Grassland Songbird Community Relationships Mediated by Cattle Stocking

Rates and Plant Community Composition in Two Habitats in a Northern

Mixed Grass Prairie

By

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ABSTRACT

Grassland birds are experiencing the most significant declines of any avian guild in North America. Grazing is an important tool to manage habitats for these species, as they respond to structural changes in vegetation, and grazing affects vegetation structure. I studied the impact of cattle stocking rates grassland songbird abundances, with upland and lowland habitats in Grasslands National Park, Saskatchewan, Canada, 2006 to 2012. I also examined relationships between songbird abundance and plant community composition. Generalized linear mixed models were used for analyses. Species differed in responses to increased grazing (0 to 0.85 AUM/ha); Sprague's pipit responded negatively, whereas chestnut-collared longspur responded positively. Above average precipitation during the study likely reduced the grazing effects. Overall, a range of cattle stocking rates makes habitat available for a complete songbird community. Efforts focused on prairie conservation should manage grazing at stocking rates that produce habitats that are under-represented relative to surrounding grasslands.

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CHAPTER 1: INTRODUCTION

Background

Worldwide, grasslands are one of the biomes most at risk, and the prairies of North America are no exception, as over 50% of the biome has been converted to other land uses (Hoekstra et al. 2005). Mixed-grass prairie has been reduced to only 29% of its original range (Samson et al. 2004). Grassland birds in North America have been declining significantly due to loss, degradation, and fragmentation of habitat and other species-specific threats (Knopf 1994, Houston and Schmutz 1999, Peterjohn and Sauer 1999, Brennan and Kuvlesky 2005). Grassland birds have experienced the most severe declines of all avian guilds in North America, and are therefore of serious conservation concern (Knopf 1994, NABCI 2009).

In many areas of remaining grasslands, natural disturbance regimes, primarily landscape patterns of grazing and fire, have been altered (Samson et al. 2004). Grassland birds are adapted to ecosystems with grazing disturbance (Knopf 1994). Pre-settlement bison were an important keystone species (Knapp et al. 1999) and their grazing patterns would have interacted with fire patterns to create habitat necessary for many bird species (Fuhlendorf and Engle 2001). Cattle can create grazing disturbance in a manner similar to bison (Knapp et al. 1999). However, modern rangeland management practices are aimed at maximizing livestock production which can result in relatively homogeneous grassland structure at the landscape scale, reducing habitat for some grassland birds (Fuhlendorf and Engle 2001, Derner et al. 2009). Cattle grazing, if managed differently, can create habitat gradients important for maintaining a diversity of avian species (Brennan and Kuvlesky 2005, Derner et al. 2009). Research on grazing impacts can contribute to management for grassland songbirds in remaining grassland ecosystems (Vavra 2005).

Since they respond to structural changes caused by disturbance and their abundances are easily measured, grassland birds have the potential to be used as ecological indicators (Dale and Beyeler 2001, Browder et al. 2002). They may be especially useful as indicator species for butterflies (Swengel and Swengel 1999).

In 2006, Parks Canada initiated the Biological and Grazing Management Area (BAGMA) project in Grasslands National Park in southern Saskatchewan, in an effort to restore ecological integrity to the park (Parks Canada 2006). As part of the BAGMA project, I examined the connection between stocking rate (AUM/ha), vegetation composition, and songbird communities. I integrated 2 years of pre-grazing data (2006-2007) and 4 years of grazing data (2008-2011) to provide a comprehensive analysis of the avian community changes which occurred at different stocking rates in two different habitats. I also examined how avian species responded to vegetation composition, in order to determine if not just vegetation structure, but composition has an effect on grassland songbirds

Research objectives

As part of the BAGMA experiment, my research determined how vegetation composition and grazing intensity in upland and lowland habitats affected bird communities. My research objectives were to:

1) determine how cattle grazing at different stocking rates can change the composition of songbird communities over time; and

2) determine how the effects of plant species composition and richness can lead to changes in songbird richness, diversity, and abundance.

Hypotheses

If grassland songbirds species are sensitive to grazing and grazing influences habitat structure, (increased grazing leading to increased bare ground cover, decreased litter depth and vegetation cover (Bai et al. 2001, Gillen et al. 2000)), then I hypothesize that songbirds will respond positively or negatively to increased stocking rate, according to their habitat needs in terms of habitat structure. Species that require short vegetation (e.g. horned lark (*Eremophila alpestris*)) should respond positively to heavy grazing, while species that require high vegetation cover will respond negatively to increased grazing (e.g. Baird's sparrow (*Ammodramus bairdii*)).

If changes in vegetation composition affect structure and food availability, then I predict that changes in plant community composition will lead to changes in bird communities.

