or recovering areas available for grazing-sensitive species such as Baird's sparrow due to the foraging behaviors of bison, particularly when managed in a large enclosure and at stocking rates that allow selectivity across the pastures (Brennan and Kuvlesky 2005). Often, the effects of grazing will only accumulate for a period of years before the bison herd moves to a new area of the park. This assumption is consistent with my findings because the bison paddock in Grasslands National Park had extensive ungrazed areas that supported grazing-sensitive species in high abundances. Because cattle grazing is concentrated within groups of pastures, managing cattle grazing to simulate bison grazing will require a thorough understanding of bison movements and how heavily they impact the areas in which they graze, as well as an attempt at understanding the historical impacts of bison. Utilizing a variety of stocking rates among a group of pastures could simulate the historical patterns of bison grazing more effectively than maintaining all pastures at the same moderate stocking rate. Further, cattle may be moderately effective at simulating effects of bison grazing, as my

results suggest that there were similar impacts of bison and cattle on most habitat structure variables and songbirds; while effects of bison and cattle were not identical, the economic and practical advantages of managing cattle rather than bison might outweigh the small ecological differences between the two grazers in some conservation environments. If the bison herd is permitted to grow, their impacts on the landscape and songbirds may change or become more pronounced, and understanding what patterns and density to mimic with cattle grazing will require continued research.

6.6 Management Implications

Both bison and cattle grazing positively and negatively influenced a number of songbird species, due to the impacts of both grazers on habitat structure. Some songbird species have had their habitats severely reduced due to the homogenizing effect of either grazing exclusion or long-term moderate grazing on the prairies (Brennan and Kuvlesky 2005, Askins et al. 2007), but the impacts of carefully managed grazing can be beneficial for many species. One of the most frequent recommendations for the conservation of grassland birds is to manage the landscape for heterogeneity to provide the various habitats required by different bird species (Temple et al. 1999, Vickery et al. 1999, Walk and Warner 2000, Fuhlendorf and Engle 2001). My results suggest that both bison and cattle grazing can be used as a management tool for helping to provide increased habitat for species at risk, such as the chestnut-collared and McCown's longspurs.

Deciding whether to use bison or cattle for creating this habitat will depend on ecological, economic, logistic, and societal interests, as well as which bird species are of concern in a given region. The main ecological differences I found between bison and cattle were slightly greater effects of bison on vegetation height and litter depth, and a

stronger negative impact of bison grazing on Sprague's pipits. Because Sprague's pipits are an endangered species in Canada, their conservation is important for restoring ecological integrity. Also, cattle are more likely to be accepted by the local ranching community, but bison are likely of more interest to the public in a park setting. There are also different fencing and management requirements for the two species; two benefits of choosing bison over cattle may be the reduced need for cross fencing and little requirement for management over winter. Cattle, on the other hand, can be easily concentrated in a desired area, and can also be kept away from sensitive areas, such as streams or archeological sites, if managed properly. Because Grasslands National Park is required to restore ecological integrity (Parks Canada 2009), and the landscape was home to free-roaming bison in the past, bison may be the appropriate choice for Grasslands National Park, with the stipulation that Sprague's pipit populations be monitored through time.

7.0 MANAGEMENT CONSIDERATIONS

Because Sprague's pipits and Baird's sparrows are experiencing severely declining populations (Knopf 1994, Herkert 1995), their protection often supersedes that of other species. Many studies have been conducted to understand how grazing impacts these species (Griebel et al. 1998, Davis et al. 1999, Fritcher et al. 2004, Derner et al. 2009); most found that these two species were fairly insensitive to low levels of grazing. However, my results contradict previous studies and showed that populations of these two species begin to decline at even low levels of grazing in mixed-grass prairies. Conversely, two other species at risk in Canada, chestnut-collared and McCown's longspurs, preferred grazed areas. It is clear that a variety of grazing pressures will be required to provide habitat for each of these threatened species, as well as those species that make up the songbird community as a whole. Therefore, the suggestion to manage the landscape for large-scale heterogeneity (Saab et al. 1995, Vickery et al. 1999, Walk and Warner 2000, Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006) is supported by this study.

Cattle ranching is the predominant land use on the remaining native mixed-grass prairies (Brown and McDonald 1995, Fuhlendorf and Engle 2001). Because most ranching management practices encourage homogeneity and moderate stocking rates for increased production and profit instead of for conservation (Bailey et al. 1996, Fuhlendorf et al. 2006), a suite of species that are part of the grassland bird community is likely not being well supported on ranchlands (Saab et al. 1995, Parks Canada 2006). This assertion is supported by the listing of specialist grassland species, such as Sprague's pipit and McCown's longspur, but not generalist species, such as Savannah

and vesper sparrows (COSEWIC 2010). Therefore, I suggest that the park provide habitat at least for those species that require habitat types that are undesirable from a ranching perspective: heavily overgrazed and/or burned areas, and areas that are ungrazed (Parks Canada 2002). Because Grasslands National Park has already invested in infrastructure in the East Block for the Biodiversity and Grazing Management Area, it would be beneficial to maintain this infrastructure and use it to manage for large-scale heterogeneity, using similar stocking rates as those in the grazing experiment. Further, the land outside the experiment but within the boundary of the park should be left ungrazed so as to provide habitat for those species that are not supported at optimal densities on the majority of ranchlands (i.e. Baird's sparrows, Sprague's pipits).

