Changes in grassland songbird abundances through time in response to burning and grazing in the northern mixed-grass prairie.

By

Alexis Nicole Richardson

A Thesis Submitted to the Faculty of Graduate Studies
In Partial Fulfilment 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
May 2012

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

*****

COPYRIGHT PERMISSION

Changes in grassland songbird abundances through time in response to burning and grazing in the northern mixed-grass prairie.

By

Alexis Nicole Richardson

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.)

ABSTRACT

This study considered the long term effects and interaction between burning and grazing in the northern mixed-grass prairies on the grassland songbird community. Point counts were conducted to assess songbird species abundances in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures along with habitat structure (litter depth, vegetation height and density) over a five year period; from the first year post burn in 2007 until the fifth year post burn in 2011. Generalized linear mixed models were used to analyse the interaction between year, burning, and grazing for songbird abundances and habitat structure. As time since burned increased, species abundances in burned-grazed pastures have become more similar with those in unburned-grazed while abundances in burned-ungrazed are becoming increasingly similar to those in unburned-ungrazed pastures. The effects of burning are different than those of grazing and both disturbances should be utilised in grassland management when possible.

ACKNOWLEDGMENTS

I would like to thank my funding agencies without whose support, both financial and otherwise, my research could not have been completed. Generous support was provided by Parks Canada, the University of Manitoba, and the Natural Sciences and Engineering Research Council. I would also like to thank the biologist, staff, and asset management crew at Grasslands National Park for their time and expertise.

For providing valuable advice, my committee members Spencer Sealy, professor of Biological Sciences at the University of Manitoba and Glenn Sutter, research scientist at the Royal Saskatchewan Museum. My advisor, Nicola Koper, for providing extensive advice and guidance for both my research and my time as a student, thank you for all your time and effort on my behalf.

Finally, I would like to thank all of the graduate students and field assistants who spent their summers counting birds and measuring grass: Barbara Bleho, Barbara Carleton, Rebecca Deatsman, Jessica Lockhart, Kelsey Molloy, Laura Murray, Emily Pipher, Allison Selinger, Sheila Taillon, Adrienne Tastad, Bonnie Timshel, and Tonya Lwiwski. An extra thank you goes to Maggi Sliwinski who was willing to have long discussions about methods and statistics and to Krystle White whose data and field study I used.

Table of Contents

ABSTRACT i
ACKNOWLEDGMENTS ii
List of Tables v
List of Figures vi
List of Appendices viii
1.0 INTRODUCTION 1
1.1 Project Significance and Limitations 3
1.2 Objectives 5
1.3 Hypotheses 5
2.0 LITERATURE REVIEW 7
2.1 Grassland Songbirds – Habitat Associations and Settlement Patterns 7
2.1.1 Baird's Sparrow 9
2.1.2 Chestnut-collared Longspur 10
2.1.3 Clay-colored Sparrow 11
2.1.4 Grasshopper Sparrow 11
2.1.5 Horned Lark 12
2.1.6 McCown's Longspur 13
2.1.7 Savannah Sparrow 13
2.1.8 Sprague's Pipit 14
2.1.9 Vesper Sparrow 15
2.1.10 Western Meadowlark 15
2.2 Fire 16
2.3 Climatic Variation 19
2.4 Grazing 22
2.5 Interaction between Fire and Grazing 23
3.0 METHODS 26
3.1 Study Site 26
3.2 Experimental Design 26
3.3 Songbird Surveys 28
3.4 Habitat Structure 29
3.5 Data Analysis 29

4.0 RESULTS 32
4.1 Effects of Burning and Grazing on Grassland Songbirds 32
4.1.1 Species Abundances 32
4.1.2 Species Richness and Diversity 35
4.2 Effect of Year on Grassland Songbirds in Burned and Grazed Sites 37
4.3 Effect of Year on Vegetation Structure in Burned and Grazed Sites 44
5.0 DISCUSSION 48
6.0 MANAGEMENT IMPLICATIONS & CONCLUSIONS 58
LITERATURE CITED 62
APPENDIX I 68
APPENDIX II 69
APPENDIX III 70
APPENDIX IV 71
APPENDIX V 72
APPENDIX VI 73

List of Tables

Table 1. The average precipitation (mm) for the years 1971 through 2000 per month and the total precipitation (mm) per month per year. Data collected by Environment Canada at the Val Marie weather station (location: 49.370, - 107.848) in southern Saskatchewan (source: Government of Canada 2011).

Table 2. Top three most abundant songbird species occurring in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures from 2007 through 2011 in Grasslands National Park of Canada.

Table 3: Songbird species richness, number of species in common and Sørensen's quantitative indices for burned-grazed (BG), burned-ungrazed (BUG), unburned-grazed (UBG), and unburned-ungrazed (UBUG) pastures for 2007 through 2011.

Table 4. Results from regression analysis to determine if the Sørensen's quantitative similarity indices changed over time from 2007 through 2011 in burned-grazed (BG), burned-ungrazed (BUG), unburned-grazed (UBG), and unburned-ungrazed (UBUG) pastures.

Table 5. Interaction between year, burning, and grazing on songbird species abundances in Grasslands National Park of Canada from 2007 to 2011; year*unburned*ungrazed used as the control when analysing the interaction between year and treatment. Only species that showed at least one significant result listed.

Table 6. Interaction between year, burning, and grazing on habitat structure in Grasslands National Park of Canada from 2007 to 2010; year*unburned*ungrazed used as the control when analysing the interaction between year and treatment.

List of Figures

Figure 1. Map showing location of study plots (17 unburned-ungrazed, 21 unburned-grazed, 18 burned-grazed, and 16 burned-ungrazed) within Grasslands National Park of Canada and Mankota Community Pastures. Plots within the boundary of Grasslands National Park are ungrazed (burned or unburned), while plots in Mankota Community Pastures are grazed (burned or unburned) and burn 8 is grazed. (source: map modified from White 2009)

Figure 2. Mean abundance, per year (2007-2011), of Baird's sparrows in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

Figure 3. Mean abundance, per year (2007-2011), of chestnut-collared longspurs in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

Figure 4. Mean abundance, per year (2007-2011), of clay-colored sparrow in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid line represents a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

Figure 5. Mean abundance, per year (2007-2011), of horned larks in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid line represents a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

Figure 6. Mean abundance, per year (2007-2011), of Sprague's pipits in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

Figure 7. Mean abundance, per year (2007-2010), of western meadowlarks in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid line represents a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

Figure 8. Vegetation height in cm, per year (2007-2010), in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

Figure 9. Vegetation density (50% obstruction of a Robel pole), per year (2007-2010), in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

Figure 10. Litter depth in cm, per year (2007-2010), in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

List of Appendices

Appendix I: Average abundance of grassland songbirds observed per point count plot (3.2 hectares) in Grassland National Park in 2007 separated by treatment. Average relative abundances and standard deviations are shown for all songbird species observed.

Appendix II: Average abundance of grassland songbirds observed per point count plot (3.2 hectares) in Grassland National Park in 2008 separated by treatment. Average relative abundances and standard deviations are shown for all songbird species observed.

Appendix III: Average abundance of grassland songbirds observed per point count plot (3.2 hectares) in Grassland National Park in 2009 separated by treatment. Average relative abundances and standard deviations are shown for all songbird species observed.

Appendix IV: Average abundance of grassland songbirds observed per point count plot (3.2 hectares) in Grassland National Park in 2010 separated by treatment. Average relative abundances and standard deviations are shown for all songbird species observed.

Appendix V: Average abundance of grassland songbirds observed per point count plot (3.2 hectares) in Grassland National Park in 2011 separated by treatment. Average relative abundances and standard deviations are shown for all songbird species observed.

Appendix VI: Total songbird species abundances observed in Grasslands National Park and Mankota Community Pastures in southern Saskatchewan in 2007 through 2011.

1.0 INTRODUCTION

Worldwide, grasslands are among the most degraded and least protected habitats (Hoekstra et al. 2005). Conversion of native prairie habitat for agriculture is the largest cause of habitat loss, fragmentation, and degradation. In areas where climate and soil are particularly suited for crop production, such as the moist mixed and tall grass prairies, almost 100% of native habitat has been lost (Moen 1998, Davis 2004, Koper and Schmiegelow 2006, Brudvig et al. 2007). The steep decline in populations of many grassland songbirds is usually attributed to habitat loss and the alteration of natural ecosystem processes (i.e. fire and grazing) from the prairies (Samson and Knopf 1994, Knopf 1994, Herkert 1995, Lueders et al. 2006, Samson et al. 2004, Powell 2006). North American grasslands are disturbance-dependent ecosystems and most organisms that occur rely, at least to some extent, on periodic disturbances (Collins and Barber 1986, Fuhlendorf and Engle 2004, Koper and Schmiegelow 2006). In grasslands with favourable climatic and soil conditions, disturbances are necessary to prevent the encroachment of woody vegetation and eventual community succession into a woodland ecosystem (Joern 2005). In systems with more arid or cooler climatic conditions (i.e. dry short or mixed-grass prairies and tundra) disturbances are not required to maintain a grassland ecosystem but are important in maintaining habitat heterogeneity (Shay et al. 2001, Erichsen-Arychuk et al. 2002, Powell 2006, Askins et al. 2007).

In southwestern Saskatchewan, where less than 20% of native prairie habitat remains, natural disturbance processes might be critical in maintaining a productive, healthy grassland ecosystem (Davis et al. 1999, Davis 2004, Powell 2006). The North American grasslands evolved alongside frequent and often intense disturbances. European colonization and settlement has resulted in the removal of natural disturbance processes from the prairies; bison have been largely extirpated and wildfires are suppressed (Samson and Knopf 1994, Brawn et al. 2001, Joern 2005, Lueders et al. 2006, Brudvig et al. 2007). Grassland ecosystems become degraded when disturbances are removed and the vegetation community transitions to a later successional stage with increased shrubby and woody vegetation, taller and denser grasses, and increased litter (Madden et al. 1999, Brawn et al. 2001, Shay et al. 2001). Disturbances such as fire and grazing cause the vegetation community to transition back to an earlier successional stage (Lesica and Cooper 1999, Madden et al. 1999, Brawn et al. 2001, Fritcher et al. 2004). The resulting community is transitional and Madden (et al. 1999) found in North Dakota that it was dominated by shorter and sparser grasses with fewer forbs and persisted for approximately two to three years following a burn.

The mixed-grass prairie in Saskatchewan still supports a diverse grassland songbird community despite widespread habitat loss and degradation (Davis et al. 1999). Many endemic grassland songbirds including Sprague's pipits, Baird's sparrows, lark buntings, McCown's longspurs, and chestnut-collared longspurs are dependent on disturbances that create suitable nesting and foraging habitat (Knopf 1994). For example, both chestnut-collared and McCown's longspur require short, sparse vegetation and bare ground; these types of habitat are created by fire and/or intense grazing (Ehrlich et al. 1988, Kimberly 1994, Hill et al. 1997). Conversely, Sprague's pipit and Baird's sparrow require taller, denser vegetation and moderate litter accumulation, habitat that occurs in the absence of intense disturbances (i.e. areas with moderate grazing) (Davis et al. 1999, Robbins and Dale 1999, Green et al. 2002). Management and policy decisions should consider the ecosystem as a whole since management directed towards a single species may result in the decline of non-target species.

Ecosystem management for the mixed-grass prairies requires the reintroduction of historically important disturbances to maintain habitat heterogeneity. Traditional grassland management tends to increase habitat homogeneity by suppressing wildfires and aiming for a consistent 50% biomass removal through grazing (Knopf 1994, Shay et al. 2001, Erichsen-Arychuk et al. 2002, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006). However, a study in the tallgrass prairie found that fire and grazing interact through a series of positive and negative feedback loops where fire promotes grazing by promoting new (more palatable) growth, and grazing decreases the chances of a fire by removing standing biomass and decreasing litter (Fuhlendorf and Engle 2004). The interaction between fire and grazing creates a patchy habitat mosaic that supports increased species richness and diversity (Bakker et al. 2002, Chapman et al. 2004, Danley et al. 2004, Fuhlendorf and Engle 2004).

1.1 Project Significance and Limitations

Fire and grazing were historically important processes in the North American grasslands (Collins and Barber 1986, Shay et al. 2001). Since only a small percentage of native prairie habitat remains, it is important that we optimize our management of disturbances on the remaining prairie ecosystems. Conservation and management have begun to incorporate disturbance processes into modern management plans and as such it is important that research be conducted to determine the impact that fire and grazing will have on the grassland community (Madden et al. 2000, Fuhlendorf and Engle 2004, Lueders 2006).

Environmental conditions such as soil type, moisture regime, and plant species composition and structure can vary greatly across both the east-west and north-south gradient (Madden et al. 2000). Differences in the vegetation community could have a dramatic impact on the songbird community since vegetation structure is a major factor in songbird habitat selection (Brawn et al. 2001, Bakker et al. 2002, Fondell and Ball 2004). Consequently, studies conducted in other areas of the North American grasslands, even within the northern mixed-grass prairie, cannot be directly extrapolated across the entire ecosystem due to potentially significant temporal and spatial differences (Madden et al. 2000, Bakker et al. 2002, Chapman et al. 2004).

Few studies have investigated the interaction between fire and grazing (i.e. Fuhlendorf and Engle 2004, tallgrass prairie), especially in the northern mixed-grass prairies in southern Saskatchewan. Another limitation of previous studies on fire in the prairies is that most have been restricted to a single burn (pseudoreplication of plots). Replication can be a difficult or impossible condition to meet in a natural experiment. In contrast, in the area in and around the East Block of Grasslands National Park, multiple wildfires occurred in the summer of 2006, covering both grazed and ungrazed pastures.

This study investigated the interaction between burning and grazing and the effect of this interaction on vegetation structure and the songbird community. Due to budget and time restrictions data could not be collected to determine nest success, brood parasitism, predation risk, food quality or abundance. Vegetation structure and relative songbird abundance were recorded for each year from first year post burn until fifth year post burn, 2007 through 2011. The relationship between songbirds and vegetation structure may help explain some of the underlying reasons for the decline of grassland songbirds over the past century (i.e. lack of early successional vegetation community may correspond with the decline of some endemic songbirds; Davis et al. 1999). Relative songbird species abundances were determined using point counts, which previous studies have found to be reliable predictors of reproductive success and habitat quality (Betts et al. 2005).

1.2 Objectives

The focus of this study was to determine how the interaction between fire and cattle grazing influenced the songbird community and how it might have changed over time since burned.

The objectives of the study were:

1. Evaluate relative songbird species abundances and species richness in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed sites in the northern mixed-grass prairie.
2. Determine effects of time since burned, from first to fifth year post burn, on the songbird community in grazed and ungrazed pastures.
3. Develop management recommendations for optimizing songbird diversity within the northern mixed-grass prairies.

1.3 Hypotheses

Burning and grazing are both disturbances that result in changed vegetation structure. Fire results in short, sparse vegetation that tends to be dominated by grass and greatly reduced litter. Similarly, grazing reduces vegetation height, density, and litter (Madden et al. 1999, Shay et al. 2001). Grassland songbirds evolved alongside frequent disturbances that created early successional habitats; consequently, many species are associated with low to mid vegetation height and density, and little litter accumulation (Ehrlich et al. 1988, Davis et al.

1999, Madden et al. 2000). Consequently, I predict that species abundance and richness of grassland songbirds should be highest in disturbed pastures, both grazed and burned, and lowest in unburned-ungrazed pastures as more grassland species are attracted to early successional habitat. I predict that the different disturbances will independently or in concert create habitat that supports a unique grassland songbird community with species preferring sparse vegetation and bare ground being more abundant in burned-grazed pastures while species that prefer tall, dense vegetation with moderate litter being more abundant in unburned-ungrazed pastures. For example, the community found in burned-grazed pastures will support more McCown’s and chestnut-collared longspurs than the unburned-ungrazed pastures which will in turn support more Sprague’s pipits and Baird’s sparrows. Additionally, I expect that McCown’s longspur abundances to be greatest in burned-grazed pastures in the first year post burn, with their numbers declining with time as the vegetation community recovers. As the time since burned increases, I expect that the songbird community in burned patches will begin to resemble those on unburned patches as the effects of fire decline over time and the vegetation community returns to a later successional stage. Previous studies (in the tall grass prairie) suggest that grazing and burning interact through a series of positive and negative feedback loops with recently burned patches being preferentially grazed by cattle (Fuhlendorf and Engle 2004). Thus I predicted that the effects of fire, as time progresses, will continue to have a greater influence on the songbird community in grazed pastures when compared to ungrazed pastures as the vegetation community will be maintained at an earlier successional stage.