Project significance

Vavra (2005) identified the need for information on optimal grazing management systems for non-game species. I aimed to provide some information about the use of seasonal grazing in mixed-grass prairies as a management tool for grassland songbird communities and individual species. This project should help Grasslands National Park of Canada manage for species of concern such as Sprague's pipit, chestnut-collared longspur, and Baird's sparrow and the grassland songbird community in general. Much of the land surrounding the park is used for commercial cattle grazing. The findings of this project therefore also have relevance to regional knowledge and conservation efforts. Kantrud and Kologiski (1983) found that avian species' responses to grazing varied by region and Johnson and Igl (2001) found that species abundances can vary regionally. These factors make it important to have regionally specific studies, in order to create management recommendations best suited to the area. Additionally there is a shortage of information on the effects of grazing in the mixed-grass prairie ecosystem (Symstad and Jonas

2011) and on the effects of songbird associations with plant communities and this project contributes to that body of knowledge.

This project also addresses an important research need. It examines bird community responses to stocking rate as a continuous, rather than a categorical, variable. There is a need for more research on the impacts of a continuum of stocking rates (Symstad and Jonas 2011). Most studies examining grazing intensity use a light, moderate, heavy categorization of grazing intensity and some use qualitative estimates of grazing intensity rather than stocking rate or biomass removal (e.g. Kantrud and Kologiski 1983, Biondini et al. 1998, Davis et al. 1999, Bai et al. 2001). Treating stocking rate as a continuous variable allows for more complex results to be uncovered. Additionally, using actual stocking rates (AUM/ha) as a variable, rather than categories of grazing, has more relevance for managers.

CHAPTER 2: LITERATURE REVIEW

The Great Plains ecosystem

The grassland ecosystems of North America were shaped by a combination of abiotic (drought, fire) and biotic elements (grazing) (Anderson 2006). Worldwide temperate grasslands are one of the biomes most at risk, with over 50% of the biome having been converted for other uses in North America (Hoekstra et al. 2005). The grasslands of North America have been greatly reduced since European settlement, with an overall reduction of 70% on the Great Plains (Samson et al. 2004). Many of the grassland ecosystems that remain are degraded and fragmented by crop fields, roads, railways, energy extraction infrastructure, etc. (Houston and Schmutz 1999, Brennan and Kuvlesky 2005). Mixed-grass prairie has declined to only 29% of its original area (Samson et al. 2004).   About 9 million hectares of native grassland remain as pasture in the Canadian prairie eco-zone (Thorpe 2011).

Cattle use of lowland areas

Riparian zones in arid systems are areas of high productivity and biodiversity in rangelands and serve as important water sources for wildlife (Belsky et al. 1999). Riparian and low-lying areas in grasslands contain a mix of plant habitats (Coupland 1950, Ballard and Krueger 2005) creating complex mosaics (Belsky et al. 1999). Being tropically-derived in Africa and Asia, cattle concentrate use in areas near water sources and riparian zones (Kauffman and Krueger 1984, Pinchak et al. 1991, Fontaine et al. 2004). Additionally, cattle grazing intensity varies with slope (Milchunas 1989, Teague and Dowhower 2003), generally increasing in low-lying areas. Cattle use riparian areas as water sources, thermal refugia, and forage sites (Belsky et al. 1999, Allred et al. 2013). Cattle use of areas around water sources increases with air temperature (Allred et al. 2013). Both cattle and bison show this greater preference for riparian

areas as air temperatures rise; however, cattle move into these areas as thermal refugia at lower temperatures (24 C) than bison (Allred et al. 2013). Livestock grazing in the arid and semi-arid west is generally considered to have negative ecological consequences in riparian areas (Fleischner 1994, Belsky et al. 1999). Although bison select for areas and vegetation closer to water they use larger landscapes and will travel further from water than cattle, and spend less time at water (Kohl et al. 2013). However, they do show a preference for riparian vegetation communities over other communities, similar to cattle (Kohl et al. 2013).

There is little information available on cattle grazing impacts on grassland birds in low-lying and riparian areas. Renfrew and Ribic (2001) found that use of riparian areas by grassland birds was higher in grazed pastures than in ungrazed buffer areas along streams, suggesting that grazing in lowlands provides a benefit to grassland birds. However, their sites had little shrub cover, and the ungrazed sites were located primarily in crop fields. Most other studies on cattle grazing impacts on birds in riparian areas focus on more treed or mountainous sites (e.g. Finch 1986, Knopf et al. 1988) and may not be relevant to grassland ecosystems.