Because bison were able to graze the land in such a way that no management was required to maintain biodiversity, continuing to use bison for management in the West Block is likely a sustainable option for the full songbird community. One potential benefit of using bison instead of cattle is the less intensive infrastructure and management required for bison. There is no need for cross-fencing, water troughs, minerals, or moving animals during the winter months if bison are the management tool selected. These benefits may prove to be substantial for a fiscally constrained national park. Further, because I did find a number of small differences between bison and cattle, continuing to use bison is likely to result in a more historically accurate landscape.

It will be important for the park to continue monitoring wildlife response to grazing by both bison and cattle because there may be impacts beyond what I have uncovered after two years. For instance, many studies indicated that songbirds require heterogeneity of habitat because they require different types of habitat to meet various

needs during their lifecycle (i.e. Fuhlendorf and Engle 2001, Derner et al. 2009). The heavy grazing in pastures 3, 4, and 8 may be providing suitable habitat for certain species after two years because the pastures were still quite heterogeneous, but after five years of heavy grazing the pastures may become unsuitable to those species that have varying habitat requirements. Other species, such as the mountain plover (*Charadrius montanis*), which generally require sparse vegetation and bare ground throughout their life cycle (Derner et al. 2009) and used to occur in the park, may be able to move into the heaviest grazed habitat. Continued heavy grazing may also promote the invasion of shrubs (Campbell et al. 1994) or the degradation of the soil crust layer (Pieper et al. 1994, Temple et al. 1999). Time is the critical element left in this study to understand the full impacts of cattle and bison grazing on the landscape and on birds of the mixed-grass prairie.

To help promote large-scale management practices, the landowners surrounding the park should be included in management planning discussions for both within and outside the park, and it is also important to encourage landowners to manage their land for the benefit of wildlife (Fuhlendorf and Engle 2001). If landowners are to be encouraged to manage their land for biodiversity, it will be crucial to show them that managing for landscape heterogeneity is an economically viable option (Derner et al. 2009). Cattle production is generally not diminished when it is used for the purpose of managing for a heterogeneous landscape (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006). The Biodiversity and Grazing Management Area could be used as a teaching tool in the future to help inform local ranchers about grazing management for heterogeneity and wildlife management. If it can be shown that management for biodiversity in

southwestern Saskatchewan is economically feasible, then ranchers may be more easily convinced of its benefits and be willing to manage for biodiversity. The park has a mandate to protect and restore its own native prairies, but it also has an opportunity to inform the management of surrounding lands for the benefit of wildlife.

8.0 LITERATURE CITED

Abouguendia, Z.M. 1990. A practical guide to planning for management and improvement of Saskatchewan rangeland: Range plan development. New Pastures and Grazing Technology Project, Saskatchewan Rural Development. Regina SK.

Ahlering, M. A., D. H. Johnson, and J. Faaborg. 2009. Factors associated with arrival densities of grasshopper sparrow (*Ammodramus savannarum*) and Baird's sparrow (*A. bairdii*) in the upper Great Plains. The Auk 126:799-808.

Anderies, J. M., M. A. Janssen, and B. H. Walker. 2002. Grazing management, resilience, and the dynamics of a fire-driven rangeland system. Ecosystems 5:23-44.

Anderson, D. C., K. T. Harper, and S. R. Rushforth. 1982. Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. Journal of Range Management 35:355-359.

Anderson, V. J., and D. D. Briske. 1995. Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance? Ecological Applications 5:1014-1024.

Askins, R. A., F. Chávez-Ramírez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, and P. D. Vickery. 2007. Conservation of grassland birds in North America: Understanding ecological processes in different regions. Ornithological Monographs 64:1-46.

Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49:386-400.

Bakker, E. S., M. E. Ritchie, H. Olff, D. G. Milchunas, and J. M. H. Knops. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecology Letters 9:780-788.

Bakker, K. K., D. E. Naugle, and K. F. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. Conservation Biology 16:1638-1646.

Beason, R. C. 1970. The annual cycle of the Prairie Horned Lark in west-central Illinois. Master's Thesis. Western Illinois University at Macomb.

Beason, R. C. 1995. Horned Lark (*Eremophila alpestris*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/195.

Belovsky, G. E., and J. B. Slade. 1986. Time budgets of grassland herbivores: body size similarities. Oecologia 70:53-62.

Biondini, M. E., and L. Manske. 1996. Grazing frequency and ecosystem processes in a northern mixed prairie, USA. Ecological Applications 6:239-256.

Biondini, M. E., B. D. Patton, and P. E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. Ecological Applications 8:469-479.

Biondini, M. E., A. A. Steuter, and R. G. Hamilton. 1999. Bison use of fire-managed remnant prairies. Journal of Range Management 52:454-461.

Bleho, B. 2009. Passerine relationships with habitat heterogeneity and grazing at multiple scales in northern mixed-grass prairie. Master's thesis, University of Manitoba.

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and Environment 2:403-410.

Bock, C. E., and B. Webb. 1984. Birds as grazing indicator species in southeastern Arizona. Journal of Wildlife Management 48:1045-1049.

Bork, E. W., and S. J. Werner. 1999. Viewpoint: implications of spatial variability for estimating forage use. Journal of Range Management 52:151-156.