2.0 LITERATURE REVIEW

2.1 Grassland Songbirds – Habitat Associations and Settlement Patterns

Songbirds are often used as indicators of ecosystem health because they respond quickly to changes in habitat and the environment (Brawn et al. 2001). North American grasslands are a disturbance-dependent ecosystem characterized by periodic (i.e. grazing) and sometimes intense disturbances (i.e. fire and drought). These disturbances can result in dramatica changes in vegetation structure and habitat suitability from year to year. Since songbird habitat selection is strongly influenced by vegetation structure, breeding locations can change rapidly in response to a disturbance (Davis et al. 1999, Brawn et al. 2001, Bakker et al. 2002, Fondell and Ball 2004).

Consequent to the potential for extreme habitat variability between years, many grassland bird species appear to be partially nomadic, shifting their preferred nesting areas in response to habitat disturbance (Madden et al. 2000, Green et al. 2002, Ahlering et al. 2006, Jones et al. 2007, Skagen and Adams 2010). A study on the annual return rates of breeding grassland songbirds in North Dakota by Jones et al. (2007) found a return rate of 8.9% for grasshopper sparrows, 5.4% for Savannah sparrows, 5.1% for Baird's sparrows, and 2.1% for Sprague's pipits. This flexibility can result in large variations in population and breeding densities between years with species either abandoning or discovering new habitats each season (Ahlering et al. 2006, Jones et al. 2007, Skagen and Adams 2010). Nomadic behaviour is often advantageous to site fidelity in unstable environments as suitable nesting locations will change between years and it may be disadvantageous for young to return to their natal site.

This nomadic and/or semi-colonial (i.e. erratic and patchy) territoriality of grassland songbirds has implications for conservation and management (Ahlering et al. 2006). For woodland species that exhibit site fidelity, important breeding habitat can be identified and protected. Since individual grassland songbirds often do not return to the same patch for consecutive seasons, protecting a patch that appeared important for the current year may not actually protect any breeding habitat for the following year.

Using songbird densities as a metric for habitat quality and nesting success can be problematic if higher densities are actually linked to lower nesting success due to increased predation and disease. Predation is responsible for the majority of nest failures in the prairies. In the northern mixed-grass prairies of southern Saskatchewan, 24-32% of total nests were successful and predation was responsible for 88% of failed nesting attempts (Davis 2003). Disturbances can have either negative or positive effects on nesting success depending on the species. Grazing reduces standing vegetation biomass and density, which can affect nesting success by increasing nest vulnerability to certain predators (Davis 2003, Fondell and Ball 2004). Many species use dense stands of grass for nest concealment, a habitat feature that is lost when burning or intense grazing occur. Studies have found that nest density is strongly correlated with vegetation density and that seral stage can be used as an effective predictor of songbird species found in the community (Fondell and Ball 2004, Fritcher et al. 2004). Another study that investigated the effects of local and landscape factors found that nesting success and species abundances were associated with vegetation height, density and litter depth (Koper and Schmiegelow 2006). Local habitat patch characteristics appear to be more important in determining habitat suitability, species abundance, and nesting success than larger landscape characteristics (Bakker et al. 2002, Fondell and Ball 2004, Fritcher et al. 2004, Koper and Schmiegelow 2006). Thus the ability of grassland songbirds to react quickly to changes in their environment and the impact that disturbances have on habitat suitability through vegetation structure indicates that grassland management will need to include some form of disturbance management and that songbird populations should perhaps be managed based on long term trends rather than year to year fluctuation.

2.1.1 Baird's Sparrow

Baird's sparrows *(Ammodramus bairdii)* arrive to the North American short and mixed-grass prairies in the first two weeks of May and lay a single clutch of four to five eggs in a small, well constructed nest of dried grasses in shallow depression on the ground (Ehrlich et al. 1988, National Audubon Society 2001, Davis 2003). The young are fed insects while adults will eat a variety of seeds gleaned from the ground or vegetation and insects (Ehrlich et al. 1988, National Audubon Society 2001).

Densities of Baird's sparrows are positively associated with cover (grasses over 10cm) and negatively associated with increasing grazing intensity (prefer lightly grazed or ungrazed pastures) due to their preference for tall, dense vegetation with substantial litter accumulation (Davis et al. 1999, Green et al. 2002). A recent study in GNPC found that Baird's sparrows decreased linearly with increased cattle stocking rates (Sliwinski 2011). They are generally most abundant in moist mixed-grass prairies with few disturbances (Davis et al. 1999, Green et al. 2002). Baird's sparrows are semi-colonial nesters. They were once among the most abundant songbird species in the moist mixed-grass prairie, but are now experiencing steep declines, at 2.4% per year in Saskatchewan, and throughout most of their range as native prairie continues to be converted for agricultural purposes (Ehrlich et al. 1988, Green et al.

2002, Sauer et al. 2011). They are now a candidate species being considered by COSEWIC (COSEWIC 2009).

2.1.2 Chestnut-collared Longspur

Chestnut-collared longspurs *(Calcarius ornatus)* arrive on the short and mixed-grass prairies in the third week of April and usually produce two clutches with four eggs (Ehrlich et al. 1988, Davis 2003). Nests are constructed using grass, feathers, and hair in a shallow depression in the ground and are concealed beneath an overhanging tuft of grass. The young are fed insects but adults will eat both insects and seeds gleaned on the ground or off vegetation (Ehrlich et al. 1988, Hill et al. 1997, National Audubon Society 2001). Chestnut-collared longspurs prefer short (<20-30cm), sparse vegetation with minimal litter accumulation and are negatively associated with litter depth and vegetation density. They are most abundant in recently disturbed patches (mowed, grazed, and/or burned) and occur mainly in the dry short and mixed-grass prairie (Ehrlich et al. 1988, Hill et al. 1997, Davis et al. 1999, Madden et al. 2000). In 2009 and 2010 chestnut-collared longspur abundances at GNPC remained relatively low in light to moderately grazed pastures (i.e. abundances increased in pastures stocked at 0.4 AUM/ha or above, Sliwinski 2011). Chestnut-collared longspurs are currently declining at a rate of 4.6% per year in Saskatchewan (Saeur et al. 2011) and the Committee on the Status of Endangered Wildlife in Canada has proposed that the species be listed under the Species at Risk Act (Government of Canada 2009). They are currently expected to be listed under SARA in the next 2 years (S. Davis, 2010, pers. comm.).

2.1.3 Clay-colored Sparrow

Clay-colored sparrows (*Spizella pallid*) are late migrants, arriving at their breeding grounds in late April to early May. Nests are built in shrubs, often snowberry (*Symphoricarpos* spp.) in the mixed-grass prairie, close (<30cm) to the ground. Adults feed their young invertebrates and generally forage outside of their breeding territory, thus breeding territories are selected based on potential nest cover and not food availability (Ehrlich et al. 1988, Knapton 1994). Clay-colored sparrows are a common open shrubland species and among the most abundant low shrub nesting songbirds in the prairies. Fire suppression in the prairies has resulted in increased local populations where aspen groves and snowberry stands proliferate in once open grasslands (Knapton 1994). Although clay-colored sparrow populations remain fairly high and are well adapted to human settlement their overall populations are currently declining at a rate of 2.2% per year across the prairies (Knapton 1994, Sauer et al. 2011).

2.1.4 Grasshopper Sparrow

Grasshopper sparrows *(Ammodramus savannarum)* are late migrants and may not arrive at their breeding grounds until late April. Nests are built on the ground and hidden by overhanging grasses. Despite being a relatively late arrival, a pair can have two clutches per season. Summer forage consists of insects with grasshoppers being the main source of food (Ehrlich et al. 1988, Vickery 1996).

Grasshopper sparrows prefer open grasslands with bare ground but will select areas with more shrubs and denser vegetation cover in arid ecosystems. Studies have found that grasshopper sparrows, with their preference for moderate vegetation and litter accumulation, often occupy similar habitats to Savannah and Baird’s sparrows (Vickery 1996, Madden et al.

2000) and showed population declines at moderate to high cattle stocking rates (i.e. declines occur at 0.3-0.4 AUM/ha, Sliwinski 2011). Grasshopper sparrows are currently declining in Saskatchewan at a rate of 5.2% per year (Sauer et al. 2011) and are listed as a candidate species for COSEWIC (COSEWIC 2009). Their requirements for large habitat patches, 134 hectares, is likely a major factor in the steep population decline (Davis 2004).

2.1.5 Horned Lark

The horned lark *(Eremophila alpestris)* is the only lark species native to North America and is widespread across the continent occupying habitats as diverse as the desert, tundra, and grasslands. There are 26 subspecies of horned larks and depending on habitat larks will vary in size, behaviour, and colour (Beason 1995, National Audubon Society 2001). Horned larks prefer short, sparse vegetation (<5cm) and bare ground, and are most abundant in the years immediately following a fire (Ehrlich et al. 1988, Beason 1995, National Audubon Society 2001). They require relatively barren ground for nesting, and sites that were suitable in April are often unsuitable by June since vegetation has grown too tall and/or dense. Consequently, horned larks will abandon their breeding grounds after the first brood unless they are heavily grazed throughout the season (Ehrlich et al. 1988, Beason 1995, National Audubon Society 2001). They arrive on the Canadian prairies by early April and construct a nest in a shallow depression in the ground near shelter (grass, rocks, etc.). Adults consume mostly seeds but display flexible foraging behaviour, and young are fed insects (Ehrlich et al. 1988, National Audubon Society 2001). The horned lark is not currently listed under COSEWIC (Government of Canada 2009, COSEWIC 2009) but is experiencing a decline of 5.1% per year in Saskatchewan (Sauer et al. 2011).

2.1.6 McCown's Longspur

McCown's longspur *(Calcarius mccownii)* prefer short, sparse vegetation and open bare ground and are found in the dry short and mixed-grass prairie (Ehrlich et al. 1988, Kimberly 1994). The highest abundances occur in patches that have been recently burned or are heavily grazed; however, McCown's longspurs are listed as special concern under both COSEWIC and SARA for the province of Saskatchewan (Government of Canada 2009, COSEWIC 2009). McCown's longspurs are currently declining at a rate of 7.3% per year (Sauer et al. 2011), one of the steepest rates among grassland songbirds, a fact which is sometimes considered surprising, since much of the remaining prairie habitat is heavily grazed, or is in fair or poor condition, usually associated with overgrazing (Ehrlich et al. 1988, National Audubon Society 2001).

McCown's longspur eat a variety of seeds and insects and will stalk and pursue large insects (grasshoppers and moths). They arrive to their breeding grounds in April. Nest are built on the ground next to shelter (cactus, tuft of grass, shrub), and both male and female will take turns brooding and feeding their young (Kimberly 1994). While chestnut-collared longspurs also breed in short and mixed-grass prairies, it is rare for the two species to have overlapping home ranges as chestnut-collared longspurs prefer slightly taller and denser vegetation (Kimberly 1994).

2.1.7 Savannah Sparrow

Savannah sparrows *(Passerculus sandwichensis)* are widely dispersed throughout North America and are generally considered habitat generalists. They sometimes show a preference for lightly grazed pastures with tall, dense vegetation and substantial litter accumulation (Madden et al. 2000, National Audubon Society 2001, Wheelwright and Rising 2008); and showed population declines in heavily grazed pastures (i.e. abundances declined above 0.4 AUM/ha, Sliwinski 2011). Four to five eggs are laid per clutch (and rear one or two depending on habitat) in a nest built using grasses in a shallow depression and concealed by surrounding vegetation. Adults eat a wide variety of insects and seeds and will run mouselike along the ground while foraging (Ehrlich et al. 1988). The Savannah sparrow is not currently listed under COSEWIC (Government of Canada 2009, COSEWIC 2009) with the population remaining relatively stable and only declining by 0.2% per year in Saskatchewan (Sauer et al. 2011).

2.1.8 Sprague's Pipit

Sprague's pipits *(Anthus spragueii)* are most common in the dry mixed and short grass prairie and are negatively associated with heavy grazing. Their preferred habitat is open grasslands with grasses of intermediate height and density with moderate litter accumulation; lightly grazed and ungrazed pastures generally provide this habitat. Sprague's pipits are negatively associated with both increasing shrubs and habitat fragmentation (Ehrlich et al. 1988, Davis et al. 1999, Robbins and Dale 1999, Madden et al. 2000) and increasing cattle stocking rates (Sliwinski 2011). Pipits arrive on the North American prairies in late April to early May and lay four to five eggs in a ground nest that is usually covered by a canopy of woven grasses (Ehrlich et al. 1988, National Audubon Society 2001). The display flight of the males is unique among songbirds and can last over 40 minutes during which the male will fly up to 90 m and sing dozens of songs (Ehrlich et al. 1988, Robbins and Dale 1999, National Audubon Society 2001). Currently experiencing a 4.7% population decline per year (Davis et al. 1999, Sauer et al. 2011), pipits are listed as threatened under both COSEWIC and SARA for the province of Saskatchewan (Government of Canada 2009, COSEWIC 2009).

2.1.9 Vesper Sparrow

Vesper sparrows *(Pooecetes gramineus)* are considered grassland generalists, but some authors suggest that they prefer short, sparse vegetation with minimal litter accumulation in the dry short and mixed-grass prairie (Ehrlich et al. 1988, National Audubon Society 2001, Jones et al. 2002). Vesper sparrows are commonly found in areas dominated by cropland and pastures, especially those dominated by crested wheatgrass, and their abundances were negatively correlated with native vegetation in Manitoba (Jones et al. 2002). Rocks, shrubs, or tall vegetation are used for perching, whereas nests are built in a shallow depression in the ground and concealed using surrounding vegetation. Vesper sparrows can have up to three clutches in a season and lay three to four eggs per brood (Ehrlich et al. 1988, National Audubon Society 2001, Jones et al. 2002), although it is likely that they have fewer broods in more northern populations, such as those in Canada. Vesper sparrows are not currently listed under COSEWIC (COSEWIC 2009) with the population only declining by 0.5% per year in Saskatchewan (Sauer et al. 2011).

2.1.10 Western Meadowlark

Western meadowlarks (*Sturnella neglecta*) are one of the most abundant and widely distributed grassland songbird species with their range expanding farther eastward following the conversion of woodlands into agricultural lands. Western meadowlarks prefer sites with moderately dense vegetation and litter accumulation and are negatively associated with tall, dense, and/or woody vegetation with total abundances highest in lightly to moderately disturbed habitat (Ehrlich et al. 1988, National Audubon Society 2001, Fritcher et al. 2004, Davis et al. 2008). Breeding territories tend to be larger than most other grassland species with meadowlarks often being negatively associated with fragmentation and non-native habitat in the larger landscape (Davis et al. 2008).

Western meadowlarks arrive on the northern prairies in late March to early April and build a domed nest in a shallow depression in the ground with interwoven grass and forbs. Individual pairs can have up to two broods with three to seven eggs in more temperate climates. Diet consists of a mixture seeds, grains, and insects with insects being the main food consumed during the breeding season (Ehrlich et al. 1988, National Audubon Society 2001). Western meadowlarks are not currently listed under COSEWIC (COSEWIC 2009) but are declining by 2.8% per year in Saskatchewan (Sauer et al. 2011)

2.2 Fire

The effect of fire on grasslands is dependent on season, intensity, frequency, topography, and climate (Wright and Bailey 1982, Collins and Barber 1986, Wendtland and Dodd 1990, Shay et al. 2001). A study on charcoal fragments found in four lakes in North and South Dakota and northeastern Montana concluded that the fire return interval in the mixed-grass prairies was extremely variable and could not accurately be assessed (Umbanhowar 1996). Nonetheless, there have been some attempts to quantify the historical fire return interval. For grassland ecosystems with rolling hills it was estimated that the fire return interval was likely very short and was probably every 2 to 5 years. In areas with more variable topography (i.e. larger hills and coulees can act as a barrier to fire movement) it was estimated that the return frequency might be closer to every 20 to 30 years (Wright and Bailey 1982).

The estimated return interval for fires in the Canadian mixed-grass prairies, pre-colonization, has been estimated to be 5 to 10 years (Wright and Bailey 1982). Regardless of the actual historical fire return interval, most authors agree that managers should vary the time between prescribed fires to better mimic the highly variable nature of the prairies (Wendtland and Dodd 1990, Umbanhowar 1996).