Grazing on the Great Plains

Pre-settlement, bison played a keystone role in grassland ecosystems (Knapp et al. 1999) and their grazing patterns created landscape heterogeneity (Fuhlendorf and Engle 2001). Bison grazing was a periodic disturbance and herds would have moved across the landscape in response to fire and vegetative changes (Samson et al. 2004). Bison were all but removed from the plains following settlement (Knapp et al. 1999), after which they were replaced with domestic open-range cattle. Now North American grasslands are fenced, although cattle still graze most available rangelands (Fleischner 1994). Cattle can have a similar ecological function as bison under some management scenarios (Knapp et al. 1999, Milchunas et al. 1998) and can

be used in the conservation of prairie resources (Steuter and Hidinger 1999). There are some differences in foraging behavior between cattle and bison as cattle spend more time actually foraging compared to other behaviors (Plumb and Dodd 1993, Kohl et al. 2013). Cattle trampling may cause similar effects as bison rubbing on shrubs (Plumb and Dodd 1993). Bison grazing would have created a mosaic of patches of varying structures on the landscape (Samson et al. 2004). In contrast, current rangeland management practices aimed at livestock production often result in habitat homogeneity through grazing practices aimed at an even distribution of grazing (Fuhlendorf and Engle 2001). Birds that need habitats maintained by either light or heavy grazing intensities are therefore at a disadvantage with current systems of cattle production (Derner et al. 2009).

Grazing theories

Range succession model

The range succession model is the classic theory that describes ecosystem changes in rangeland (Westoby et al. 1989, Briske et al. 2003). This model holds that a rangeland ecosystem without disturbance moves towards a climax successional stage (Westoby et al. 1989). Grazing or other disturbances will move the ecosystem towards an earlier successional stage. Removal of a disturbance will reverse the vegetative changes that occurred. However, there are numerous examples where this model does not correspond with empirical data, as many changes on rangelands are not reversible or continuous (Westoby et al. 1989, Briske et al. 2005).

State and transition model

The state-and-transition model was proposed as an alternative to the range succession model to account for discontinuities from linear changes in succession (Westoby et al. 1989, Briske et al. 2005). Rather than a continuous movement between stages, this model suggests that

an ecosystem remains at a certain "state" until an event (e.g. fire, change in stocking rate, drought) causes it to transition to another state (Westoby et al. 1989). This model therefore allows multiple equilibrium stages to be possible in an ecosystem. The events that cause transitions can be natural or anthropogenic and transitions can occur at different rates (Westoby et al. 1989).

MSL model

Milchunas et al. (1988) created the Milchunas-Sala-Lauenroth (MSL) which predicts that grazing impacts on vegetation communities will be based primarily on moisture and evolutionary history of grazing in the ecosystem. The MSL model predicts that grazing will have little impact on plant species composition in semi-arid ecosystems with long grazing histories because of natural selection for both drought and grazing-tolerant plants (Milchunas et al. 1988). This part of the model applies to the semi-arid mixed-grass prairie of the northern Great Plains.

Synthesis of models

The MSL model and state-and-transition model are the two theories primarily referred to today (Briske et al. 2005, Cingolani et al. 2005). The state-and-transition model can apply to grazing disturbances, but does not provide an explanation of how grazing will impact the vegetation community. Cingolani et al. (2005) proposed modifications of the MSL model to include the state-and-transition model within it. Rather than a moisture gradient as a factor, Cingolani et al. (2005) proposed a productivity gradient to allow for soil differences. Additionally, Cingolani et al. (2005) state that in areas with a long evolutionary grazing history, grazing pressure would not have been constant. This would have allowed two groups of plant communities to exist: grazing-resistant plant species and species more sensitive to grazing but also more resource efficient. In these systems grazing should, therefore, change plant species

composition rather than diversity (Cingolani et al. 2005). In contrast, the MSL model holds that all species in these systems will be adapted to both grazing and drought. Finally, Cingolani et al. (2005) specify that systems with a short history of grazing are more likely to experience non-reversible changes, whereas systems with a long history of grazing are more resilient to the impacts of grazing. These modifications change the MSL model to better reflect systems with a long grazing history.

Grazing intensity

In the literature, measures of grazing intensity vary considerably among studies. Some of the key papers on grazing effects on grassland birds (e.g. Kantrud and Kologiski 1983, Milchunas et al. 1998, Davis et al. 1999) and on vegetation (e.g. Biondini et al. 1998, Bai et al. 2001, Hart et al. 2001) use categories of ungrazed, light, moderate, and heavy grazing intensities. Among these, some studies (Kantrud and Kologiski 1983, Davis et al. 1999, and Bai et al. 2001) used ocular estimates compared to nearby ungrazed sites to determine which grazing intensity category to place study sites in. Other studies (Biondini et al. 1998, Hart et al. 2001) used estimated biomass removal to place study sites into these categories. Although both Hart et al. (2001) and Milchunas et al. (1998) performed research as part of the same long term project, Milchunas et al. (1998) also included stocking rates for the years this information was available. A few other studies I referenced did report stocking rates (e.g. Gillen et al. 2000, AUD/ha) used in their study.