Boyd, D. P., and C. C. Gates. 2006. A brief review of the status of plains bison in North America. Journal of Wildlife Management 45:15-21.

Brennan, L. A., and W. P. Kuvlesky. 2005. North American grassland birds: An unfolding conservation crisis? Journal of Wildlife Management 69:1-13.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smiens. 2003. Vegetation dynamics on rangelands: a critique of the current paradigms. Journal of Applied Ecology 40:601-614.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smiens. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. Rangeland Ecology and Management 58:1-10.

Brown, J. H., and W. McDonald. 1995. Livestock grazing and conservation on southwestern rangelands. Conservation Biology 9:1644-1647.

Campbell, C., I. D. Campbell, C. B. Blyth, and J. H. McAndrews. 1994. Bison extirpation may have caused aspen expansion in western Canada. Ecography 17:360-362.

Cid, M. S., J. K. Detling, A. D. Whicker, and M. A. Birzuela. 1991. Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. Journal of Range Management 44:100-105.

Cingolani, A. M., I. Noy-Meir, and S. Diaz. 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. Ecological Applications 15:757-773.

Cody, M. L. 1985, Habitat selection in grassland and open-country birds. In Habitat Selection in Birds, M. L. Cody, ed. Academic Press, Inc., Orlando, FL, USA, pages 191-226.

Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecology 68:1243-1250.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745-747.

Collins, S. L., and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio 64:87-94.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Coppedge, B. R., and J. H. Shaw. 1997. Effects of horning and rubbing behavior by bison (*Bison bison*) on woody vegetation in a tallgrass prairie landscape. American Midland Naturalist 138:189-196.

Coppedge, B. R., J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. Journal of Range Management 51:258-264.

Coppedge, B. R., and J. H. Shaw. 2000. American bison (*Bison bison*) wallowing behavior and wallow formation on tallgrass prairie. Acta Theriologica 45:103-110.

Coppedge, B. R., S. D. Fuhlendorf, W. C. Harrell, and D. M. Engle. 2008. Avian community response to vegetation and structural features in grasslands managed with fire and grazing. Biological Conservation 141:1196-1203.

COSEWIC. 2009. Canadian Wildlife Species at Risk. Committee on the Status of Endangered Wildlife in Canada. Accessed online February 26, 2010 from <http://www.cosewic.gc.ca/eng/sct0/rpt/dsp_booklet_e.htm>.

COSEWIC. 2010. Candidate Wildlife Species. Committee on the Status of Endangered Wildlife in Canada. Accessed online February 28, 2010 from <http://www.cosewic.gc.ca/eng/sct3/index_e.cfm>.

Coughenour, M. B. 1991. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. Journal of Range Management 44:530-542.

Coupland, R. T. 1950. Ecology of mixed prairie in Canada. Ecological Monographs 20:271-315.

Damhoureyeh, S. A., and D. C. Hartnett. 1997. Effects of bison and cattle on growth, reproduction, and abundances of five tallgrass prairie forbs. American Journal of Botany 84:1719-1728.

Davis, S. K. 2003. Nesting ecology of mixed-grass prairie songbird in southern Saskatchewan. The Wilson Bulletin 115:119-130.

Davis, S. K. 2004. Area sensitivity in grassland passerines: effects of patch size, patch shape, and habitat structure on bird abundance and occurrence in southern Saskatchewan. The Auk 4:1130-1145.

Davis, S. K. 2005. Nest-site selection patterns and influence of vegetation on nest survival of mixed-grass prairie passerines. The Condor 104:605-616.

Davis, S. K., and D. C. Duncan. 1999. Grassland songbird occurrence in native and crested wheatgrass pastures of southern Saskatchewan. Studies in Avian Biology 19:211-218.

Davis, S. K., D. C. Duncan, and M. A. Skeel. 1996. The Baird's Sparrow: status resolved. Blue Jay 54:185-191.

Davis, S. K., D. C. Duncan, and M. Skeel. 1999. Distribution and habitat associations of three endemic grassland songbirds in southern Saskatchewan. Wilson Bulletin 111:389-396.

Davis, S. K., and W. E. Lanyon. 2008. Western Meadowlark (*Sturnella neglecta*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/104.

Dechant, J. A., M. F. Dinkins, D. H. Johnson, L. D. Igl, C. M. Goldade, and B. R. Euliss. 2003. Effects of management practices on grassland birds: Vesper Sparrow. Northern Prairie Wildlife Research Center, Jamestown, ND. Accessed online March 1, 2010 at <http://www.npwrc.usgs.gov/resource/literatr/grasbird/vesp/vesp.htm> (Version 28 MAY 2004).

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

Derner, J. D., W. K. Lauenroth, P. Stapp, and D. J. Augustine. 2009. Livestock as ecosystem engineers for grassland bird habitat in the western great plains of North America. Rangeland Ecology and Management 62:111-118.

Dinkins, M. F., A. L. Zimmerman, J. A. Dechant, B. D. Parkin, D. H. Johnson, L. D. Igl, C. M. Goldade, and B. R. Euliss. 2003. Effects of management practices on grassland birds: Horned Lark. Northern Prairie Wildlife Research Center,

Jamestown, ND. Accessed online March 1, 2010 at <http://www.npwrc.usgs.gov/resource/literatr/grasbird/hola/hola.htm> (Version 28 MAY 2004).