My study examined the effects of wildfires, which may have a different effect on vegetation than prescribed burns. Prescribed burns are generally set in the spring or fall, while wildfires tend to occur in the late summer when drought conditions arise and vegetation biomass is at a peak. As such, prescribed burns tend to have less of an impact on the vegetation community than wildfires since they tend to burn less intensely (vegetation is still green in the spring) or occur after the growth season has ended (and after the songbird breeding season has passed). However, both prescribed burns and wildfires significantly impact litter accumulation and reduce standing biomass (Shay et al. 2001, Erichsen-Arychuk et al. 2002). Thus while the results from this study are based on the effects of a late summer wildfire they should still be used to guide the use of prescribed burns provided they are set in the fall. Early spring burns might disrupt songbird species that have already established breeding territories while fall burns, like late summer burns, would have a smaller impact on the songbird community as nesting has already finished and the young fledged. Additionally, in a semi-arid climate such as the northern mixed-grass prairie, vegetation growth may be largely finished due to a lack of available moisture further making the effects of a fall prescribed burn and late summer wildfire similar.

Fire is an important factor in maintaining a healthy grassland ecosystem. In general, a fire reduces standing biomass, vegetation becomes shorter and sparser, the community becomes grass dominated with fewer forbs (early successional), and litter accumulation is greatly reduced (Madden et al. 1999, Shay et al. 2001, Collins and Smith 2006). This change in the vegetation community is transitional, and grasslands tend to return to a pre-burned state within 2 to 5 years, depending on climatic conditions and the intensity of the burn. The vegetation will become taller, denser, with more shrubs and forbs, and more litter (Madden et al. 1999). In semi-arid areas typical of the northern mixed-grass prairies, litter can take years to re-accumulate to pre-burn levels. One study in western North Dakota concluded that a *Stipa comata*-dominated community required at least four years to recover after an August wildfire; more northern and/or arid grassland ecosystems may take considerably longer to recover (Erischsen-Arychuk et al. 2002).

Some studies have found a decrease in grassland production in the years immediately following a burn. This decrease is believed to be caused by the removal of accumulated litter and standing biomass, leading to lower soil moisture availability and increased topsoil erosion (Shay et al. 2001, Erichsen-Arychuk et al. 2002). In contrast, other studies have found an increase in grassland production in the years immediately following a burn, which is believed to be due to an increase in available nutrients and an increase in topsoil temperature leading to earlier seed germination (Shay et al. 2001, Erichsen-Arychuk et al. 2002). Whether a system has increased or decreased productivity following a burn is strongly tied to climatic conditions; a year with sufficient rain may have increased growth, while a drier year may have decreased growth. Since water availability is the most limiting factor for plant growth in the northern mixed-grass prairie, fire may have an overall negative impact on vegetation growth in GNPC (Shay et al. 2001, Erichsen-Arychuk et al. 2002). Studies have found that northern grassland productivity declined by 30-40% up to 3 years after the initial fire. This decrease was linked to the amount of rainfall in the growing season as the removal of litter increases water evaporation from the soil and makes the system more dependent on rainfall (Shay et al. 2001, Erichsen-Arychuk et al. 2002).

2.3 Climatic Variation

The North American mixed-grass prairie ecosystem has variable climatic conditions with years of drought interspersed with years of increased precipitation (Shay et al. 2001, Bailey et al. 2010). Thus a long-term study with a sampling period that includes at least one wet-dry cycle is needed to determine the long-term effects of fire and to make recommendations on conditions under which it would be most beneficial to allow wildfires to burn.

The climate has a major impact on wildfires over a wide range of spatial and temporal scales. At an annual time scale, the amount of precipitation strongly influences fuel loads as vegetation growth increases with moisture availability. Additionally, an increase in the frequencies of intense storms also increases the chances that there will be lighting strike that will ignite a wildfire (McKenzie et al. 2011). Over a longer time scale, climatic variability often results in wet and dry cycles that can last for a decade or more (Shay et al. 2001, Bailey et al. 2010). Current climate change models predict that the North American prairies will see an increase in wildfires as temperatures and the frequency of intense thunderstorms increase (Bailey et al. 2010, McKenzie et al. 2011). Increased precipitation has actually been linked to an increase in wildfires in ecosystems such as the prairie, where vegetation growth is restricted by lack of precipitation. The fuel load in these ecosystems tends to be patchy and the increase in vegetation growth associated with a wet summer results in a significant increase in the potential fuel load. Wildfires are most common during dry spells in a wet climate cycle (McKenzie et al. 2011).

The 20th century has been an anomaly for the prairies. Outside of the 1930's there have not been any prolonged droughts. There was a severe but short drought from 1999 to 2002 but otherwise the century has been well above average for precipitation. Historical data indicates that there was much more variability in precipitation in previous centuries, with one long term drought predicted to occur every 50 years (Bailey et al. 2010). The average historical monthly precipitation and the total monthly precipitation for each study year are listed in Table 1. Unfortunately, data for June through August 2010 and May through August 2011 were gathered by an alternate, although nearby, weather station as Environment Canada only listed data for the Val Marie southeast station. Due to differences in topography and the variability and patchiness of the local weather, the data collected from the Val Marie station versus the Val Marie southeast station varied, sometimes significantly, for the months where data were collected for both. The summer of 2009 was significantly drier than normal and June and August 2008 appear to have been unusually wet. April, May, and August in 2010 and May and July in 2011 were significantly wetter than the historical average and discussions with local landowners indicated that 2010 and 2011 were among the wettest springs in the last 50 years. Overall there was a large annual variation between years and months in total precipitation and this likely had a significant impact on vegetation growth and in turn on the settlement patterns of local songbirds. This large variation in precipitation supports the need for long term studies in the mixed-grass prairie since conclusions drawn from short-term studies cannot be used in guiding management over the long term.

Table 1. The average precipitation (mm) for the years 1971 through 2000 per month and the total precipitation (mm) per month per year for 2007 through 2011. Data collected by Environment Canada at the Val Marie weather station (location: 49.370, -107.848) in southern Saskatchewan (source: Government of Canada 2011).

Month	Avg. precipitation 1971-2000 (mm)	Year	Total precipitation (mm)
April	23.4	2007	50.8
		2008	6.2
		2009	15.6
		2010	43.4
		2011	21.5*
May	51.7	2007	43.8
		2008	43.4
		2009	21.7
		2010	72.9
		2011	88.4*
June	65.3	2007	66.9
		2008	130.6
		2009	37.8
		2010	27.6*
		2011	75.0*
July	54.0	2007	33.8
		2008	50.8
		2009	34.8
		2010	22.8*
		2011	71.3*
August	33.8	2007	35.8
		2008	49.2
		2009	31.8
		2010	63.2*
		2011	40.1*

*data is collected from the Val Marie southeast station located at 49.058, -107.586

2.4 Grazing

Grazing by livestock, usually cattle, is one of the primary economic uses of mixed-grass prairies (Fondell and Ball 2004). Long-term selective grazing can lead to significant changes in vegetation structure and species composition (Milchunas et al. 1988, Gordon and Prins 2008). Light to moderate grazing has been found to increase vegetation diversity and productivity, while heavy grazing can result in decreased diversity and productivity (Collins and Baber 1986, Harrison et al. 2003). Similar to fire, the effects of grazing can be highly variable and are impacted by topography, climate, intensity, seasonality, and evolutionary history of the ecosystem (West 1993, Harrison et al. 2003). Grazing results in a reduction in biomass (defoliation and shorter and sparser grasses) and a decrease in litter accumulation and soil compaction through trampling (Fondell and Ball 2004). In short and mixed-grass prairies (i.e. semiarid ecosystems) with a stronger evolutionary history of grazing, moderate grazing intensities tend to have a relatively small effect on the vegetation community when compared to similar grazing intensities in the tall grass prairie (Milchunas et al. 1988, Milchunas and Lauenroth 1993, West 1993).

Grazing intensity varies in time and space as animals preferentially select patches with a greater abundance of palatable plants and/or closer to shelter and water (Collins and Smith 2006). In small pastures where cattle are unable to selectively forage, vegetation structure tends to be the same throughout the pasture and the habitat is homogenous. One way to maintain habitat heterogeneity is to manage livestock in larger pastures, where cattle have the freedom to preferentially forage in the most desirable locations (Koper et al. 2008). It has been hypothesised that grazing, at moderate to light intensities, enhances vegetation diversity by reducing biomass and reducing above-ground competition among species and is expected to have a stronger positive effect on diversity in systems that have higher productivity due to increased precipitation and/or nutrient rich soil (i.e. tall grass prairie). The mixed-grass prairies, with a long evolutionary history of grazing and low productivity (semi-arid), is relatively resilient to grazing intensities and vegetation species richness is not expected to be significantly impacted by light to moderate grazing (Milchunas et al. 1988, Milchunas and Lauenroth 1993, Harrison et al. 2003, Gordon and Prins 2008). However, many songbird species are sensitive to grazing intensity since it is primarily vegetation structure, and not species composition, that drives habitat selection (Davis et al. 1999, Brawn et al. 2001, Bakker et al. 2002). Grazing at light intensities is unlikely to greatly impact vegetation structure but moderate intensities or higher will have a significant impact on the abundances of some species. While overall songbird species richness may not change with increasing grazing, the community may shift towards species that prefer bare ground and sparse vegetation (Brawn et al. 2001, Gordon and Prins 2008).

2.5 Interaction between Fire and Grazing

Spatial and temporal heterogeneity is found in all natural ecosystems and is the result of multiple interactions between abiotic (i.e. fire, topography, climate) and biotic (i.e. animal grazing, vegetation community) factors operating at multiple scales (Collins and Smith 2006). Heterogeneity is generally recognized as being an important factor in maintaining high species diversity. Disturbances, such as fire and grazing, are often responsible for creating habitat heterogeneity and promoting species diversity (Brawn et al. 2001, Harrison et al. 2003, Fuhlendorf and Engle 2004, Joern 2005, Ahlering et al. 2006). Disturbed patches usually support a novel community compared with undisturbed patches but this community is temporary and will eventually return to a pre-disturbance community. Thus disturbances and the resulting habitat heterogeneity create a mosaic of habitat types at multiple successional stages that support different species and varied ecosystem processes (Ahlering et al. 2006, Collins and Smith 2006, Fuhlendorf et al. 2006).

Grassland conservation in North America must consider the interaction between fire and grazing since they are the primary drivers of the ecosystem. Fire and grazing interact through a series of positive and negative feedback loops; the sum of the interaction is greater than either disturbance alone (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006). Several studies have found that cattle are attracted to recently burned areas. For example, cattle may spend over 70% of their time grazing in burned plots, even if only one-third of the pasture had been burned (Fuhlendorf and Engle 2004). Recently burned areas have younger above-ground vegetation, which is higher in protein and lower in crude fibre, and is more palatable to grazers. Further, the removal of litter and canopy makes the forage more accessible (Erichsen-Arychuk et al. 2002, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006, Powell 2006).

Fire and grazing interact to create a shifting mosaic of vegetation communities at various stages of succession (Fuhlendorf and Engle 2004, Joern 2005, Powell 2006). Fire and grazing tend to create a negative feedback loop. Since grazing animals such as cattle preferentially select vegetation in recently burned patches, fire effectively promotes local grazing. Grazing, in turn, suppresses the chance of a future fire by maintain a lower fuel load. Patches that have not been burned for several years are selected against by grazing animals and the increasing fuel load increases the chance of an intense fire occurring (Harrison et al. 2003, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006). Mixed-grass prairies that are grazed after burning require 3 to 5 years to recover to a pre-burned vegetation community, especially litter accumulation, compared to ungrazed-burned areas that require 2 to 3 years (Erichsen-Arychuk et al. 2002). As with all disturbances in the mixed-grass prairie, the return interval and recovery rate is highly variable and dependent on several factors. Depending on the current climatic cycle (i.e. wet vs. dry) recovery can take significantly longer since it is the rate of vegetation growth that largely determines recovery length. Additionally, the intensity of burning and grazing can vary greatly at the local scale and are impacted by topography, creating a patchy habitat within a uniform treatment.

North American grassland birds evolved in the presence of frequent and often intense disturbances. The declines in grassland species is often attributed to changing land use practices, including the conversion of native habitat to agricultural lands and the removal of disturbances (Herkert 1995). Habitat heterogeneity has largely been lost from the prairies now that fires are suppressed and bison have mostly disappeared. Cattle, the most common ungulate to replace bison, are usually managed to acheive 50% removal of biomass across the entire landscape, creating a relatively homogeneous habitat (Fuhlendorf and Engle 2004). Grassland songbirds use vegetation structure as a cue for habitat suitability; fire and grazing both have a strong impact on vegetation structure. Vegetation structure influences the availability of food, nesting materials, and the risk of predation (Davis et al. 1999, Brawn et al. 2001, Fondell and Ball 2004, Fritcher et al. 2004). A study in western Montana found that all common grassland species were strongly correlated with vegetation structure and that vegetation density and height were the best predictors of presence or absence for each species (Fondell and Ball 2004). Therefore, grazing and burning are likely to have strong effects on the densities and occurrences of many grassland songbird species.

3.0 METHODS

3.1 Study Site

The study area is the East Block of Grasslands National Park of Canada (GNPC) and the adjacent Mankota Community Pastures (MCP), which are located in the northern mixed-grass prairies of southern Saskatchewan. The park was founded in 1988 and encompasses a large area of relatively undisturbed (most of the land has never been cultivated or heavily grazed) and continuous prairie habitat (Henderson 2006, Koper et al. 2008). The average annual precipitation is 324.5 mm with a mean temperature of 18.8^{o}C in July. The soil is relatively nutrient poor and the growing season averages 170 days although the length of day during the summer (sunshine hours) is among the highest in the prairies (Parks Canada 2005). Thus the potential for vegetation growth is high, although growth is usually limited by water availability, and woody vegetation is limited to shrubs (Csillag et al. 2001). Indeed, there are no trees in this study area. The upland vegetation community is dominated by needle-and-thread grass (*Stipa comata*), June grass (*Koeleria macrantha*), blue grama grass (*Bouteloua gracilis*), western wheatgrass (*Pascopyrum smithii*), sage (*Artemisia* spp.), sedge (*Carex* spp.), and western snowberry (*Symphoricarpos occidentalis*).

3.2 Experimental Design

Songbird and vegetation surveys, in 2008 and 2009, were conducted in 72 plots with 17 plots in unburned-ungrazed, 21 in unburned-grazed, 18 in burned-grazed, and 16 in burned-ungrazed (Fig. 1). Due to time and budget constraints in 2007 only 51 plots were sampled and a change in grazing treatment in a grazed pasture in 2010 resulted in only 65 plots being studied for both 2010 and 2011. The study sites were limited to upland pastures within GNPC and MCP. My study is a part of a larger ten year adaptive management grazing experiment, the "Biodiversity and Grazing Management Area Experiment" that will examine the effects of grazing intensity on songbird and vegetation biodiversity in native mixed-grass prairie (Henderson 2006). The unburned plots used in my study were previously established in experimental pastures within GNPC and MCP. Pastures in MCP have been moderately grazed (removal of 50% of biomass) for the last 20 years, while pastures used for this study in GNPC have been ungrazed for the last 20 years (Parks Canada 2005). Burned sites were the result of multiple wildfires in late summer 2006 ranging in size from 70 to 750 ha; plots were established in both grazed and ungrazed upland sites that had been burned. Songbird data was collected for 2007 through 2011 and vegetation data was collected for 2007 through 2010.