Grazing effects on vegetation structure

Grazing can have a number of impacts on vegetation in grasslands. Cattle grazing can impact primary production, nutrient cycling, decomposition rates, and amount of litter biomass (Biondini et al. 1998). Different stocking rates of cattle impact these factors at varying levels.

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Grazing also impacts vegetation structure (e.g. vegetation height and density), heterogeneity, and creates structural gradients across the landscape (Fuhlendorf and Engle 2001, Chapman et al. 2004).

Grazing decreases litter and dead vegetation on pastures by as much as 97 % (Biondini et al. 1998), with heaviest grazing intensities having the strongest effect (Biondini et al. 1998, Gillen et al. 2000, Bai et al. 2001). Increases in grazing also decrease the biomass on pastures (Gillen et al. 2000, Hart 2001). The effect size of grazing on plant biomass decreases from 0.5 to almost 0 with increased precipitation as precipitation reaches 1200 mm annually (Chase et al. 2000). Cattle grazing results in a piosphere, or zone of impact, around water sources. This piosphere results in a gradient of litter around water sources, with lowest litter depths near water (Fontaine et al. 2004). Cattle grazing can also increase bare ground cover (Bai et al. 2001).

Grazing effects on vegetation composition

Studies have found mixed results for the effects of grazing on plant species composition. Biondini et al. (1998) found that climate variation was the primary driver of changes in plant species composition in mixed-grass prairie, with grazing causing no major changes in composition. However, another study in short-grass prairie found increased plant diversity at moderate and high grazing intensities compared to low grazing intensity (Hart 2001). This study also found that grazing at different intensities led to changes in dominant species. Grazing can increase plant diversity by increasing heterogeneity and the availability of resource niches (Wrage et al. 2011). Although grazing may not always affect species richness or presence it does change plant species abundances (Bai et al. 2001, Willms et al. 2002, Dumont et al. 2009). For example, Milchunas et al. (1998) found increases in *Bouteloua gracilis* cover with grazing. Some grass species have been found to increase in abundance with grazing (e.g. june grass

(*Koeleria macrantha*), western wheatgrass (*Pascopyrum smithii*), while others decrease (e.g. northern wheatgrass (*Elymus lanceolatus*), winterfat (*Krascheninnikovia lanata*) (Bai et al. 2001). Gillen et al. (2000) found that grazing intensity only impacted the tall-grass species found in southern mixed-grass prairie Grazing has also been found to increase forb cover at some sites (Bai et al. 2001), but not in others (Gillen et al. 2000, Bai et al. 2001).

Songbird communities of the Great Plains

North American grassland songbirds are adapted to grassland ecosystems and rely on them for survival (Vickery et al. 1999). Avian diversity in the Great Plains of North America is primarily restricted to a relatively low level by drought pressures (Zimmerman 1992). In addition to evolving with periods of low precipitation and fire, these species are adapted to grazing disturbances (Knopf 1999).

Habitat selection occurs at different scales from the selection of food items up to geographic range (Johnson 1980). Grassland birds require specific structural vegetation traits (e.g. height and density) (Chapman et al. 2004). Many species differ in their habitat requirements, making habitat gradients created by grazing especially important (Fuhlendorf and Engle 2001). For example, Horned Lark (*Eremophila alpestris*) selects for low vegetation height (Davis and Duncan 1999). In contrast, Baird's sparrow (*Ammodramus bairdii*) selects for increased grass cover and selects against bare ground (Sutter et al. 1995). Individual songbird species may also select for specific plant communities (Rotenberry 1985, Haire et al. 2000, Paczek and Krannitz 2005).

Grazing impacts on songbird communities

Birds exhibit strong and complex responses to grazing intensity (Milchunas et al.1998). Kantrud and Kologiski (1983) found that highest avian richness occurred with moderate grazing

in mixed-grass prairie overall, but in the northern mixed-prairie highest songbird densities were found with heavy grazing. Grazing impacts on structure may also have other impacts besides those on habitat selection. McCown's longspurs (*Rhyncophanes mccowni*) faced increased predation in pastures with moderate grazing, and this may have been due to increased shrub cover compared to heavily grazed pastures (With 1994). Through changes in vegetation cattle grazing can also impact arthropod populations, including grasshopper communities (Stoner and Joern 2004, Branson and Sword 2010). These arthropod species are an important food resource for grassland songbirds (Wiens and Rotenberry 1979, Hill and Gould 1997, Davis and Lanyon 2008). Avian responses to grazing intensity vary by region and dominant habitat type (Kantrud and Kologiski 1983).