Dyksterhuis, E. J. 1949. Condition and management of rangeland based on quantitative ecology. Journal of Range Management 2:104-115.

Efford, M. G., and D. K. Dawson. 2009. Effect of distance-related heterogeneity on population size estimates from point counts. The Auk 126:100-111.

Ellis, J. E., J. A. Wiens, C. F. Rodell, and J. C. Anway. 1976. Conceptual-model of diet selection as an ecosystem process. Journal of Theoretical Biology 60:93-108.

England, R. E., and A. DeVos. 1969. Influence of animals on pristine conditions on Canadian grasslands. Journal of Range Management 22:87-94.

Environment Canada. 2011. National Climate Data and Information Archive. Accessed online 8 May 2011 at <http://www.climate.weatheroffice.gc.ca/climateData/dailydata_e.html?timeframe=2&Prov=SK&StationID=3196&dlyRange=1937-04-01|2010-05-24&cmdB1=Go&Month=6&Year=2009&Day=7>.

Fritcher, S. C., M. A. Rumble, and L. D. Flake. 2004. Grassland bird densities in seral stages of mixed-grass prairie. Journal of Range Management 57:351-357.

Fuhlendorf, S. D., and D. M. Engle. 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. Journal of Applied Ecology 41:604-614.

Fuhlendorf, S. D., B. W. Allred, and R. G. Hamilton. 2010. Bison as keystone herbivores on the Great Plains: can cattle serve as proxy for evolutionary grazing patterns? American Bison Society Working Paper No. 4.

Fuhlendorf, S. D., and F. E. Smiens. 1999. Scaling effects of grazing in a semi-arid grassland. Journal of Vegetation Science 10:731-738.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie, Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706-1716.

Gates, C.C., Freese, C.H., Gogan, P.J.P. and Kotzman, M. (eds. and comps.) 2010. American Bison: Status Survey and Conservation Guidelines 2010. Gland, Switzerland: IUCN.

Gillen, R. L., J. A. Eckroat, F. T. McColum III. 2000. Vegetation response to stocking rate in southern mixed-grass prairie. Journal of Range Management 53:471-478.

Goguen, C. B., and N. E. Mathews. 1999. Review of the causes and implications of the association between cowbirds and livestock. In Research and management of the brown-headed cowbird in western landscapes. Studies in Avian Biology 18:10-17.

Goguen, C. B., and N. E. Mathews. 2000. Local gradients of cowbird abundance and parasitism relative to livestock grazing in a western landscape. Conservation Biology 14:1862-1869.

Goguen, C. B., and N. E. Mathews. 2001. Brown-headed cowbird behavior and movements in relation to livestock grazing. Ecological Applications 11:1533-1544.

Government of Canada. 2009. Species at Risk Public Registry. Accessed online March 1, 2010 at <http://www.sararegistry.gc.ca/species/schedules_e.cfm?id=1>.

Green, M. T., P. E. Lowther, S. L. Jones, S. K. Davis and B. C. Dale. 2002. Baird's Sparrow (*Ammodramus bairdii*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/638.

Griebel, R. L., S. L. Winter, and A. A. Steuter. 1998. Grassland birds and habitat structure in sandhills prairie managed using cattle or bison plus fire. Great Plains Research 8:255-268.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242: 344–347.

Hafez, E. S. E., M. W. Schein, and R. Ewbank. 1969. The behaviour of cattle in The Behaviour of Domestic Animals, E. S. E. Hafez, ed. Baillere, Tindall & Cassell, London, England.

Harris, R. D. 1933. Observations on a nest of Sprague's Pipit (*Anthus spragueii*). Canadian Field-Naturalist 47:91-95.

Hart, R. H. 2001. Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. Plant Ecology 155:111-118.

Hart, R. H., J. Bissio, M. J. Samuel, and J. W. Waggoner, Jr. 1993. Grazing systems, pasture size, and cattle grazing behavior, distribution, and gains. Journal Range Management 46:81-87.

Hart, R. H., and J. A. Hart. 1997. Rangelands of the Great Plains before European settlement. Rangelands 19:4-11.

Hart, R. H., M. J. Samuel, P. S. Test, and M. A. Smith. 1988. Cattle, vegetation, and economic responses to grazing systems and grazing pressure. Journal of Range Management 41:282-286.

Hartnett, D. C., K. R. Hickman, and L. E. Fischer Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. Journal of Range Management 49:413-420.

Hartnett, D. C., A. A. Steuter, and K. R. Hickman. 1997. Comparative ecology of native and introduced ungulates. In Ecology and Conservation of Great Plains Vertebrates. F. L. Knopf and F. B. Samson, eds, pp.72-101.

Herkert, J. R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. Ecological Applications 4:461-471.

Herkert, J. R. 1995. An analysis of Midwestern breeding bird population trends: 1966–1993. American Midland Naturalist 134:41–50.

Hickman, K. R., D. C. Hartnett, R. C. Cochran, and C. E. Owensby. 2004. Grazing management effects on plant species diversity in tallgrass prairie. Journal of Range Management 57:58-65.

Hill, D. P. and L. K. Gould. 1997. Chestnut-collared Longspur (*Calcarius ornatus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/288.

Hurley, R. J., and E. C. Franks. 1976. Changes in the breeding ranges of two grassland birds. The Auk 93:108-115.

Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. The Auk 103:593-602.

Johnson, D. H. 2008. In defense of indices: the case of bird surveys. Journal of Wildlife Management 72:857-868.

Johnson, D. H., and J. W. Grier. 1988. Determinants of breeding distribution of ducks. Wildlife Monographs 100:3-37.

Johnson, D. H., and L. D. Igl. 2001. Area requirements of grassland birds: a regional perspective. The Auk 118:24-34.

Jones, S. L., J. S. Dieni, M. T. Green, and P. J. Gouse. 2007. Annual return rates of breeding grassland songbirds. The Wilson Journal of Ornithology 119:89-94.

Jones, S. L., and J. E. Cornely. 2002. Vesper Sparrow (*Pooecetes gramineus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology;

Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/624.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren. Data analysis in community and landscape ecology. 1995. Cambridge University Press, Great Britain.

Julander, O. 1955. Determining grazing use by cow-chip counts. Journal of Range Management 8:182.

Kantrud, H. A. 1981. Grazing intensity effects on the breeding avifauna of North Dakota native grasslands. Canadian Field-Naturalist 95:404-417.

Kantrud, H. A., and R. L. Kologiski. 1983. Avian associations of the northern Great Plains grasslands. Journal of Biogeography 10:331-350.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. BioScience 49:39-50.

Knopf, F. L. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15:67-84.

Knopf, F. L. 1996. Prairie legacies—birds. In: F. B. Samson and F. L. Knopf (eds.). Prairie conservation: preserving North America's most endangered ecosystem. Washington, DC, USA: Island Press. p. 135–148.

Koper, N., D. C. Henderson, J. F. Wilmshurst, P. J. Fargey, and R. A. Sissons. 2008. Design and analysis of rangeland experiments along continuous gradients. Rangeland Ecology and Management 61:605-613.

Koper, N., and F. K. A. Schmiegelow. 2006. Effects of habitat management for ducks on target and nontarget species. Journal of Wildlife Management 70:823-834.

Lauenroth, W.K., D. G. Milchunas, J. L. Dodd, R. H. Hart, R. K. Heitschmidt, and L. R. Rittenhouse. 1994. Effects of grazing on ecosystems of the Great Plains. pp. 69-100, in Ecological implications of livestock herbivory in the West, M. Vavra, W.A. Laycock and R.D. Pieper (eds.). Denver, Colorado, USA: Society for Range Management.

Lesica, P., and S. V. Cooper. 1999. Succession and disturbance in sandhills vegetation: constructing models for managing biological diversity. Conservation Biology 13:293-302.

Lueders, A. S., P. L. Kennedy, and D. H. Johnson. 2006. Influences of management regimes on breeding bird densities and habitat in mixed-grass prairie: an example from North Dakota. Journal of Wildlife Management 70:600-606.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

Madden, E. M., R. K. Murphy, A. J. Hansen, and L. Murray. 2000. Models for guiding management of prairie bird habitat in northwestern North Dakota. American Midland Naturalist 144:377-392.

Madden, E. M. 1996. Passerine communities and bird-habitat relationships on prescribe-burned, mixed-grass prairie in North Dakota. MSc Thesis. Montana State University, Bozeman, MT.

Malainey, M. E., and B. L. Sherriff. 1996. Adjusting our perceptions: historical and archeological evidence of winter on the plains of western Canada. Plains Anthropologist 41:333-357.

Mickey, F. W. 1943. Breeding habits of McCown's longspurs. The Auk 60:181-209.

Milchunas, D. G., W. K. Lauenroth, and I. C. Burke. 1998. Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. Oikos 83:65-74.

Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. Vegetatio 80:11-23.

Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist 132:87-106.

Oesterheld, M., J. Loreti, M. Semmartin, and J. M Paruelo. 1999. Grazing, fire, and climate effects on primary productivity of grasslands and savannas. Pages 287-306 in Ecosystems of the World: Ecosystems of Disturbed Ground, L. R. Walker, ed., Elsevier, New York City, NY.

Osenberg, C. W., R. J. Schmitt, S. J. Holbrook, K. E. Abu-Saba, and A. R. Flegal. 1994. Detection of environmental impacts: natural variability, effect size, and power analysis. Ecological Applications 4:16–30.

Owens, R. A., and M. T. Myres. 1973. Effects of agriculture upon populations of native passerine birds of an Alberta fescue grassland. Canadian Journal of Zoology 51:697-713.

Parks Canada. 2002. Grasslands National Park of Canada: Management Plan. Parks Canada, Western Canada Service Centre. Winnipeg MB.

Parks Canada. 2004. The Reintroduction of Plains Bison (*Bison bison bison*) to Grasslands National Park. Grasslands National Park of Canada, Parks Canada, Val Marie, SK.

Parks Canada. 2006. Restoring grazing-induced heterogeneity in Grasslands National Park of Canada. Grasslands National Park of Canada, Parks Canada, Val Marie, SK.

Parks Canada. 2009. Draft – Grasslands National Park of Canada Proposed Management Plan. Grasslands National Park of Canada, Parks Canada, Val Marie, SK.

Patterson, M. P., and L. B. Best. 1996. Bird abundance and nesting success in Iowa CRP fields: the importance of habitat structure and composition. American Midland Naturalist 135:153-167.