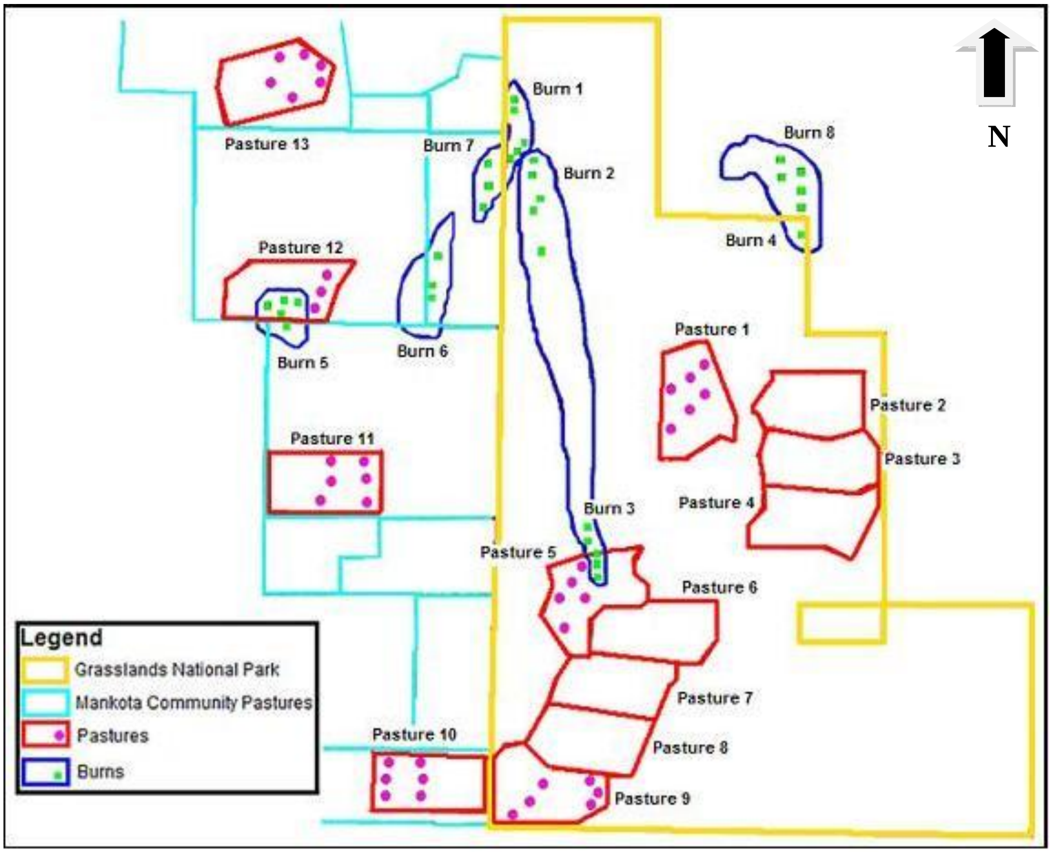

Figure 1. Map showing location of study plots (17 unburned-ungrazed, 21 unburned-grazed, 18 burned-grazed, and 16 burned-ungrazed) within Grasslands National Park of Canada and Mankota Community Pastures. Plots within the boundary of Grasslands National Park are ungrazed (burned or unburned), while plots in Mankota Community Pastures are grazed (burned or unburned) and burn 8 is grazed.

3.3 Songbird Surveys

Relative songbird abundances were assessed using five-minute, 100 m radius point count plots; all birds seen or heard within the plot were recorded. Point count plot centers were placed at least 250 m apart to ensure that birds were not counted in more than one plot. Surveys were not conducted when raining, foggy, or if wind exceeded 16 km/hr (Lueders et al. 2006; Koper and Schmiegelow 2006). Surveys were conducted between sunrise and 1000 hours in the first two weeks of June. All observers were trained in visual and auditory identification prior to conducting point counts to ensure accurate detection and identification and point counts were kept short so that individual birds were not double counted and to maximize sampling efficiency (Dettmers et al. 1999). Songbird data in 2007 and 2008 was collected by Krystle White and 2 assistants, in 2009 by Maggi Sliwinski and 4v assistants, 2010 by both Maggi Sliwinski and myself plus 2 additional assistants, and in 2011 by myself plus 4 assistants.

3.4 Habitat Structure

Vegetation structure including height, density, and litter depth was measured at each point-count plot in July. Vegetation density was determined using a visual obstruction reading (VOR) on a Robel pole based on the height of the vegetation that visually obstructed 50% of the pole (at a distance of 4 m and a height of 1 m) (Robel et al. 1970). Vegetation height (height of the tallest plant within a 1x0.5m frame against the Robel pole) and litter depth (litter layer on the ground) was measured using a metre stick. The number of vegetation samples taken per plot varied between years and burned and unburned plots; a minimum of four samples per plot (one in each cardinal direction) per site were measured each year. In 2007, vegetation structure was only measured in three point counts per pasture (compared with six points in all other years) and only four (compared with eight for all other years) frames per point count.

3.5 Data Analysis

Eleven songbird species, those that occurred in at least 10% of point count plots, were analysed: Baird’s sparrow, brown-headed cowbird, chestnut-collared longspur, clay-colored sparrow, grasshopper sparrow, horned lark, McCown’s longspur, Sprague’s pipit, Savannah sparrow, vesper sparrow, and western meadowlark. The results presented in this paper focus on the interaction between year, burning, and grazing to evaluate how differences in the effects of burning and grazing changed with time since burned. To standardize sampling efforts across years, only one round of songbird surveys was used (the second round, which was collected in the first and second week of June) as only one round was collected in burned plots in 2007. The interactions between year and treatment were also analysed for vegetation height, density, and litter depth.

Species richness was calculated using the total number of songbird species (raptors and shores birds were excluded) per point-count plot. The Shannon-Wiener heterogeneity index was used to calculate heterogeneity since it is sensitive to rare species within the community (Kempton 1979). Rare species are of special interest because they may include species that are at risk in the northern mixed-grass prairies.

Sørensen's quantitative index was used to test for similarity (songbird species abundance and richness) between treatments across years. Sørensen's quantitative index considers differences in species abundances between two treatments and measures community similarity based on species diversity and relative abundances (Jongman et al. 1995, Huste and Boulinier 2011). Since the index is sensitive to sample size, I randomly selected 15 plots to represent each treatment type as there were only 15 unburned-ungrazed plots in 2010. Regression analysis was used to test for changes in Sørensen's quantitative index over time from 2007 to 2011.

I used generalized linear mixed models (GLMMs), in SAS version 9.2, to analyze songbird and vegetation data. Mixed models are beneficial when analysing data from a clustered study design as a random variable (i.e. a grouping variable) can be incorporated to control for correlation among plots within sites. For clustered study designs, the statistical power of GLMMs is optimized since the values per plot do not need to be averaged across site and more information about the variation among plots can be retained (Quinn and Keough 2002, Bolker et al. 2008). Incorporating both random (pasture and point-count plots) and fixed effects (burned, grazed, year) also allows for inferences to be made beyond the sites surveyed (Bolker et al. 2008). Additionally, GLMMs can accommodate non-normal distributions of response variables, and both categorical (burned and grazed) and continuous (year) independent variables (Quinn and Keogh 2002). Unburned-ungrazed plots were used as controls to assess songbird abundances and vegetation measurements in burned-grazed, burned-ungrazed, and unburned-grazed plots.

An alpha value of 0.10 was used for all analyses to reduce the chances of a Type II error (determining that there is no effect when one did occur as compared to a Type I error were an effect is found when one did not occur). While an alpha value of 0.05 is often used in biological studies, reducing the risk of committing a Type I error, it is generally more important for studies that focus on environmental monitoring and conservation to ensure that a potential effect is not missed (i.e. concluding that a treatment had no effect) (Quinn and Keough 2002).

4.0 RESULTS

4.1 Effects of Burning and Grazing on Grassland Songbirds

4.1.1 Species Abundances

A total of 16 songbird species was observed during surveys from 2007 through 2011 (Appendix VI). The most abundant species, occurring in 90% of point count plots, were Sprague's pipits. Baird's sparrows and chestnut-collared longspurs occurred in 80% of plots and horned larks and Savannah sparrows occurred in 50% of plots; all remaining species occurred in 20% of plots or less. Although both grasshopper sparrows and McCown's longspurs occurred in 10% of plots, the statistical models could not converge; thus a brief qualitative discussion is presented for both species. McCown's longspurs were generally most abundant in grazed plots and only occurred in unburned-ungrazed plots in 2007. Conversely, grasshopper sparrows were most abundant in unburned-ungrazed plots and did not occur in burned-grazed plots until 2011. The mean abundance and standard deviation for each species per plot, treatment, and year are listed in Appendices I through V.

The top three most abundant songbird species per treatment for each year are listed in Table 2. In 2007, 2008, and 2009 chestnut-collared longspurs were the most abundant species in both burned-grazed and burned-ungrazed pastures. They remained the most abundant species in burned-grazed pastures in 2010 while Baird's sparrow became the most abundant species in burned-ungrazed pastures in 2010 and burned-grazed pastures in 2011. Overall, Baird's sparrows, chestnut-collared longspurs, and Sprague's pipits were the three most abundant songbirds within the study area for all years.

Table 2. Top three most abundant songbird species occurring in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures from 2007 through 2011 in Grasslands National Park of Canada.

Year	**Treatment**	**Species**	**Mean abundance per plot**
2007	Burned-grazed	Chestnut-collared longspur	2.94±1.66
		Horned lark	1.06±1.06
		Baird's sparrow	0.89±1.08
	Burned-ungrazed	Chestnut-collared longspur	2.38±1.50
		Baird's sparrow	1.19±1.17
		Horned lark	1.13±0.72
	Unburned-grazed	Baird's sparrow	2.10±1.09
		Sprague's pipit	1.81±0.75
		Chestnut-collared longspur	1.57±1.40
	Unburned-ungrazed	Baird's sparrow	2.94±1.34
		Sprague's pipit	1.82±0.95
		Horned lark	0.41±0.71
2008	Burned-grazed	Chestnut-collared longspur	2.50±1.47
		Baird's sparrow	1.50±1.50
		Horned lark	1.11±1.02
	Burned-ungrazed	Chestnut-collared longspur	2.69±1.58
		Baird's sparrow	1.38±1.02
		Sprague's pipit	1.13±0.72
	Unburned-grazed	Chestnut-collared longspur	2.71±1.45
		Baird's sparrow	2.29±1.31
		Sprague's pipit	2.05±1.20
	Unburned-ungrazed	Baird's sparrow	3.00±1.22
		Sprague's pipit	2.00±0.71
		Chestnut-collared longspur	1.06±1.03
2009	Burned-grazed	Chestnut-collared longspur	3.00±1.19
		Baird's sparrow	1.11±1.13
		Horned lark	1.11±0.90
	Burned-ungrazed	Chestnut-collared longspur	2.13±1.31
		Baird's sparrow	1.63±1.31
		Sprague's pipit	1.13±0.81
	Unburned-grazed	Chestnut-collared longspur	2.29±1.10
		Sprague's pipit	1.81±0.81
		Baird's sparrow	1.67±0.80
	Unburned-ungrazed	Baird's sparrow	2.29±0.99
		Sprague's pipit	2.18±1.01
		Grasshopper sparrow	0.94±0.97

Table 2. continued

Year	**Treatment**	**Species**	**Mean abundance per plot**
2010	Burned-grazed	Chestnut-collared longspur	3.11±1.68
		Sprague's pipit	2.00±0.59
		Baird's sparrow	1.28±1.13
	Burned-ungrazed	Baird's sparrow	2.81±1.05
		Sprague's pipit	2.38±1.09
		Chestnut-collared longspur	1.56±0.89
	Unburned-grazed	Chestnut-collared longspur	3.00±1.41
		Baird's sparrow	2.53±0.74
		Sprague's pipit	2.33±0.82
	Unburned-ungrazed	Baird's sparrow	2.94±0.90
		Sprague's pipit	2.35±0.86
		Chestnut-collared longspur	1.65±1.00
2011	Burned-grazed	Baird's sparrow	1.83±0.92
		Chestnut-collared longspur	1.83±1.25
		Sprague's pipit	1.56±0.78
	Burned-ungrazed	Baird's sparrow	1.67±1.05
		Sprague's pipit	1.60±0.63
		Chestnut-collared longspur	1.53±1.06
	Unburned-grazed	Sprague's pipit	2.33±0.49
		Chestnut-collared longspur	2.00±1.00
		Baird's sparrow	1.80±0.56
	Unburned-ungrazed	Baird's sparrow	2.00±0.94
		Sprague's pipit	1.88±0.86
		Grasshopper sparrow	1.12±0.86
		Savannah sparrow	1.12±0.86

4.1.2 Species Richness and Diversity

Songbird species richness and diversity were both positively associated with time ($\beta=1.1706$, $p=<0.0001$ and $\beta=0.8270$, $p=<0.0001$ respectively) but were not significantly associated with burning or grazing. Based on regression analysis (Tables 3,4), the only treatments that increased or decreased significantly in Sørensen's quantitative similarity index from 2007 to 2011 were the unburned-ungrazed and burned-ungrazed pastures ($R^2=0.7574$, $p=0.0550$) which showed an increased from 51.49% similarity in 2007 to 82.20% similarity in 2011. The difference between burned-grazed and burned-ungrazed plots increased slightly with time since burned, from 84.11% to 80.37%. The difference between burned-grazed and unburned-grazed decreased (from 68.20% in 2007 to 79.87% in 2010) until the fifth year post burn when it increased to 51.81% in 2011. The communities in burned-ungrazed and unburned-grazed pastures and unburned-ungrazed and unburned-grazed pastures have remained similar over time. The similarity between burned-grazed and unburned-ungrazed pastures was quite variable (48.04% in 2007, 61.42% in 2008, and 50.00% in 2009).

Table 3: Songbird species richness, number of species in common and Sørensen's quantitative indices for burned-grazed (BG), burned-ungrazed (BUG), unburned-grazed (UBG), and unburned-ungrazed (UBUG) pastures for 2007 through 2011.

Year	Total no. of species per treatment		No. of species in common	Sørensen's Quantitative index
	BG	**BUG**		
2007	12	10	10	84.11
2008	11	11	10	82.28
2009	10	9	8	82.24
2010	11	12	9	69.62
2011	12	10	10	80.37
	BG	**UBG**		
2007	12	9	8	68.20
2008	11	10	9	75.84
2009	10	10	8	79.46
2010	11	12	9	79.87
2011	12	11	10	51.81
	BG	**UBUG**		
2007	12	11	10	48.08
2008	11	11	8	61.42
2009	10	9	7	50.00
2010	11	12	8	66.24
2011	12	10	10	63.06
	UBUG	**BUG**		
2007	11	10	10	51.49
2008	11	11	9	58.96
2009	9	9	7	56.19
2010	12	12	10	87.23
2011	10	10	10	82.20
	UBUG	**UBG**		
2007	11	9	9	76.10
2008	11	10	8	68.84
2009	9	10	7	60.91
2010	12	12	11	82.39
2011	10	11	9	75.35

Table 3. continued

Year	Total no. of species per treatment		No. of species in common	Sørensen's Quantitative index
	BUG	**UBG**		
2007	10	9	8	72.99
2008	11	10	9	83.00
2009	9	10	7	84.40
2010	12	12	11	79.88
2011	10	11	9	70.53

Table 4. Results from regression analysis to determine if the Sørensen's quantitative similarity indices changed over time from 2007 through 2011 in burned-grazed (BG), burned-ungrazed (BUG), unburned-grazed (UBG), and unburned-ungrazed (UBUG) pastures.

Treatment	R^2	*p*-value
BG-BUG	0.3013	0.3380
BG-UBG	0.1503	0.5190
BG-UBUG	0.4525	0.2134
UBUG-BUG	0.7574	**0.0550**
UBUG-UBG	0.0055	0.7055
BUG-UBG	0.0430	0.7378

4.2 Effect of Year on Grassland Songbirds in Burned and Grazed Sites

Species abundances and vegetation height, density, and litter depth all increased with time. Thus an increase in any of these variables was only potentially driven by grazing or burning if the rate of change was different from that in the unburned-ungrazed plots. The parameter estimates for effect of year, burning, grazing, and the interaction between burning and grazing, and year*burning*grazing for songbird species and vegetation structure respectively are listed in Tables 5 and 6. To further illustrate the results of Tables 5 and 6, the mean abundances in burned-grazed, burned-ungrazed, unburned-grazed, unburned-ungrazed pastures for songbird species and vegetation structure respectively were graphed against year in Figures 2 through 7 and 8 through 10. A lack of significance in the year*burned*grazed interaction term does not mean that burning or grazing alone did not significantly impact the species; just that the impact did not significantly change over time.

Baird's sparrow abundances increased over time in burned pastures, both grazed (β=0.2138, *p*=0.0059) and ungrazed (β=0.2314, *p*=0.0019) (Fig. 2), and were negatively associated with burning but not grazing. Chestnut-collared longspurs decreased over time in burned-grazed (β=-0.1996, *p*=0.0212) and burned-ungrazed (β=-0.2767, *p*=0.0029) (Fig. 3) pastures and were positively associated with burning and grazing. Clay-colored sparrows were negatively associated with grazing and showed a significant interaction between burning and grazing (β=4.8663, *p*=0.0760) and over time in unburned-grazed (β=0.7732, *p*=0.0598) (Fig. 4) pastures. Horned larks were positively associated with both burning and grazing and significantly associated with time in burned-ungrazed (β=-0.2837, *p*=0.0863) (Fig. 5) pastures. Sprague's pipit abundances increased over time in burned-grazed (β=0.2301, *p*=0.0062) and burned-ungrazed (β=0.2004, *p*=0.0170) pastures (Fig. 6) and were negatively associated with burning but not grazing. Western meadowlarks were significantly associated with time in burned-grazed pastures (β=0.3663, *p*=0.0844) (Fig. 7) but not with burning or grazing. Species that showed no significant association with time or treatment included brown-head cowbirds, Savannah and vesper sparrows.