Plant species composition impacts on songbird communities

There is very little research relating grassland songbirds to plant composition on native prairie. Some species (e.g. Baird's sparrow, Sprague's pipit (*Anthus spragueii*) can respond negatively to non-native grasslands, which often have significantly reduced plant diversity (Wilson and Belcher 1989, Davis and Duncan 1999).

It appears that both plant community composition and structure can influence grassland songbirds; however it is generally believed that structure is more important (Chapman et al. 2004, but see Rotenberry 1985). Chapman et al. (2004) found that seeded pastures had fewer plant species than native grassland but were structurally similar, and grassland birds occurred in both types of pasture. This suggests that bird species may select for structural vegetation elements rather than for specific plant species communities (Sutter et al. 1995, Chapman et al. 2004). However, other studies (Wilson and Belcher 1989, Davis and Duncan 1999) found that some species (i.e. Sprague's pipit, chestnut-collared longspur (*Calcarius ornatus*), clay-colored

sparrow (*Spizella pallida*) and upland sandpiper (*Bartramia longicauda*)) occurred more often in native prairie than seeded grassland.   This suggests that plant species composition does have some impact when there are large differences in overall composition or diversity.

Not all species exhibit avoidance of non-native habitats, so it is possible that some species are more sensitive than others to differences in plant composition (Davis and Duncan 1999). Paczek and Krannitz (2005) found relationships between several songbird species, including western meadowlark, vesper sparrow, and Brewer's sparrow, and specific plant species present in the sagebrush habitat of British Columbia. Additionally, Haire et al. (2000) found that overall community composition (e.g. a mid-grass community compared to a tall grass plant community) shaped responses of grassland songbirds to habitat. Some grassland songbird species show strong preferences for very specific plant communities (Haire et al. 2000). Rotenberry (1985) also found that although there were some correlations with plant structure and plant composition, a large portion of the variation in bird communities can be attributed to variation in plant community composition. Rotenberry (1985) suggests that birds may select a habitat due to overall structure, and then refine habitat selection based on the plant taxonomic composition. Additional research is necessary to determine what differences in plant species composition in native habitats might have an impact on my study species.

Natural history of study species

Baird's sparrow (Ammodramus bairdii)

Baird's sparrows are associated with high-quality grassland (Green et al. 2002). Historically, they were a common songbird in the northern Great Plains, but are now rare throughout their range, having declined by 75% since 1968 (Green et al. 2002, Sauer et al. 2014). They exhibit area sensitivity, with a minimum patch size of 25 ha required (Davis 2004). The

species has been shown to prefer native prairie compared to less diverse, non-native grassland (Wilson and Belcher 1989, Sutter et al. 1995, Dale et al. 1997). Baird's sparrow is negatively associated with increases in bare ground (Sutter et al. 1995). Baird's sparrow shows a positive response to litter depth and grass cover (Sutter and Brigham 1998). It appears to prefer moister habitats with taller vegetation cover than other songbird species (Davis et al. 1999). The species selects areas of low shrub cover (Davis et al. 1999). Davis et al. (1999) also found Baird's sparrows to have more flexible site selection requirements than other species studied. A study by Davis et al. (1999) found no effect of grazing on Baird's sparrows in Saskatchewan rangelands. However, Kantrud and Kologiski (1983) found the species to be associated with light grazing, whereas Sutter et al. (1995) found the species most commonly on ungrazed grasslands. Sutter et al. (1995) found that Baird's sparrow is more heavily impacted by grazing than by plant species composition.

Brewer's Sparrow (Spizella breweri)

Brewer's sparrow is a bird of shrublands that generally nests in sagebrush (*Artemisia* spp.) (Rotenberry et al. 1999). This species has been experiencing declines along with other songbirds of the Great Plains (Rotenberry et al. 1999). It prefers areas that are both open and have tall shrubs, but will avoid areas of dense shrub (Williams et al. 2011). It is generally found in habitats with moderate patchiness (Kantrud and Kologiski 1983). In British Columbia, Brewer's sparrow showed positive associations with two forb species, parsnip-flowered buckwheat (*Eriogonum heracleoides*) and lupines (*Lupinus* sp.) (Paczek and Krannitz 2005).