Peden, D. G., G. M. van Dyne, R. W. Rice, and R. M. Hansen. 1974. The trophic ecology of *Bison bison* L. on shortgrass plains. Journal of Applied Ecology 11:489-498.

Pickwell, G. B. 1931. The prairie horned lark. St. Louis Academy of Science Transactions 27:1-153.

Pieper, R. D. 1994. Ecological implications of livestock grazing. In Ecological Implications of Livestock Herbivory in the West, Vavra, M, W. A. Laycock, and R. D. Pieper, eds. Society for Range Management.

Plumb, G. E., and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. Ecological Applications 3:631-643.

Polley, H. W., and S. L. Collins. 1984. Relationships of vegetation and environment in buffalo wallows. American Midland Naturalist 112:178-186.

Porter, D. K., and R. A. Ryder. 1974. Avian density and productivity studies and analysis on the Pawnee site in 1972. Grassland Biome, U.S. International Biological Program Technical Report No. 252.

Pratt, M., and A. Rasmussen. 2001. Determining your stocking rate. Utah State University Cooperative Extension. Utah State University, Logan, UT.

Pylypec, B., and J. T. Romo. 2003. Long-term effects of burning festuca and stipa-agropyron grasslands. Journal of Range Management 56:640-645.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, New York.

Ratliff, R. D. 1993. Viewpoint: trend assessment by similarity: a demonstration. Journal of Range Management 46:139-141.

Robbins, M. B., and B. C. Dale. 1999. Sprague's Pipit (*Anthus spragueii*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/439.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295-297.

Robinson, S. K., S. I. Rothstein, M. C. Brittingham, L J. Petit, and J. A. Grzybowski. 1995. Ecology and behavior of cowbirds and their impact on host populations. In: T. E. Martin and D. M. Finch [EDS.]. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. New York, NY, USA: Oxford University Press. p. 428–460.

Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. Ecology 57:773-782.

Saab, V. A., C. E. Bock, T. D. Rich, and D. S. Dobkin. 1995. Livestock grazing effects in western North America. In: T. E. Martin and D. M. Finch [EDS.]. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. New York, NY, USA: Oxford University Press. p. 311–353.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. Bioscience 44:418-421.

SAS Institute, Inc. 2008. SAS 9.2, Cary, North Carolina: SAS Institute Inc.

Schaefer, A. L., B. A. Young, and A. M. Chimwano. 1978. Ration digestion and retention times of digesta in domestic cattle (*Bos taurus*), American bison (*Bison bison*), and Tibetan yak (*Bos grunniens*). Canadian Journal of Zoology 56:2355-2358.

Schwartz, C. C., and J. E. Ellis. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. Journal of Applied Ecology 18:343-353.

Severson, K. E., and P. J. Urness. 1994. Livestock grazing: a tool to improve wildlife habitat. In Ecological Implications of Livestock Herbivory in the West, Vavra, M, W. A. Laycock, and R. D. Pieper, eds. Society for Range Management.

Shaffer, J. A., C. M. Goldade, M. F. Dinkins, D. H. Johnson, L. D. Igl, and B. R. Euliss. 2003. Brown-headed cowbirds in grasslands: their habitats, hosts, and response to management. Prairie Naturalist 35(3):145-186. Jamestown, ND: Northern Prairie Wildlife Research Center Online. http://www.npwrc.usgs.gov/resource/literatr/grasbird/bhco/bhco.htm (Version 28MAY2004).

Steuter, A. A., E. M. Steinauer, G. L. Hill, P. A. Bowers, and L. L. Teiszen. 1995. Distribution and diet of bison and pocket gophers in a sandhills prairie. Ecological Applications 5:756-766.

Swanson, D. A. 2003. Effects of management practices on grassland birds: Savannah Sparrow. Northern Prairie Wildlife Research Center, Jamestown, ND. Accessed online March 1, 2010 at

<http://www.npwrc.usgs.gov/resource/literatr/grasbird/savs/savs.htm> (Version 12 AUG 2004).

Tate, K. W., E. R. Atwill, N. K. McDougald, M. R. George. 2003. Spatial and temporal patterns of cattle feces deposition on rangeland. Journal of Range Management 56:432-438.

Temple, S. A., B. M. Fevold, L. K. Paine, D. L. Undersander, and D. W. Sample. 1999. Nesting birds and grazing cattle: accommodating both on Midwestern pastures. Studies in Avian Biology 19:196-202.

Towne, E. G., D. C. Hartnett, and R. C. Cochran. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. Ecological Applications 15:1550-1559.

Underwood, A. J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecological Applications 4:3-15.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Vickery, Peter D. 1996. Grasshopper Sparrow (*Ammodramus savannarum*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/239.

Vickery, P. D., P. L. Tubaro, J. M. Cardoso da Silva, B. G. Peterjohn, J. R. Herkert, R. B. Cavalcanti. 1999. Conservation of grassland birds in the Western Hemisphere. Studies in Avian Biology 19:2-26.

Vinton, M. A., D. C. Hartnett, E. J. Finck, and J. M. Briggs. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. American Midland Naturalist 129:10-18.

Wagnon, K.A. 1963. Behavior of beef cows on a California range, California Agricultural Experiment Station Bulletin, 799, pp. 58.