Table 5. Interaction between year, burning, and grazing on songbird species abundances in Grasslands National Park of Canada from 2007 to 2011; year*unburned*ungrazed used as the control when analysing the interaction between year and treatment. Only species that showed at least one significant result listed.

Species	**Fixed Variable**	**Estimate**	***p*-value**
Baird's sparrow	Year	-0.0877	**0.0342**
	Burned	-1.1137	**0.0094**
	Grazed	-0.3716	0.2656
	Burned*Grazed	0.1391	0.7868
	Year*Burned*Grazed	0.2138	**0.0059**
	Year*Burned*Ungrazed	0.2314	**0.0019**
	Year*Unburned*Grazed	0.0389	0.5339
Chestnut-collared longspur	Year	0.1390	**0.0580**
	Burned	1.5803	**0.0041**
	Grazed	1.3116	**0.0106**
	Burned*Grazed	-1.1147	**0.0678**
	Year*Burned*Grazed	-0.1996	**0.0212**
	Year*Burned*Ungrazed	-0.2767	**0.0029**
	Year*Unburned*Grazed	-0.09431	0.2758
Clay-colored sparrow	Year	-0.1472	0.2489
	Burned	-1.2033	0.3889
	Grazed	-4.7110	**0.0444**
	Burned*Grazed	4.8663	**0.0760**
	Year*Burned*Grazed	0.2715	0.2149
	Year*Burned*Ungrazed	0.3363	0.1719
	Year*Unburned*Grazed	0.7732	**0.0598**
Horned lark	Year	-0.1048	0.3790
	Burned	1.3485	**0.0416**
	Grazed	1.1655	**0.0622**
	Burned*Grazed	-1.3551	**0.0912**
	Year*Burned*Grazed	-0.0486	0.7339
	Year*Burned*Ungrazed	-0.2837	**0.0863**
	Year*Unburned*Grazed	-0.1905	0.2015

Table 5. continued

Species	**Fixed Variable**	**Estimate**	**p-value**
Sprague's pipit	Year	0.0073	0.8763
	Burned	-0.9985	**0.0074**
	Grazed	-0.1497	0.5380
	Burned*Grazed	-0.0779	0.8600
	Year*Burned*Grazed	0.2301	**0.0062**
	Year*Burned*Ungrazed	0.2004	**0.0170**
	Year*Unburned*Grazed	0.0558	0.3916
Western meadowlark	Year	-0.1473	0.3529
	Burned	-0.3447	0.6625
	Grazed	-0.3650	0.6397
	Burned*Grazed	0.0819	0.9403
	Year*Burned*Grazed	0.3663	**0.0844**
	Year*Burned*Ungrazed	0.3130	0.1433
	Year*Unburned*Grazed	0.1859	0.3825

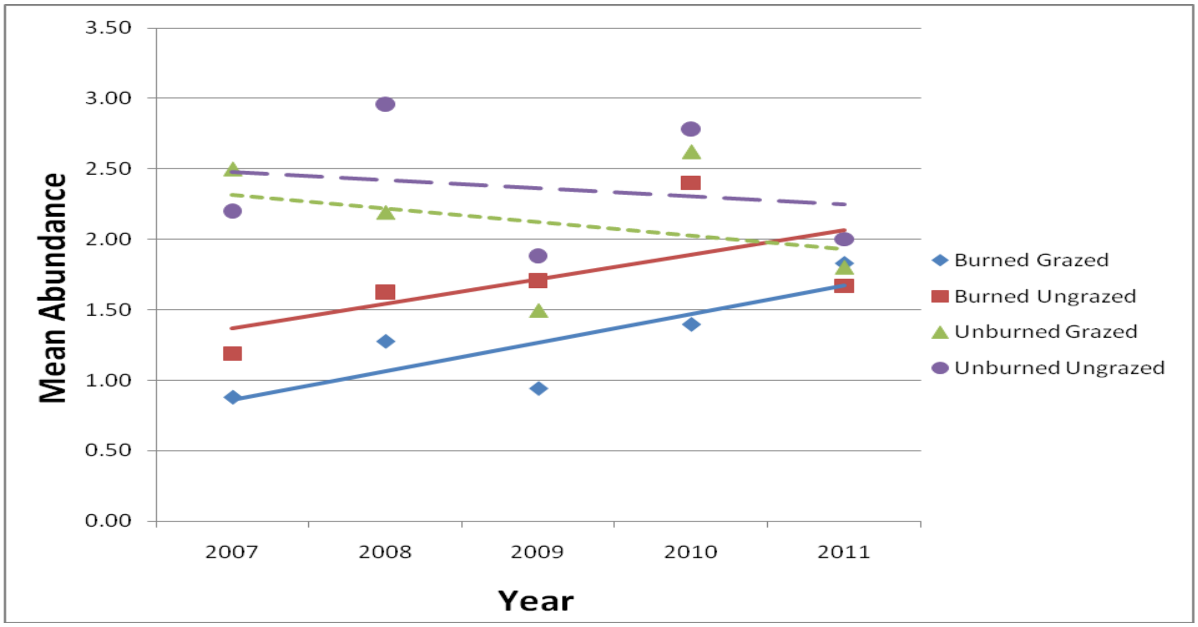

Figure 2. Mean abundance, per year (2007-2011), of Baird's sparrows in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

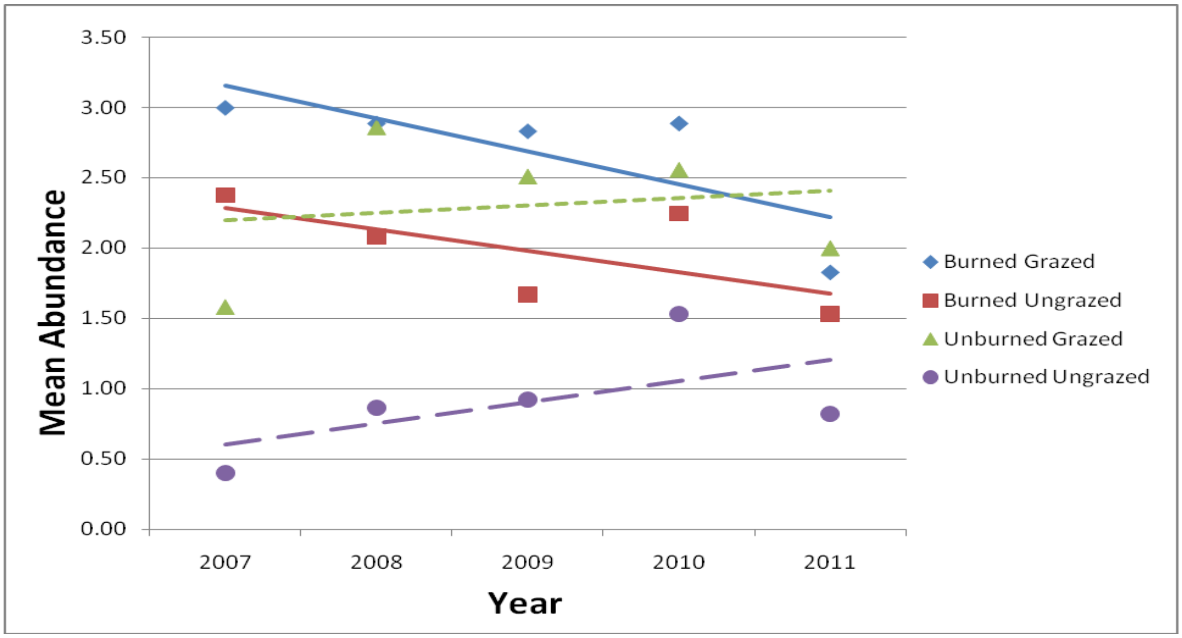

Figure 3. Mean abundance, per year (2007-2011), of chestnut-collared longspurs in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

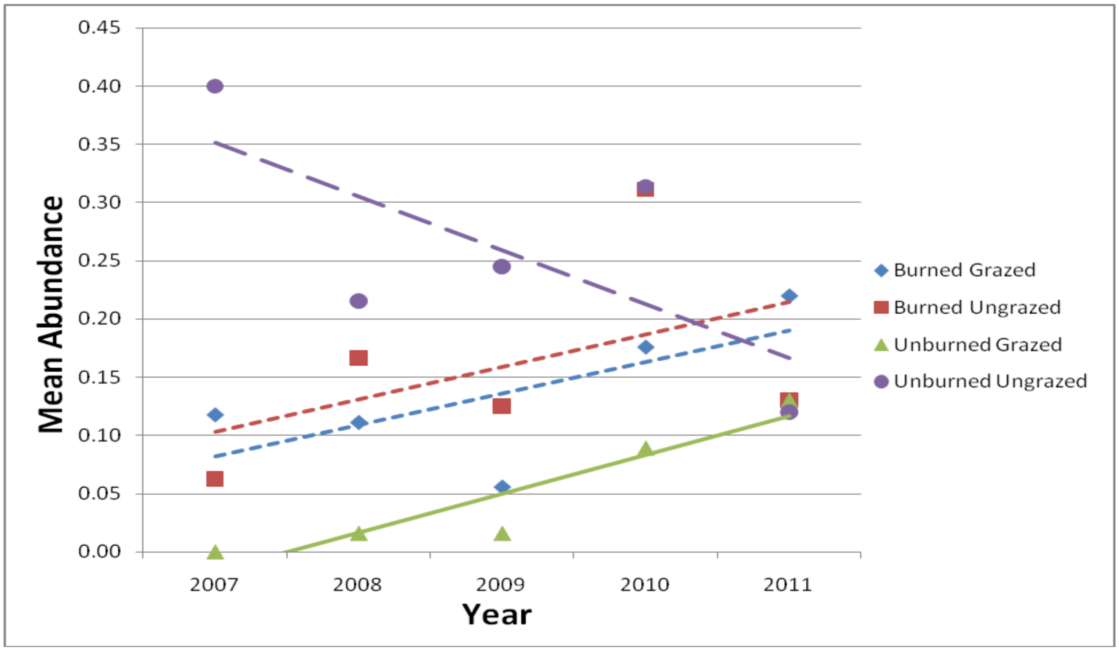

Figure 4. Mean abundance, per year (2007-2011), of clay-colored sparrow in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid line represents a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

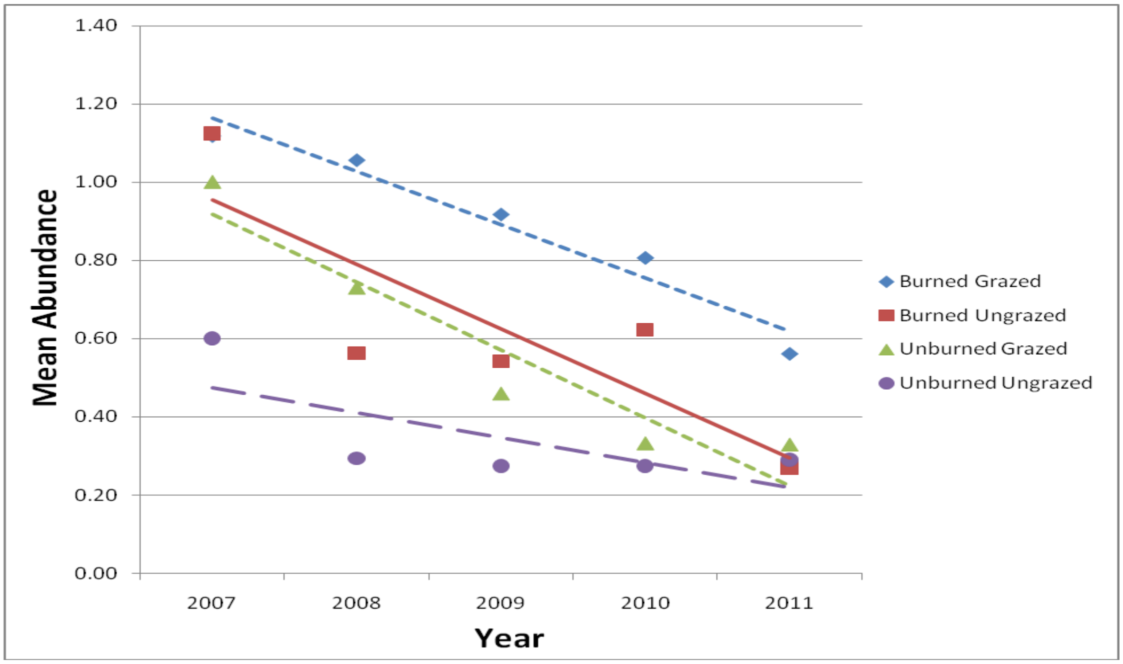

Figure 5. Mean abundance, per year (2007-2011), of horned larks in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid line represents a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

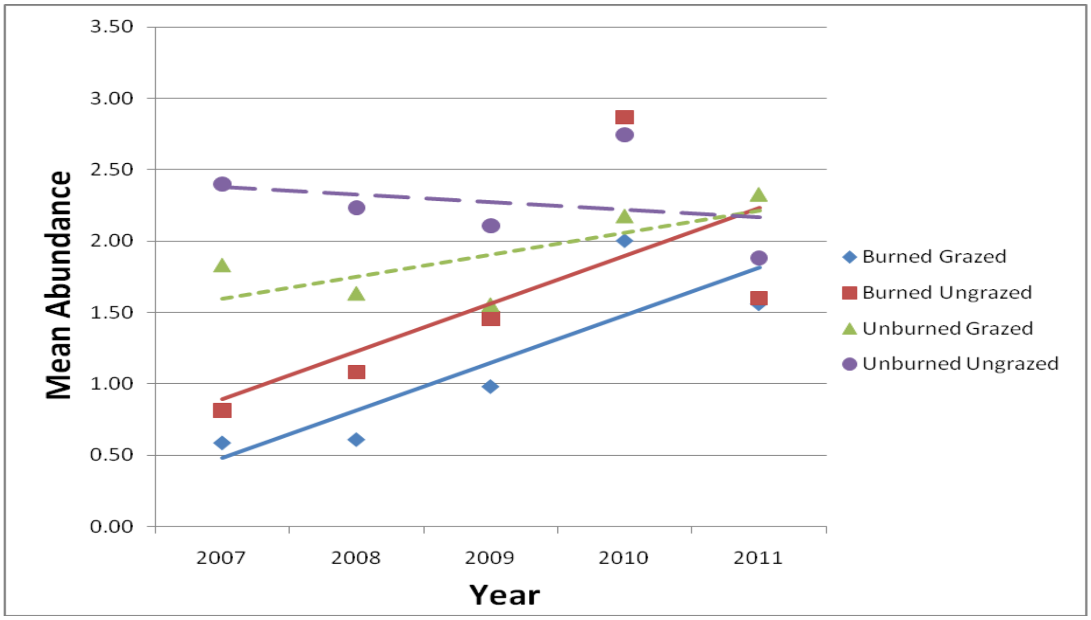

Figure 6. Mean abundance, per year (2007-2011), of Sprague's pipits in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

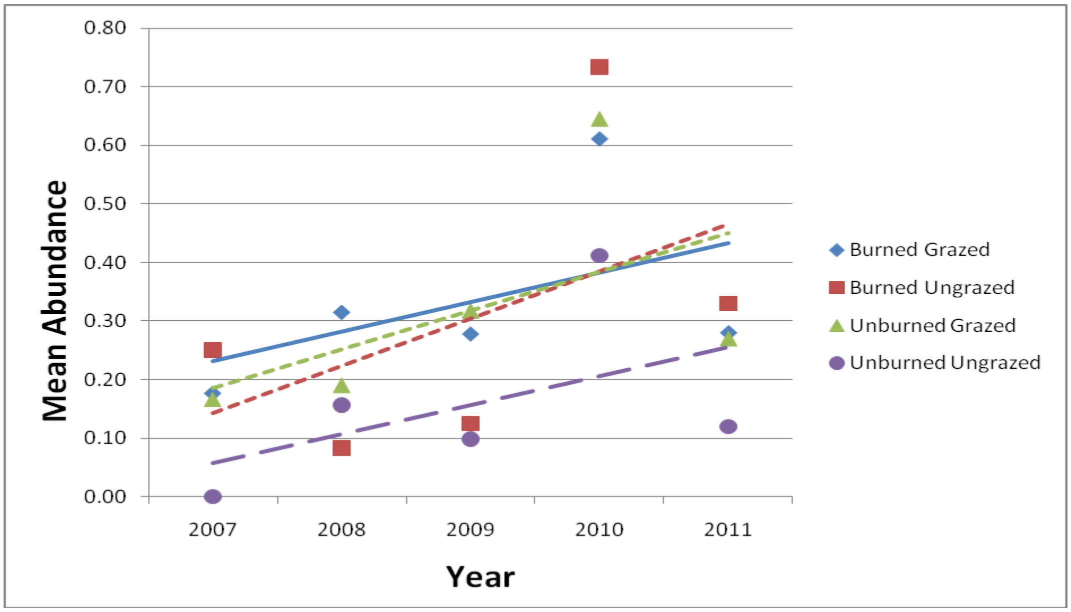

Figure 7. Mean abundance, per year (2007-2010), of western meadowlarks in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid line represents a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

4.3 Effect of Year on Vegetation Structure in Burned and Grazed Sites

Similar to songbird species richness and diversity, vegetation height (β=0.1608, *p*=<0.0001), density (β=0.8094, *p*=<0.0001), and litter depth (β=1.2957, *p*=<0.0001) were all positively associated with time. Vegetation height was significantly associated with time in burned-grazed, burned-ungrazed, and unburned-grazed pastures (Fig. 8). Vegetation density was significantly associated with time in burned-grazed and unburned-grazed pastures (Fig. 9) and positively associated with grazing (β=0.9192, *p*=0.0092). Litter depth was significantly associated with time in burned-grazed and unburned-grazed pastures (Fig. 10).