Chestnut-collared Longspur (Calcarius ornatus)

Chestnut-collared longspurs are restricted to the short and mixed-grass prairies of North America (Hill and Gould 1997). Their breeding distribution has been reduced greatly due to prairie conversion (Hill and Gould 1997). They are listed as threatened under the Species at Risk Act (Government of Canada 2012). Chestnut-collared longspurs are a native grassland specialist, and will avoid non-native grasslands (Hill and Gould 1997, Davis and Duncan 1999, but see Lloyd and Martin 2005). Additionally, they exhibit reduced nesting success in non-native prairie (Lloyd and Martin 2005). The species has also been found to be area sensitive (Davis and Brittingham 2004). Historically they were found in areas disturbed by recent grazing or fire (Hill and Gould 1997). Davis et al. (1999) found this species exhibited no response to grazing intensity in a study conducted in Saskatchewan. In contrast, in the same province Maher (2008) found the species to be positively associated with grazing. Chestnut-collared longspurs are found in areas with low litter and vegetation densities (Davis et al. 1999). Their nest locations have been found to be associated with the presence of cattle dung nearby (Davis 2005).

Clay-colored sparrow (Spizella pallida)

Clay-colored sparrow is a low-shrub-associated grassland songbird which is often found in areas of snowberry (*Symphoricarpos occidentalis)* (Knapton 1994, Davis and Duncan 1999). The occurrence of this species is best predicted by shrub cover, with a 69% probability of occurrence at 3% shrub cover, increasing to almost 100 % probability of occurrence at 20 % shrub cover (Madden et al. 2000) and it is often found in riparian zones in mixed-grass prairie which are highly associated with shrub cover. It is known to prefer native habitat over seeded pastures (Davis and Duncan 1999). One study in Alberta found that clay-colored sparrows had the highest abundances under moderate grazing (Saunders and Hurly 2000). It often occupies habitat types similar to that of Brewer's sparrow (Knapton 1994).

Grasshopper Sparrow (*Ammodramus savannarum*)

The grasshopper sparrow is found in open habitats across much of North America, including the Great Plains. It has declined by 74% since 1968 across the continent, in large part due to habitat conversion (Vickery 1996, Peterjohn and Sauer 1999, Sauer et al. 2014). It does not show a preference for native grassland over planted grasslands (Chapman et al. 2004). It requires areas of bare ground for foraging and therefore may need patchy habitats (Vickery 1996). However, in other studies, it has been found to be most abundant in areas of low patchiness/ heterogeneity (Wiens 1974, Chapman et al. 2004). This species selects habitat with moderate vegetation heights (<0.5 m) and low to moderate litter depths in mixed-grass prairie and selects shorter, drier areas in the eastern portion of its range (Wiens 1973, Patterson and Best 1996, Vickery et al. 1996, Madden et al. 2000, Swengel and Swengel 2001). In eastern areas where it overlaps with Savannah sparrows it selects for more open habitat, and generally avoids areas of high shrub (Vickery 1996). The grasshopper sparrow prefers lightly grazed habitats (Kantrud and Kologiski 1983) and it exhibits area sensitivity (Herkert 1994, Davis and Brittingham 2004). This species has a diet containing Lepidoptera larvae, weevils, and seeds (Wiens 1973)

Horned Lark (Eremophila alpestris)

The horned lark is a common species found in open areas of sparse vegetation across North America (Beason 1995). This songbird is found in areas of low vegetation height with bare ground (Wiens 1973, Beason 1995, Davis and Duncan 1999). They create a small cavity or scrape in the ground as a nest site. Adults feed primarily on seeds, but feed their young insects (Beason 1995). Horned larks are generally associated with areas of high grazing intensity

(Kantrud and Kologiski 1983, Maher 2008). Fontaine et al. (2004) found increased abundances of horned larks near water in areas with heavy grazing.

Savannah Sparrow (Passerculus sandwichensis)

Savannah sparrows are abundant throughout North America in a variety of open habitats (Wheelright and Rising 2008). This species nests in tall grass clumps, often near decaying dung (Davis 2005) and overall prefers denser, taller vegetation (Davis and Duncan 1999). Savannah sparrow is positively associated with litter cover and depth (Sutter and Brigham 1998). It is often associated with moderate grazing intensities (Kantrud and Kologiski 1983). Wilson and Belcher (1989) found that Savannah sparrows were more positively correlated with native vegetation than introduced grasses. It is an area-sensitive species (Herkert 1994).