Walk, J. W., and R. E. Warner. 2000. Grassland management for the conservation of songbirds in the Midwestern USA. Biological Conservation 94:165-172.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42:266–274

Wheelwright, N. T., and J. D. Rising. 2008. Savannah Sparrow (*Passerculus sandwichensis*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/045.

Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs 8:1-93.

Wiens, J. A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. American Midland Naturalist 91:195-213.

Wiens, J. A. 1985. Vertebrate responses to environmental patchiness in arid and semiarid ecosystems. In The Ecology of Natural Disturbance and Patch Dynamics, S. T. A. Pickett and P. S. White, eds. Academic Press. San Diego, CA.

Wiens, J. A. 1989. The ecology of bird communities, vol. 1: foundations and patterns. Cambridge University Press, New York, NY.

Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21-41.

Willms, W. D., and P. G. Jefferson. 1993. Production characteristics of the mixed prairie: constraints and potential. Canadian Journal of Animal Science 73:765 - 778.

Wilson, S. D., and J. W. Belcher. 1989. Plant and bird communities of native prairie and introduced Eurasian vegetation in Manitoba, Canada. Conservation Biology 3:39-44.

With, Kimberly A. 1994a. McCown's Longspur (*Calcarius mccownii*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/096.

With, Kimberly A. 1994b. The hazards of nesting near shrubs for a grassland bird, the McCown's longspur. The Condor 96:1009-1019.

WWF (World Wildlife Fund). 2001. Nebraska sand hills mixed grasslands. Accessed online 5 March 2011 at < http://www.worldwildlife.org/wildworld/profiles/terrestrial/na/na0809_full.html>.

APPENDIX I.

Set of models tested in Proc NLMixed for Biodiversity and Grazing Management Area.

```
Title 'model null';
proc nlmixed data=BAGMA alpha=0.1;
parms intercept = 2;
      num = intercept + u ;
model SW ~ normal (num,s2e);
random u ~ normal(0,s2u) subject=site;
run;


Title 'model AUM;
proc nlmixed data=BAGMA alpha=0.1;
parms intercept = 2 A = 1;
      num = intercept + A*AUM + u ;
model SW ~ normal (num,s2e);
random u ~ normal(0,s2u) subject=site;
run;


Title 'model grazing duration;
proc nlmixed data=BAGMA alpha=0.1;
parms intercept = 2 y = 1;
      num = intercept + y*years + u ;
model SW ~ normal (num,s2e);
random u ~ normal(0,s2u) subject=site;
run;


Title 'model linear1';
proc nlmixed data=BAGMA alpha=0.1;
parms intercept = 2 A y = 1;
      num = intercept + A*AUM + y*years + u ;
model SW ~ normal (num,s2e);
random u ~ normal(0,s2u) subject=site;
run;


Title 'model linear2';
proc nlmixed data=BAGMA alpha=0.1;
parms intercept = 2 A y i1 =1;
      num = intercept + A*AUM + y*years + i1*AUM*years + u ;
model SW ~ normal (num,s2e);
random u ~ normal(0,s2u) subject=site;
run;


Title 'model quadratic1';
proc nlmixed data=BAGMA alpha=0.1;
parms intercept = 2 A A2 y = 1;
      num = intercept + A*AUM + A2*AUM*AUM + y*years + u;
model SW ~ normal (num,s2e);
random u ~ normal(0,s2u) subject=site;
run;
```

```
Title 'model quadratic2';
proc nlmixed data=BAGMA alpha=0.1;
parms intercept = 2 A A2 y i1 i2= 1;
      num = intercept + A*AUM + A2*AUM*AUM + y*years + i1*AUM*years +
      i2*AUM*AUM*years + u;
model SW ~ normal (num,s2e);
random u ~ normal(0,s2u) subject=site;
run;


Title 'model cubic1';
proc nlmixed data=BAGMA alpha=0.1;
parms intercept = 2 A A2 A3 y = 1;
      num = intercept + A*AUM + A2*AUM*AUM + A3*AUM**3 + y*years + u;
model SW ~ normal (num,s2e);
random u ~ normal(0,s2u) subject=site;
run;


Title 'model cubic2';
proc nlmixed data=BAGMA alpha=0.1;
parms intercept = 2 A A2 A3 y i1 i2 i3 = 1;
      num = intercept + A*AUM + A2*AUM*AUM + A3*AUM**3 + y*years +
      i1*aum*years + i2*aum*aum*years + i3*aum*aum*aum*years + u;
model SW ~ normal (num,s2e);
random u ~ normal(0,s2u) subject=site;
run;


Title 'model quartic1';
proc nlmixed data=BAGMA alpha=0.1;
parms intercept = 2 A A2 A3 A4 y = 1;
      num = intercept + A*AUM + A2*AUM*AUM + A3*AUM**3 + A4*AUM**4 +
      y*years + u;
model SW ~ normal (num,s2e);
random u ~ normal(0,s2u) subject=site;
run;


Title 'model quartic2';
proc nlmixed data=BAGMA alpha=0.1;
parms intercept = 2 A A2 A3 A4 y i1 i2 i3 i4 = 1;
      num = intercept + A*AUM + A2*AUM*AUM + A3*AUM**3 + A4*AUM**4 +
      y*years + i1*aum*years + i2*aum*aum*years
      + i3*aum*aum*aum*years + i4*years*aum**4 + u;
model SW ~ normal (num,s2e);
random u ~ normal(0,s2u) subject=site;
run;
```

APPENDIX II.