Since burning and grazing were not individually statistically significant when all four years of data were analysed together I separated vegetation data by year to evaluate effects of burning and grazing alone. Several additional relationships with burning and grazing appear when vegetation height and litter depth are separated by year. Vegetation height was negatively associated with burning in 2007 (β=-3.8906, *p*=0.0775), 2009 (β=-7.0685, *p*=0.0792), and 2010 (β=-10.3622, *p*=0.0262) while litter depth was negatively associated with burning in 2008 (β=-2.1972, *p*=-1.9007) and 2009 (β=-1.9007, *p*=0.0209) and with grazing in 2008 (β=-1.4914, *p*=0.0035), 2009 (β=-2.3556, *p*=0.0057), and 2010 (β=-1.8681, *p*=0.0724).

Table 6. Interaction between year, burning, and grazing on habitat structure in Grasslands National Park of Canada from 2007 to 2010; year*unburned*ungrazed used as the control when analysing the interaction between year and treatment.

Habitat characteristic	**Fixed Variable**	**Estimate**	**p-value**
Vegetation height	Year	0.1608	**<0.0001**
	Burned	0.1457	0.1762
	Grazed	0.1593	0.1453
	Burned*Grazed	-0.2120	0.1421
	Year*Burned*Grazed	-0.08078	**0.0042**
	Year*Burned*Ungrazed	-0.08589	**0.0031**
	Year*Unburned*Grazed	-0.07990	**0.0066**
Vegetation density	Year	0.8094	**<0.0001**
	Burned	0.1827	0.5394
	Grazed	0.9192	**0.0092**
	Burned*Grazed	-0.5358	0.1896
	Year*Burned*Grazed	-0.3331	**<0.0001**
	Year*Burned*Ungrazed	-0.0619	0.4404
	Year*Unburned*Grazed	-0.4524	**<0.0001**
Litter depth	Year	1.2957	**<0.0001**
	Burned	-0.6674	0.3256
	Grazed	0.4791	0.4832
	Burned*Grazed	0.5133	0.5605
	Year*Burned*Grazed	-0.8122	**<0.0001**
	Year*Burned*Ungrazed	-0.2701	0.1894
	Year*Unburned*Grazed	-0.8035	**0.0002**

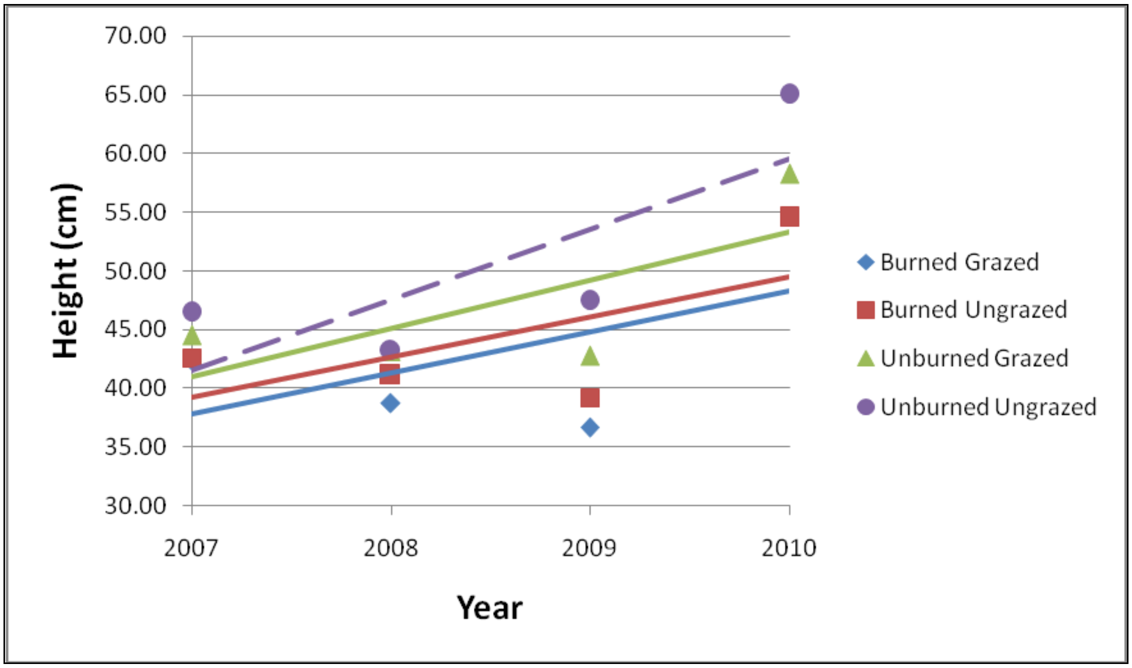

Figure 8. Vegetation height in cm, per year (2007-2010), in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

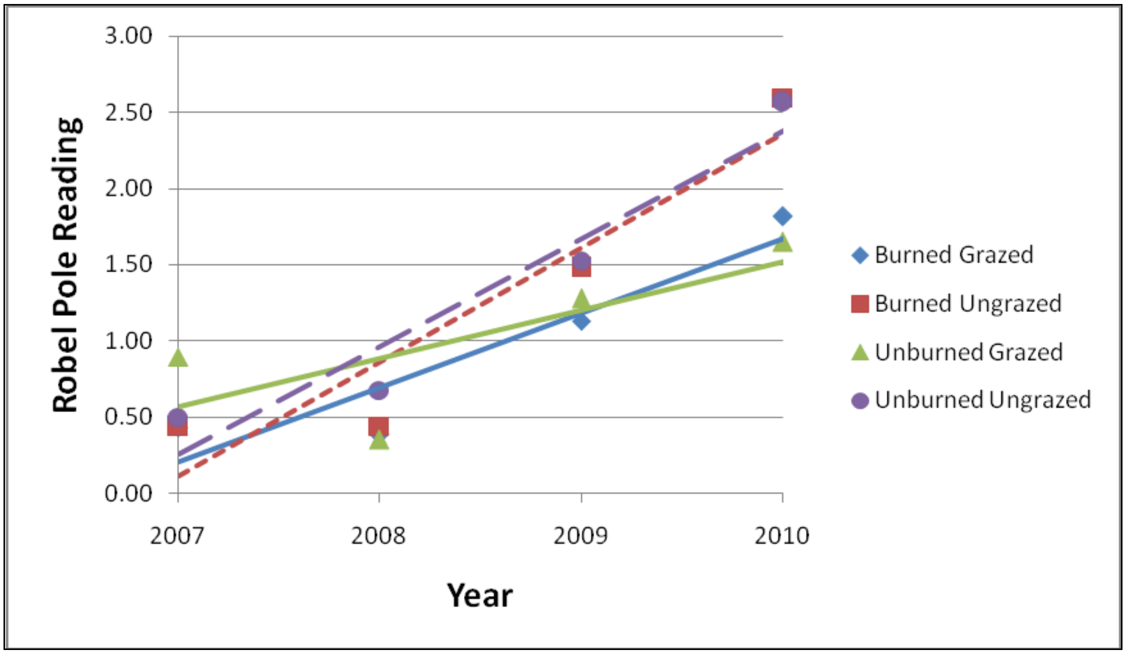

Figure 9. Vegetation density (50% obstruction of a Robel pole), per year (2007-2010), in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

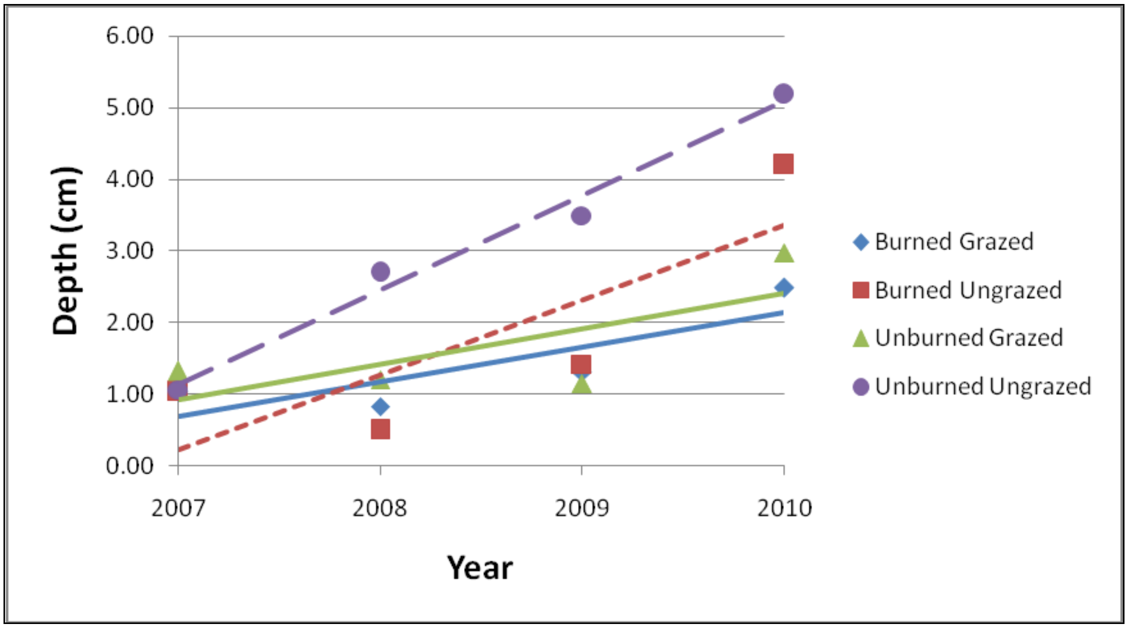

Figure 10. Litter depth in cm, per year (2007-2010), in burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures in Grasslands National Park and adjacent Mankota Community Pastures in southern Saskatchewan. Solid lines represent a significant interaction between year and treatment when compared to abundances in unburned-ungrazed pastures.

5.0 DISCUSSION

In general, songbird species that prefer short, sparse vegetation were positively associated with burning and grazing while species that prefer taller, denser vegetation were negatively associated with these disturbances. Since these habitat preferences are already well documented this study was more concerned with how these associations changed over time since burned. Baird’s sparrows, chestnut-collared longspurs, clay-colored sparrows, horned larks, Sprague’s pipits, and western meadowlarks all showed significant changes over time in at least one treatment (i.e. burned-grazed, burned-ungrazed, unburned-grazed).

There have not been any previous studies that assessed the changes over time in the interaction between fire and grazing on the songbird community and habitat structure in the northern mixed-grass prairies. I am aware of only two previous studies in the mixed-grass prairie that considered burned-grazed, burned-ungrazed, unburned-grazed, and unburned-ungrazed pastures; a study by Kruse and Bowen (1996) that focused on the nesting success of waterfowl, and a study by White (2009) in Grasslands National Park on the short-term effects of burning and grazing on songbirds and vegetation structure. Most of the studies on the interaction between fire and grazing have been conducted in the tallgrass prairies (i.e. Fuhlendorf and Engle 2004) and have not focused on the songbird community. Due to the differences in environmental conditions including soil type, moisture regime, growing seasons, and plant species composition these studies are of limited use in informing grazing and fire management practices in the northern mixed-grass prairie (Wright and Bailey 1982, Madden et al. 2000).

Species richness and diversity were significantly associated with time but not burning or grazing. The increase in both richness and diversity is most likely linked with the overall increase in vegetation growth. Increased vegetation may have increased foraging opportunities through an increase in seeds and insects or may have improved nesting success by providing better cover (Davis 2003, Fondell and Ball 2004). However, given the nomadic tendencies of grassland songbirds it is also possible that more individuals 'discovered' the study site as time progressed and that the arrival of more individuals in turn attracted even more in the following year due to conspecific attractions (Ahlering et al. 2006, Jones et al. 2007, Skagen and Adams 2010). These results contradict several previous studies in the fescue and mixed-grass prairies that found an increase in species richness after a disturbance (Pylypec 1991, Madden et al. 1999, 2000, Danley et al. 2004). This increase in species has generally been explained by the preference by most endemic grassland species for short, sparse vegetation with little litter; a preference shaped by the evolutionary history of the North American prairies, where frequent and intense disturbances are normal (Knopf 1994, Brawn et al. 2001, Fuhlendorf et al. 2006). However, of the songbird species found in my study site only chestnut-collared and McCown's longspurs are considered endemic to the short and mixed-grass prairies. Most other species such as Sprague's pipits and Baird's sparrows are endemic to the Great Plains and are less dependent on disturbances, tolerating or even preferring more dense vegetation.

As habitat structure strongly influences songbird site selection, which is in turn strongly influenced by grazing and burning (Davis et al. 1999, Davis 2003, Fondell and Ball 2004), I expected that the results for the Sørensen's quantitative index would demonstrate that community composition (i.e. species abundance and richness) varied by treatment. I predicted that burned-grazed pastures would recover more slowly than burned-ungrazed pastures, since grazing tends to maintain vegetation at an earlier successional stage, and that the similarity between these two treatments would decrease over time (Fuhlendorf et al. 2006). I also expected that these two treatments would have a high initial similarity as the differences in grazing treatment would be diminished by a recent burn (i.e. complete removal of litter layer and standing dead vegetation) and that over time the vegetation community in the ungrazed pastures would more quickly return to a pre-burned state. As predicted, burned-grazed and burned-ungrazed pastures did show a high initial songbird community similarity; however, by the fifth year post burn the similarity had not changed significantly. The only treatments that showed a significant change in similarity over time were the unburned-ungrazed pastures when compared to burned-ungrazed pastures. These results suggest that the effect of grazing since time burned has a relatively small impact on the songbird community. I predicted that grazing would slow the recovery of the vegetation community and that as time since burned increased the difference between burned-grazed and burned-ungrazed sites would increase. The lack of a significant change over time may be due, at least partially, to the relatively low grazing intensity that occurred on my study site, which I suspect was significantly below the 50% biomass removal that was the original goal. This was especially the case in 2009, 2010, and 2011 where a wet spring resulted in higher than normal vegetation growth.

The significant increase in songbird community similarity in burned-ungrazed and unburned-ungrazed pastures showed that over time the effects of burning are decreasing and that the communities in burned and unburned pastures are slowly converging. The similarity between the other songbird communities remained relatively stable and did not show a significant increase or decrease since time burned. The communities found in burned-grazed pastures when compared to those in unburned-grazed and unburned-ungrazed were relatively low (<60%) while the communities in unburned-grazed pastures when compared to unburned-ungrazed and burned-ungrazed were moderately similar at >70%. The relative stability of the different communities regardless of treatment was unexpected as previous studies investigating the effects of fire (i.e. Fuhlendorf et al. 2006, Madden et al. 1999) suggested that the community in the burned habitat was transitional and that the similarity to unburned habitat should increase over time. Additionally, it seems likely that the cattle were preferentially foraging in burned pastures at a rate much lower than observed by Fuhlendorf and Engle (2004) as the songbird community in burned-grazed and burned-ungrazed was not significantly different several years after the wildfires. Overall these results suggest that the songbird community has not yet completely recovered from the wildfires in 2006 as there is still a difference in community similarity in burned versus unburned pastures in the fifth year post burned, and that burning has a larger impact on the community than grazing.