Sprague's Pipit (Anthus spragueii)

Sprague's pipit is a grassland songbird endemic to the northern Great Plains (Robbins and Dale 1999). Sprague's pipit is listed as threatened under Canada's Species at Risk Act (Government of Canada 2012) and is a candidate species for listing in the United States, due to population declines (Peterjohn and Sauer 1999, Robbins and Dale 1999, US Fish and Wildlife Service 2012). Sprague's pipits are area-sensitive (Davis and Brittingham 2004, Davis et al. 2006) and prefer native grassland to non-native habitat (Davis and Duncan 1999). They nest in dense areas that are taller than the surrounding vegetation (Sutter 1997, Davis 2005). They prefer intermediate cover height (Sutter and Brigham 1998). Fledglings also favor areas of taller vegetation (25 cm) (Fisher and Davis 2011b). Sprague's pipit has an average home range of 1.9 ha (Fisher and Davis 2011a). The species is less likely to be found on heavily grazed pastures (Davis et al. 1999) and generally prefers ungrazed to lightly grazed areas (Maher 2008, Kantrud and Kologiski 1983). They have been found to have a positive association with dead litter

(Davis and Duncan 1999), moderate litter depth (Robbins and Dale 1999) and areas of low visual obstruction (Madden et al. 2000).

Vesper Sparrow (Pooecetes gramineus)

The vesper sparrow is a generalist passerine of open habitats, and is found across much of North America (Jones and Cornely 2002). Along with other grassland songbirds, it has been experiencing continental population declines (Peterjohn and Sauer 1999). It selects habitat with some shrub cover and patchy vegetation and prefers areas of low vegetation heights (Jones and Cornely 2002). It is associated with moderate grazing regimes (Kantrud and Kologiski 1983); however Harrison et al. (2010) found no significant difference in abundance between grazed and ungrazed sites in short-grass prairie. This species is not strongly influenced by patch size (Mcmaster et al. 2005). Lower nest success has been observed at nests in shorter vegetation (Harrison et al. 2011). Vesper sparrow has been shown to be positively associated with pasture sage (*Artemisia frigida)* cover, rock and selaginella cover and negatively associated with big sagebrush (*Artemisia tridentata*) cover (Paczek and Krannitz 2005).

Western Meadowlark (Sturnella neglecta)

The western meadowlark is a common, widely distributed bird across much of western North America (Davis and Lanyon 2008). It can be found in a variety of grassland types, including planted grasslands (Chapman et al. 2004, Davis and Lanyon 2008). However, studies have found that the species has a negative correlation with introduced vegetation (Wilson and Belcher 1989, Haire et al. 2000). Nests are concealed in dense vegetation (Davis and Lanyon 2008). This species needs a moderate amount of grass and litter cover (Madden et al. 2000, Davis and Lanyon 2008) and prefers habitat that is ungrazed to lightly grazed (Maher 2008, Kantrud and Kologiski 1983). It seems to prefer homogeneous habitat (Chapman et al. 2004).

Western meadowlarks are primarily carnivorous, feeding on beetles, grasshoppers and

Lepidoptera larvae (Wiens 1973, Wiens and Rotenberry 1979) and are known to depredate

songbird nests (Powell et al. 2012).

CHAPTER 3: METHODS

Study area

The study site was located in southern Saskatchewan, within the East Block of Grasslands National Park (GNP) at approximately latitude 49°01'00"N and longitude 106°49'00"W (Koper et al. 2008). The topography of the area was mixed, with hills and flat lowland areas, ranging from 750 to 850 m above sea level. The upland areas were primarily glacial till and the valley soils are a mix of alluvial deposits and till (Saskatchewan Soil Survey 1992, Parks Canada 2006). The area was primarily native mixed-grass prairie dominated by grass species such as *Elymus lanceolatus*, *Pascopyrum smithii, Bouteloua gracilis,* and *Hesperostipa comata*; shrub species such as *Artemisia cana* and *Symphoricarpos occidentalis*; and forb species such as *Phlox hoodii* and *Artemisia frigida* (Parks Canada 2006). Annually the area experienced approximately 350 mm of precipitation (Parks Canada 2006).

The study area consisted of 9 pastures of approximately 300 ha each, 3 of which were ungrazed throughout the study (Koper et al. 2008) (Figure 1). The other 6 GNP pastures were stocked with yearling steers with a season-long continuous grazing system in the summers. Cattle were usually brought into the pastures between mid-May and early June and remained there for four months, until early September. The study area had not been grazed by cattle for at least 20 years (Parks Canada 2006). Two years of pre-grazing data were collected before yearling steers were put on the pastures in 2008 (Koper et al. 2008). The pastures were then grazed annually, each summer, 2008-2011 at stocking intensities which varied slightly by year, ranging from approximately 0 to 0.85 AUM/ ha (Table 1). The pastures were ungrazed in 2012, but all infrastructure and fencing remained in place. Within each pasture 10 points were surveyed, 4 in the lowland area and 6 in the upland area (Parks Canada 2006; Figure 1).