Set of Generalized Linear Mixed Models (Proc Glimmix) models run for bison variables including birds, diversity, and habitat structure.

```
TITLE "stdev_density50 1a";
proc GLIMMIX method = laplace data=bison;
 class intensity site plot year;
 model stdev_density50= / solution dist=normal ddfm=betwithin CL
alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run;


TITLE "stdev_density50 1b";
proc GLIMMIX method = laplace data=bison;
 class intensity site plot year;
 model stdev_density50= year/ solution dist=normal ddfm=betwithin CL
alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run;


TITLE "stdev_density50 1c";
proc GLIMMIX method = laplace data=bison;
 class intensity site plot year;
 model stdev_density50= patties/ solution dist=normal ddfm=betwithin CL
alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run;

TITLE "stdev_density50 2";
proc GLIMMIX method = laplace data=bison;
 class intensity site plot year;
 model stdev_density50= patties year / solution dist=normal
ddfm=betwithin CL alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run;


TITLE "stdev_density50 3";
proc GLIMMIX method = laplace data=bison;
 class intensity site plot year;
 model stdev_density50= patties year patties*year/ solution dist=normal
ddfm=betwithin CL alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run;
```

```
TITLE "stdev_density50 4";
proc GLIMMIX method = laplace data=bison;
 class intensity site plot year;
 model stdev_density50= patties year patties*year patties*patties
patties*patties*year/ solution dist=normal ddfm=betwithin CL alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run;


TITLE "stdev_density50 5";
proc GLIMMIX method = laplace data=bison;
 class intensity site plot year;
 model stdev_density50= patties year patties*year patties*patties
patties*patties*year patties*patties*patties
patties*patties*patties*year/ solution dist=normal ddfm=betwithin CL
alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run;


TITLE "stdev_density50 6";
proc GLIMMIX method = laplace data=bison;
 class intensity site plot year;
 model stdev_density50= patties year patties*year patties*patties
patties*patties*year patties*patties*patties
patties*patties*patties*year patties*patties*patties*patties
patties*patties*patties*patties*year/ solution dist=normal
ddfm=betwithin CL alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run;
```

APPENDIX III

Set of Generalized Linear Mixed Models (Proc Glimmix) models run for bison and cattle comparisons, including birds, diversity, and habitat structure.

```
TITLE "BAIS 1";
proc GLIMMIX method=laplace data=cattlebison;
  class intensity grazer site plot year;
  model BAIS= / solution dist=normal ddfm=betwithin CL alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run ;

TITLE "BAIS 2";
proc GLIMMIX method=laplace data=cattlebison;
  class intensity grazer site plot year;
  model BAIS= patties / solution dist=normal ddfm=betwithin CL
alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run ;

TITLE "BAIS 3";
proc GLIMMIX method=laplace data=cattlebison;
  class intensity grazer site plot year;
  model BAIS= grazer / solution dist=normal ddfm=betwithin CL
alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run ;

TITLE "BAIS 4";
proc GLIMMIX method=laplace data=cattlebison;
  class intensity grazer site plot year;
  model BAIS= year / solution dist=normal ddfm=betwithin CL alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run ;

TITLE "BAIS 5";
proc GLIMMIX method=laplace data=cattlebison;
  class intensity grazer site plot year;
  model BAIS= patties grazer year / solution dist=normal ddfm=betwithin
CL alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run ;

TITLE "BAIS 6";
proc GLIMMIX method=laplace data=cattlebison;
  class intensity grazer site plot year;
  model BAIS= patties grazer year patties*grazer*year/ solution
dist=normal ddfm=betwithin CL alpha=0.1;
random intercept /subject=site type=vc;
```

```
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run ;


TITLE "BAIS 7";
proc GLIMMIX method=laplace data=cattlebison;
  class intensity grazer site plot year;
  model BAIS= patties grazer year patties*grazer / solution dist=normal
ddfm=betwithin CL alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run ;

TITLE "BAIS 8";
proc GLIMMIX method=laplace data=cattlebison;
  class intensity grazer site plot year;
  model BAIS= patties grazer year patties*grazer patties*patties/
solution dist=normal ddfm=betwithin CL alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run ;

TITLE "BAIS 9";
proc GLIMMIX method=laplace data=cattlebison;
  class intensity grazer site plot year;
  model BAIS= patties grazer year patties*grazer patties*patties
patties*patties*grazer/ solution dist=normal ddfm=betwithin CL
alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run ;

TITLE "BAIS 10";
proc GLIMMIX method=laplace data=cattlebison;
  class intensity grazer site plot year;
  model BAIS= patties grazer year patties*grazer
patties*patties patties*patties*grazer
patties*patties*patties / solution dist=normal ddfm=betwithin CL
alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run ;

TITLE "BAIS 11";
proc GLIMMIX method=laplace data=cattlebison;
  class intensity grazer site plot year;
  model BAIS= patties grazer year patties*grazer
patties*patties patties*patties*grazer
patties*patties*patties patties*patties*patties*grazer/ solution
dist=normal ddfm=betwithin CL alpha=0.1;
random intercept /subject=site type=vc;
output out=glimmix pred=p pearson=pearsonresid ucl=upper lcl=lower;
run ;
```