At the species level, Baird’s sparrows and Sprague’s pipits occupy similar habitats, preferring undisturbed to lightly disturbed habitats with tall, dense vegetation and minimal bare ground (Davis et al. 1999, Green et al. 2002). Thus it was expected that both species would be negatively associated with burning but possibly not grazing since it was only moderate at less than 50% biomass removal. Previous studies have found both species to be relatively insensitive to light to moderate grazing intensities (Davis et al. 1999, Koper and Schmiegelow 2006) although a concurrent study in Grasslands found that both species demonstrated a negative linear relationship with increasing grazing intensities (Sliwinski 2011). Conversely, chestnut-collared longspurs, a species that preferentially selects for disturbed habitat with sparse vegetation and minimal litter (Hill et al. 1997) showed a strong positive association with both burning and grazing. Horned larks, a species that requires barren ground for nesting

(Ehrlich et al. 1988, Beason 1995), were positively associated with both burning and grazing. Surprisingly, clay-colored sparrows, a species that requires woody vegetation (Knapton 1994) were negatively associated with grazing but not burning. It was expected that clay-colored sparrows would be negatively associated with any type of disturbance that reduced woody vegetation. Species that can be considered habitat generalists, such as western meadowlarks, Savannah and vesper sparrows, did not show any significant relationships with burning or grazing (Davis et al. 1999, National Audubon Society 2001, Davis 2003). This result was not unexpected as a previous study by White (2009) found that while most species show some correlation with habitat structure (i.e. vegetation height, percent forb, bare ground, etc.) only four species (horned lark, Sprague's pipit, Baird's sparrow, and chestnut-collared longspur) were significantly associated with treatment (i.e. burning or grazing).

The interaction between year and treatment was significant for Baird's sparrows, chestnut-collared longspurs, clay-colored sparrows, horned larks, Sprague's pipits, and western meadowlarks. I predicted that songbird abundances would remain relatively stable in unburned pastures since the grazing treatment remained the same; however, abundances for some species increased over time in unburned pastures, an increase that is most likely linked to the increase in vegetation growth as the mixed-grass prairies transitioned from dry to wet environmental conditions.

Chestnut-collared longspurs were the only species that decreased over time in burned-ungrazed pastures, while both Sprague's pipits and Baird's sparrows increased. This suggests that the habitat created by the burns, especially in the absence of grazing, is transitioning back to a later successional stage (Madden et al. 1999, Erischsen-Arychuk et al. 2002, Pylypec and Romo 2003). As time since burn increased, the effects of burning declined as the vegetation community recovered, favouring species that prefer later successional habitat, such as Baird's sparrows. With the exception of western meadowlarks and clay-colored sparrows, the mean abundance in burned-ungrazed pastures became increasingly similar to levels in unburned-ungrazed pastures, while those in burned-grazed and unburned-grazed converged. These results imply that by the fifth year post burn, the disturbance that is more strongly driving songbird habitat selection is grazing (although burning is still significant for some species) and that the presences or absences of a species could be better predicted based on grazing treatment. In contrast, burning was the more influential factor affecting settlement patterns in the first and second years post burn. However there are still more chestnut-collared longspurs and fewer Sprague's pipits in burned-grazed pastures, for all years, than in burned-ungrazed.

The significant year*burning*grazing interaction for both clay-colored sparrows and horned larks was for the unburned-grazed treatment. This was not a predicted result as grazing intensity was supposed to remain constant and in unburned sites the vegetation community should not have changed significantly over time. It is likely that due to the abnormally wet springs that grazing intensity effectively decreased over time as more cattle were not added to the pasture to compensate for increased vegetation growth. Thus horned larks lost barren ground habitat while clay-colored sparrows gained woody vegetation. Baird's sparrows, chestnut-collared longspurs, and Sprague's pipits all had a significant interaction with time in burned-grazed and burned-ungrazed pastures. For all three species, the slope in the burned pastures was the same for both grazed and ungrazed sites, but differed from unburned-ungrazed pastures. The similarity in slopes suggests that for these species that although grazing may maintain the habitat in burned sites at an earlier successional stage it does not result in a slower transition (i.e. vegetation in burned-grazed sites begins at an earlier stage than burned-ungrazed but both ‘recover’ at the same rate) further supporting that at least in my study area burning did not seem to result in a positive feedback loop of increased grazing.

McCown’s longspurs, a species of special concern, did not occur in sufficiently high numbers to allow for statistical analysis; however, there are some interesting trends that can be discussed qualitatively. McCown’s longspurs show a clear preference for heavily disturbed sites, a finding that is consistent with their preference for short, sparse vegetation and bare ground (Ehrlich et al. 1988, Kimberly 1994). In 2007 and 2011, they were most abundant in burned-grazed pastures; additionally, with the exception of 2007, they never occurred in unburned-ungrazed pastures. Surprisingly, in 2008 and 2009 the highest abundances occurred in unburned-grazed pastures perhaps indicating that the preferred habitat provided by burning may only last until the second year post burned. By 2011, McCown’s longspurs were essentially only observed in burned-grazed pastures, perhaps due to the increase in vegetation height and density associated with the wetter springs. Thus while in 2008 and 2009 burning no longer appeared to be a driving factor determining settlement with grazed and burned patches seeming about equal, in 2010 and 2011 when grazing intensity had effectively decreased, the burned patches were necessary to provide adequate nesting habitat.

Grasshopper sparrows were another species that did not occur at sufficiently high densities to allow for statistical analysis. Preferring relatively dense, tall vegetation with minimal bare ground (Vickery 1996, Madden et al. 2000), grasshopper sparrows only occurred in burned-grazed pastures in 2011 and were most abundant in unburned-ungrazed pastures in all years. Grasshopper sparrow abundances in burned pastures were still significantly lower than unburned pastures through five years post burn.

Research in the mixed-grass prairies has shown that the vegetation community can transition back to a pre-burned state within 2 to 5 years given favourable climatic conditions (i.e. moderate to heavy precipitation and early spring/late fall) (Madden et al. 1999, Erischsen-Arychuk et al. 2002, Pylypec and Romo 2003). A previous study in Grasslands National Park (White 2009) found that vegetation in burned pastures was similar regardless of grazing and suggested that grazing intensity was light, due to a lack of preferential grazing, in the burned pastures because the wildfires occurred at the end of summer a result further supported by my study and the lack of an apparent positive feedback loop between fire and grazing. Additionally, a study investigating grazing by bison found that late summer fires did not allow for adequate vegetation regrowth before the winter to attract grazers the following spring (Biondini et al. 1999). My results suggest that despite very moist and productive environmental conditions, the vegetation community has not yet fully recovered to pre-burn conditions by the fifth year post burn, since there are still some differences in the songbird community.

It was expected that grazing would increase vegetation density, whereas burning would reduce it (Holechek et al. 1998, Madden et al. 1999); however, density was only positively associated with grazing. This may be because the burns were the result of wildfires that occurred after the growing season was over and were not particularly intense (White 2009). Vegetation height was negatively associated with burning in three out of four years. The higher *p* values in two of those years may explain why when the data were pooled there was no overall (significant) trend. Surprisingly, the difference between unburned and burned pastures increased since time burned. Overall, vegetation height increased dramatically over time, especially in 2010 due to the wet spring, and the large difference in growth between treatments suggests that perhaps burning has had a major impact on something other than the vegetation structure. Burning may have altered the nutrient content of the soil, made the soil more impermeable to water, or increased evaporation rates through the removal of litter (Shay et al. 2001, Erinchsen-Arychuk et al. 2002); it is also possible that burning favoured the growth of shorter grass species to an extent that four years later the overall vegetation height is shorter than unburned since there are fewer tall grasses in each plot. Vegetation height was not significantly associated with grazing, perhaps because the grazing intensities were relatively low and precipitation was relatively high making the vegetation community resilient to grazing pressure.

It is possible that the sample size was not large enough, especially in 2007, to account for the variation in litter depth among plots resulting in a non significant association with burning and grazing when the data for all four years was pooled. Previous studies have found that burning and grazing both reduce the amount of accumulated litter (Pylypec and Romo 2003) and when the data were analysed on a year by year basis I found that litter depth was negatively associated with burning in 2008 and 2009 and grazing in 2008, 2009, and 2010. Grazing significantly reduced litter depth across all years (except 2007), as expected since grazing intensity was relatively constant over time. Unlike vegetation height, litter depth was no longer significantly associated with burning by the fourth year post burn. The extra vegetation growth that occurred in 2009 and 2010 due to the wet conditions may have contributed to the recovery of the litter layer (Madden et al. 1999).

Vegetation height increased more slowly over time in disturbed sites than in undisturbed while vegetation density and litter depth increased more slowly in grazed pastures regardless of burning. In general, both fire and grazing were maintaining the vegetation community in an earlier successional stage. This suggests that for vegetation height, burning is the most important disturbance and for litter depth, grazing was more important. Burning results in a change in the vegetation community (i.e. an increase in grasses and decrease in forbs) and a reduction in accumulated litter (Madden et al. 1999). Litter begins to re-accumulate almost immediately following a burn and accumulates at a rate that is mostly governed by vegetation growth and grazing intensity since grazing suppresses litter accumulation through the removal of dead standing vegetation (Madden et al. 1999, Shay et al. 2001, Collins and Smith 2006). Since grazing intensity remained relatively constant over the course of this study, litter accumulation in grazed plots increased at a steady rate. By the fourth year post-grazing there was no significant difference between litter accumulation in burned and unburned plots, suggesting that that the litter layer can recover within a four year interval providing there are favourable climatic conditions (Madden et al. 1999, Erischsen-Arychuk et al. 2002). Vegetation density was also affected more by grazing than burning. This is likely due to the fact that the wildfires were later in the summer and occurred towards the end of the growing season, whereas grazing occurs throughout the spring and summer and alters plant growth.

6.0 MANAGEMENT IMPLICATIONS & CONCLUSIONS

The historical fire return interval for the northern mixed-grass prairie has been estimated at every five to ten years (Wright and Bailey 1982, Madden et al. 1999). Habitat heterogeneity is important to maintaining a diverse songbird community. Fire and grazing create a patchy habitat mosaic and will vary in intensity in time and space based on many external factors including topography, climate, hydrology, and soil (West 1993, Harrison et al. 2003). Fire and grazing are additive and using both as management tools on the landscape would allow for the largest range of habitats and a disturbance gradient from burned-grazed to unburned-ungrazed.

Grasslands National Park is part of a semi-arid ecosystem, and is prone to prolonged periods of drought; consequently, management practices and grazing regimes need to be conservative (Bailey 2010). This study occurred as the mixed-grass prairies transitioned from a dry to wet cycle. The increased precipitation resulted in lush vegetation growth that supported higher abundances of most songbird species. As such, the results from this study cannot be directly applied for management during a drought. The apparent population growth of several species is most likely temporary and will not continue once precipitation returns to 'normal'.

Several songbird species did not show any significant association with treatment, a result that may be due to the inherent variability within the ecosystem and/or data and not a lack of preference. The nomadic settlement patterns of grassland songbirds is another variable that can make it difficult to interpret the effect of burning and grazing as individuals do not exhibit site fidelity and thus the reason that abundances change between years may be due to nomadic tendencies of grassland birds and not a change in habitat availability and/or quality. The low population densities of most songbird species, less than 0.5 individuals per point, within the study area and the need to standardize sampling effort across time and treatment (only one round collected in the burns for 2007) only allowed for the use of one round per year and resulted in high variability in abundance data for most species. High variability in the data can make it difficult to determine if there were any significant interactions between abundances, time, and treatment.

Species richness and diversity were not related to grazing or burning; however, the songbird community that occurred within each treatment was unique (i.e. burned-grazed vs. unburned-ungrazed), with the predominant species in burned-grazed sites being chestnut-collared longspurs, and the predominant species in unburned-ungrazed sites being Baird's sparrows and Sprague's pipits. While still evident, the effects of burning have declined with time and at five years post burned it is the difference in grazing treatment that is a better indicator of songbird species abundances. These results indicate that neither the avian nor the vegetation community has fully recovered from burning by five years post burn, although the observed trend suggests that within the next year or two there will no longer be any significant differences between burned and unburned pastures within the same grazing regime.

This study considered light to moderate grazing intensities and it should be noted that more intense grazing could have a large effect on the interaction between year, burning, and grazing. The results from this study should only be used in guiding management decisions in similarly grazed areas in the mixed-grass prairies. The effect of light to moderate grazing in the mixed-grass prairies on vegetation composition may be relatively small, especially in comparison to more productive ecosystems that would transition into a woodland if left undisturbed (Milchunas et al. 1988, Milchunas and Lauenroth 1993, West 1993). If an area is already intensely grazed, species that are intolerant of significant disturbance will decline, and using fire in conjunction with moderate to intense grazing may exacerbate this effect. Therefore, if the majority of the landscape is already grazed it may not be advisable to also use burning as there will no longer be sufficient habitat for species that avoid disturbed areas. It would also be useful if a study could more closely examine the potential for a positive feedback loop between burning and grazing in the northern mixed-grass prairie similar to the studies conducted by Fuhlendorf and Engle (2004) in the tallgrass prairie. Ideally such as a study would consider both late summer (i.e. what would occur with a wildfire) and spring fires (i.e. when most prescribed burns occur) as there is some evidence that for my study area a moderate late summer fire did not result in increased grazing the following years.

This study supports the use of fire as a management tool to create habitat for species such as McCown's and chestnut-collared longspurs, and other species that require bare ground and short, sparse vegetation. My results suggest that using a fire return interval of five years would be sufficient to maintain at least some burned habitat, although using multiple small prescribed burns each year would be ideal since that would create a gradient of burned patches and further increase heterogeneity. Additionally, longspurs were the most abundant in recently burned sites (i.e. one to two years post burn) and allowing for more frequent creation of some burned habitat would be the most efficient method of maintaining high local longspur abundances.

In the long term, fire should be re-introduced into the East Block of Grasslands National Park, likely as an early spring burn, as grazing creates some different ecological effects compared with fire (e.g. differences to nutrient cycling and early warm up of the soil).

However, due to the negative opinion held by local stakeholders towards fire, both naturally occurring and prescribed, it may not currently be possible to use fire as a management tool within the study area. In the absence of fire within the park it is vital that grazing continue with some areas being grazed intensively. Parks Canada should begin laying the foundation for the future use of fire as a management tool by gathering input from local stakeholders and providing information about the potential benefits of fire especially in regards to increased forage for cattle and weed control. It might also be worthwhile discussing, with locals, the possibility of allowing small wildfires to burn within the park. Grazing alone can be used to promote habitat heterogeneity but light to moderate grazing levels cannot mimic burning and create the heavily disturbed habitat preferred by some species.

LITERATURE CITED

Ahlering, M.A., D.H. Johnson, and J.F. Faaborg. 2006. Conspecific attraction in a grassland bird, the Baird's Sparrow. Journal of Field Ornithology 77:365-371.

Askins, R.A., F. Chavez-Ramirez, 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, A., D. McCartney, and M. Schellenberg. 2010. Management of Canadian prairie rangeland. Government of Canada. Agriculture and Agri-Food Canada, Ottawa, Ontario.

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. 1995. Horned Lark (*Eremophila alpestris*). *In* the Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology, New York.

Betts, M. G., N. P. P. Simon, and J. J. Nocera. 2005. Point count summary statistics differentially predict reproductive activity in bird-habitat relationship studies. Journal of Ornithology 146:151–159.

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.

Bolker, B.M., M.E. Brookes, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, and J.S. White. 2008. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127-135.

Brawn, J.D., S.K. Robinson, and F.R. Thompson III. 2001. The role of disturbance in the ecology and conservation of birds. Annual Review of Ecology and Systematics 32:251-276.

Brudvig, L.A., C.M. Mabry, J.R. Miller, and T.A. Walker. 2007. Evaluation of central North American prairie management based on species diversity, life form, and individual species metrics. Conservation Biology 21:864-874.

Csillag, F., M. Kertesz, A. Davidson, and S. Mitchell. 2001. On the measurement of diversity-productivity relationships in a northern mixed-grass prairie (Grasslands National Park, Saskatchewan, Canada). Community Ecology 2:145-159.

Chapman, R.N., D.M. Engle, R.E. Masters, and D.M. Leslie Jr. 2004. Grassland vegetation and bird communities in the southern Great Plains of North America. Agriculture, Ecosystems and Environment 104:577-585.

Collins, S.L., and S.C. Barber. 1986. Effects of disturbance on diversity in mixed-grass prairie. Vegetation 64:87-94.

Collins, S.L., and M.D. Smith. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. Ecology 87:2058-2067.

COSEWIC. 2009. Canadian Wildlife Species. Committee on the Satuts of Endangered Wildlife in Canada. Available: www.cosewic.gc.ca (accessed January 25, 2010).

Danchin, E., and R.H. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. Trends in Ecology and Evolution 12:342-347.

Danley, R.F., R.K. Murphy, and E.M. Madden. 2004. Species diversity and habitat of grassland and passerines during grazing of a prescribe-burned, mixed-grass prairie. Western North American Naturalist 64:72-77.

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. 2003. Nesting ecology of mixed-grass prairie songbirds in southern Saskatchewan. Wilson Bulletin 115:119-130.

Davis, S.K. 2004. Area sensitivity in grassland passerines: effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in southern Saskatchewan. Auk 121:1130-1145.

Davis, S.K., R.M. Brigham, T.L. Shaffer, and P.C. James. 2006. Mixed-grass prairie passerines exhibit weak and variable responses to patch size. Auk 123:807-821.

Davis, Stephen K. and Wesley E. Lanyon. 2008. Western Meadowlark (*Sturnella neglecta*), *In* the Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology, New York.

Dettmers, R., D.A. Buehler, J.G. Bartlett, and N.A. Klaus. 1999. Influences of point count length and repeated visits on habitat model performance. Journal of Wildlife Management 63:815-823.

Ehrlich, P.R., D.S. Dobkin, and D. Wheye. 1988. The Birder’s Handbook: a field guide to the natural history of North American birds. Simon and Schuster, New York, New York.

Erichsen-Arychuk,K., E.W. Bork, and A.W. Bailey. 2002. Northern dry mixed prairie responses to summer wildlife and drought. Journal of Range Management 55:164-170.

Fondell, T.F., and I.J. Ball. 2004. Density and success of bird nests relative to grazing on western Montana grasslands. Biological Conservation 117:203-213.

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. 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., 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.

Gordon, I.J., and H.T. Prins. 2008. The ecology of browsing and grazing. Springer-Verlag, Berlin, Germany.

Government of Canada. 2009. Species at Risk Public Registry. Available from http://www.sararegistry.gc.ca/default_e.cfm (accessed November 3, 2009).

Government of Canada. 2011. National Climate Data and Information Archive. Available from http://www.climate.weatheroffice.gc.ca (accessed October 15, 2011).

Green, M. T., P. E. Lowther, S. L. Jones, S. K. Davis, and B. C. Dale. 2002. Baird's Sparrow (*Ammodramus bairdii*). *In* the Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology, New York.

Harrison, S., B.D. Inouye, and H.D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. Conservation Biology 17:837-845.

Henderson, D.C. 2006. Restoring grazing-induced heterogeneity in Grasslands National Park of Canada: landscape-scale experiment and long-term monitoring plan, March 9, 2006. Parks Canada Agency, Western & Northern Service Center, Winnipeg, Manitoba.

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

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8:23–29.

Holechek, J.L., R.D. Pieper, and C.H. Herbel. 1998. Range management: principles and practices. Third edition. Prentice Hall, Upper Saddle River, New Jersey.

Hill, D.P., and L.K. Gould. 1997. Chestnut-collared Longspur (*Calcarius ornatus*). *In* the Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology, New York.

Huste, A., and T. Boulinier. 2011. Determinants of bird community composition on patches in the suburbs of Paris, France. Biological Conservation 144:243-252.

Joern, A. 2005. Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. Ecology 86:861-873.

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

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

Jongman, R.H.G., C.J.F. Terbraak, and O.F.R. Tongeren. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, England.

Kempton, R.A. 1979. The structure of species abundance and measurement of diversity. Biometrics 35:307-321.

Kimberly, A. 1994. McCown's Longspur (*Calcarius mccownii*). *In* the Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology, New York.

Knapton, Richard W. 1994. Clay-colored Sparrow (Spizella pallida), *In* The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology, New York.

Knopf, F.L. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15:247-257.

Koper, N., and K.A. Schmiegelow. 2006. A multi-scaled analysis of avian response to habitat amount and fragmentation in the Canadian dry mixed-grass prairie. Landscape Ecology 21:1045-1059.

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 Management 61:605-613.

Kruse, A.D., and B.S. Bowen. 1996. Effects of grazing and burning on densities and habitats of breeding ducks in North Dakota. Journal of Wildlife Management 60:233-246.

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.

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

McKenzie, D., C. Miller, and D.A. Falk. 2011. The landscape ecology of fire. Springer, New York, New York.

Madden, E.M., A.J. Hansen, and R.K. Murphy. 1999. Influence of prescribed fire history on habitat and abundance of passerine birds in northern mixed-grass prairie. Canadian Field Naturalist 113:627-640.

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.

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

Milchunas, D.G., and W.K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327-366.

Moen, J. 1998. Managing your native prairie parcels: your guide to caring for native prairie in Saskatchewan. Saskatchewan Wetland Conservation Corporation.

National Audubon Society. 2001. The Sibley Guide to Bird Life and Behavior. (C. Elphick, J.B. Dunning Jr. and D.A. Sibley Eds). New York: Alfred. A. Knopf, New York.

Parks Canada. 2005. Restoration of grazing-induced heterogeneity: large-scale experiment and long-term monitoring plan for Grasslands National Park, Canada.

Powell, A.F.L.A. 2006. Effects of prescribed burns and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. Auk 123:183-197.

Pylypec, B. 1991. Impacts of fire on bird populations in a fescue prairie. Canadian Field Naturalist 105:346–349.

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.

Robbins, M.B., and B.C. Dale. 1999. Sprague's Pipit (*Anthus spragueii*). *In* the Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology, New York.

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.

Samson, F. B., and F. L. Knopf. 1994. Prairie conservation in North America. BioScience 44:418–421.

Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great plains ecosystems: past, present, and future. Wildlife Society Bulletin 32:6–15.

Sauer, J.R., J.E. Hines, J.E. Fallon, K.L. Pardieck, D.J. Ziolkowski Jr., and W.A. Link. 2011. The North American breeding bird survey, results and analysis 1966-2009. Version 3.23.2011 USGS Patuxent Wildlife Research Center, Laurel, MD.

Shay, J., D. Kunec, and B. Dyck. 2001. Short-term effects of fire frequency on vegetation composition and biomass in mixed prairie in south-western Manitoba. Plant Ecology 155:157-167.

Skagen, S.K., and A.A.Y. Adams. 2010. Are there optimal densities for prairie birds? Condor 112:8-14.

Sliwinski, M.S. 2011. Changes in grassland songbird abundance and diversity in response to grazing by bison and cattle in the northern mixed-grass prairie. M.N.R.M. thesis, University of Manitoba, Winnipeg, Manitoba.

Vickery, P.D. 1996. Grasshopper Sparrow (*Ammodramus savannarum)*. The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology, New York.

West, N.E. 1993. Biodiversity of rangelands. Journal of Range Management. 46:2-13.

Wendtland, K.J., and J.L. Dodd. 1990. The fire history of Scotts Bluff National Monument. Proceedings of the Twelfth North American Prairie Conference 141-144.

Wheelwright, N. T. and J. D. Rising. 2008. Savannah Sparrow (*Passerculus sandwichensis*). *In* the Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology.

White, K. 2009. Songbird diversity and habitat use in response to burning on grazed and ungrazed mixed-grass prairie. M.N.R.M. thesis, University of Manitoba, Winnipeg, Manitoba.

Wright, H.A., and A.W. Bailey. 1982. Fire ecology United States and Southern Canada. John Wiley and Sons, Inc. Toronto, Ontario.

Umbanhowar, C.E.Jr. 1996. Recent fire history of the Northern Great Plains. American Midland Naturalist 135:115-121.

APPENDIX I

Average abundance of grassland songbirds observed per point count plot (3.2 hectares) in Grassland National Park in 2007 separated by treatment. Average relative abundances and standard deviations are shown for all songbird species observed.

Species	**Burned Grazed**	**Burned Ungrazed**	**Unburned Grazed**	**Unburned Ungrazed**
Baird's sparrow	0.89±1.08	1.19±1.17	2.10±1.09	2.94±1.34
Brown-head cowbird	0.28±0.57	0.25±0.45	0.00	0.06±0.24
Brewer's sparrow	0.00	0.00	0.05±0.22	0.06±0.24
Chestnut-collared longspur	2.94±1.66	2.38±1.50	1.57±1.40	0.24±0.56
Clay-colored sparrow	0.11±0.32	0.06±0.25	0.00	0.18±0.39
Eastern kingbird	0.06±0.24	0.00	0.00	0.00
Horned lark	1.06±1.06	1.13±0.72	0.95±0.97	0.41±0.71
Lark bunting	0.06±0.24	0.00	0.00	0.00
McCown's longspur	0.17±0.51	0.13±0.34	0.10±0.30	0.12±0.49
Red-winged blackbird	0.11±0.32	0.00	0.00	0.00
Savannah sparrow	0.61±0.92	0.44±0.63	0.57±0.87	0.53±0.51
Sprague's pipit	0.67±0.69	0.81±0.75	1.81±0.75	1.82±0.95
Vesper sparrow	0.06±0.24	0.44±0.81	0.10±0.30	0.12±0.33
Western meadowlark	0.17±0.38	0.25±0.45	0.10±0.30	0.12±0.33

APPENDIX II

Average abundance of grassland songbirds observed per point count plot (3.2 hectares) in Grassland National Park in 2008 separated by treatment. Average relative abundances and standard deviations are shown for all songbird species observed.

Species	Burned Grazed	Burned Ungrazed	Unburned Grazed	Unburned Ungrazed
Baird's sparrow	1.50±1.50	1.38±1.02	2.29±1.31	3.00±1.22
Brown-headed cowbird	0.39±0.78	0.06±0.25	0.05±0.22	0.00
Brewer's blackbird	0.00	0.19±0.54	0.00	0.06±0.24
Brewer's sparrow	0.00	0.00	0.00	0.76±1.71
Chestnut-collared longspur	2.50±1.47	2.69±1.58	2.71±1.45	1.06±1.03
Clay-colored sparrow	0.22±0.55	0.19±0.40	0.05±0.22	0.29±0.47
Grasshopper sparrow	0.00	0.00	0.10±0.30	0.24±0.44
Horned lark	1.11±1.02	0.75±0.77	0.81±1.12	0.41±0.87
McCown's longspur	0.11±0.32	0.19±0.40	0.33±0.58	0.00
Red-winged blackbird	0.11±0.47	0.00	0.00	0.00
Savannah sparrow	0.67±0.97	0.56±0.73	0.33±0.58	0.94±0.66
Sprague's pipit	0.89±0.83	1.13±0.72	2.05±1.20	2.00±0.71
Vesper sparrow	0.28±0.57	0.38±0.62	0.24±0.54	0.18±0.39
Western meadowlark	0.50±0.79	0.06±0.25	0.05±0.22	0.12±0.33

APPENDIX III

Average abundance of grassland songbirds observed per point count plot (3.2 hectares) in Grassland National Park in 2009 separated by treatment. Average relative abundances and standard deviations are shown for all songbird species observed.

Species	Burned Grazed	Burned Ungrazed	Unburned Grazed	Unburned Ungrazed
Baird's sparrow	1.11±1.13	1.63±1.31	1.67±0.80	2.29±0.99
Brown-headed cowbird	0.22±0.43	0.13±0.34	0.00	0.00
Brewer's sparrow	0.00	0.00	0.00	0.06±0.24
Chestnut-collared longspur	3.00±1.19	2.13±1.31	2.29±1.10	0.82±1.07
Clay-colored sparrow	0.11±0.32	0.06±0.25	0.00	0.53±0.80
Eastern kingbird	0.00	0.00	0.05±0.22	0.00
Grasshopper sparrow	0.00	0.06±0.25	0.19±0.51	0.94±0.97
Horned lark	1.11±0.90	0.50±0.89	0.52±0.75	0.18±0.39
McCown's longspur	0.06±0.24	0.00	0.29±0.64	0.00
Savannah sparrow	0.28±0.57	0.81±0.98	0.43±0.68	0.35±0.61
Sprague's pipit	1.06±1.06	1.13±0.81	1.81±0.81	2.18±1.01
Vesper sparrow	0.11±0.32	0.00	0.10±0.30	0.24±0.44
Western meadowlark	0.33±0.59	0.25±0.45	0.57±0.75	0.00

APPENDIX IV

Average abundance of grassland songbirds observed per point count plot (3.2 hectares) in Grassland National Park in 2010 separated by treatment. Average relative abundances and standard deviations are shown for all songbird species observed.

Species	Burned Grazed	Burned Ungrazed	Unburned Grazed	Unburned Ungrazed
Baird’s sparrow	1.28±1.13	2.81±1.05	2.53±0.74	2.94±0.90
Brown-headed cowbird	0.00	0.38±0.81	0.13±0.35	0.12±0.33
Brewer’s blackbird	0.28±0.67	0.00	0.00	0.00
Brewer’s sparrow	0.00	0.00	0.07±0.26	0.18±0.39
Chestnut-collared longspur	3.11±1.68	1.56±0.89	3.00±1.41	1.65±1.00
Clay-colored sparrow	0.22±0.55	0.31±0.60	0.07±0.26	0.29±0.59
Eastern kingbird	0.06±0.24	0.00	0.00	0.00
Grasshopper sparrow	0.00	0.44±0.63	0.20±0.41	0.76±0.75
Horned lark	0.72±0.75	0.31±0.60	0.40±0.63	0.24±0.56
Lark bunting	0.00	0.00	0.00	0.12±0.33
McCown’s longspur	0.61±0.85	0.06±0.25	0.07±0.26	0.00
Red-winged blackbird	0.06±0.24	0.06±0.25	0.00	0.00
Savannah sparrow	0.56±0.78	1.50±1.10	0.80±0.77	1.12±0.86
Sprague’s pipit	2.00±0.59	2.38±1.09	2.33±0.82	2.35±0.86
Vesper sparrow	0.72±0.96	0.75±0.86	0.27±0.59	0.18±0.39
Western meadowlark	0.44±0.70	0.44±0.63	0.80±0.68	0.47±0.62

APPENDIX V

Average abundance of grassland songbirds observed per point count plot (3.2 hectares) in Grassland National Park in 2011 separated by treatment. Average relative abundances and standard deviations are shown for all songbird species observed.

Species	Burned Grazed	Burned Ungrazed	Unburned Grazed	Unburned Ungrazed
Baird’s sparrow	1.83±0.92	1.67±1.05	1.80±0.56	2.00±0.94
Brown-headed cowbird	0.00	0.00	0.20±0.41	0.00
Brewer’s blackbird	0.06±0.24	0.00	0.00	0.00
Brewer’s sparrow	0.06±0.24	0.07±0.26	0.00	0.12±0.33
Chestnut-collared longspur	1.83±1.25	1.53±1.06	2.00±1.00	0.82±0.81
Clay-colored sparrow	0.22±0.55	0.13±0.52	0.13±0.35	0.12±0.33
Grasshopper sparrow	0.33±0.59	0.06±0.74	0.73±0.80	1.12±0.86
Horned lark	0.56±0.71	0.27±0.46	0.33±0.49	0.29±0.47
McCown’s longspur	0.28±0.58	0.00	0.07±0.26	0.00
Red-winged blackbird	0.22±0.55	0.00	0.00	0.00
Savannah sparrow	0.89±0.76	1.07±0.80	0.67±0.98	1.12±0.86
Sprague’s pipit	1.56±0.78	1.60±0.63	2.33±0.49	1.88±0.86
Vesper sparrow	0.44±0.62	0.33±0.82	0.07±0.26	0.12±0.33
Western meadowlark	0.28±0.46	0.33±0.49	0.27±0.46	0.12±0.33

APPENDIX VI

Total songbird species abundances observed in Grasslands National Park and Mankota Community Pastures in southern Saskatchewan in 2007 through 2011.

	Total abundance				
Species	**2007**	**2008**	**2009**	**2010**	**2011**
Baird’s sparrow	129	148	120	156	119
Brown-headed cowbird	10	9	6	10	3
Brewer’s blackbird	0	4	0	5	1
Brewer’s sparrow	2	13	1	4	4
Chestnut-collared longspur	128	163	150	154	100
Clay-colored sparrow	6	13	12	15	10
Eastern kingbird	1	0	1	1	0
Grasshopper sparrow	0	6	21	23	45
Horned lark	64	56	42	28	24
Lark bunting	1	0	0	2	0
McCown’s longspur	9	12	7	13	6
Red-winged blackbird	2	2	0	2	4
Savannah sparrow	39	44	33	65	61
Sprague’s pipit	94	111	112	149	119
Vesper sparrow	12	19	8	32	16
Western meadowlark	11	13	22	35	16