Lowland habitats were inherently more heterogeneous in structure and composition,

including shrub-dominated and grass-dominated habitats, and mudflats. A stream flowed

through the lowlands of each pasture. There was one water tank located in each pasture in the

lowland habitat, as an additional water source for cattle. In 2011, water was not pumped into the

tanks until the end of July and before this point the streams were the main water source.

Table 1. Stocking rates by pasture in 2011 in Grasslands National Park, Saskatchewan, Canada.

Pastures by stocking rate	Expected biomass removal	Stocking rate (AUM/ha)
1, 5, 9	0 %	0
2	20 %	0.24
3	57 %	0.7
4	70 %	0.77
6	33 %	0.38
7	45 %	0.55
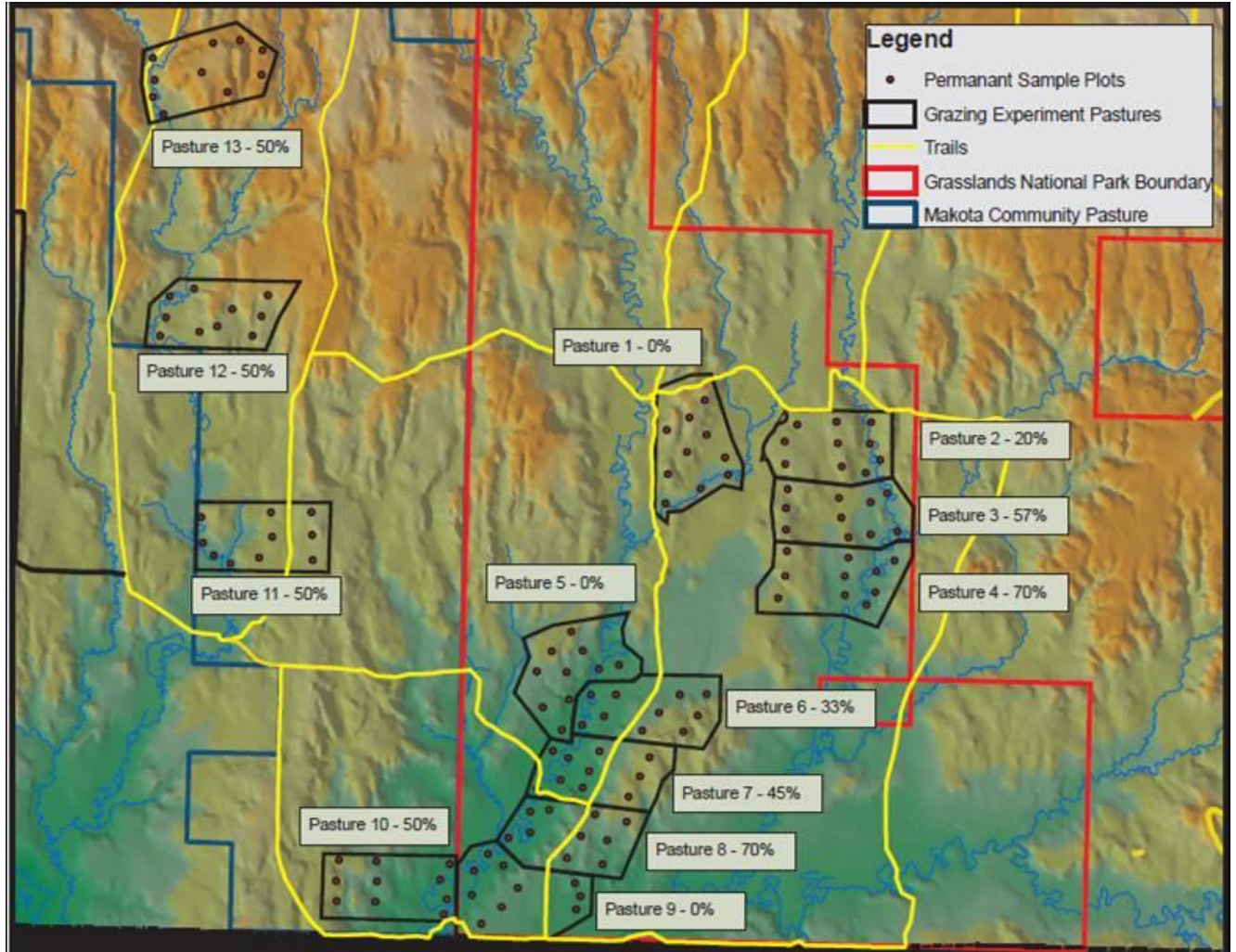
Figure 1. Location of study pastures within the East Block of Grasslands National Park,

Saskatchewan, Canada. Saskatchewan, Canada. Green shades represent lower elevations and

brown shades represent higher elevations.
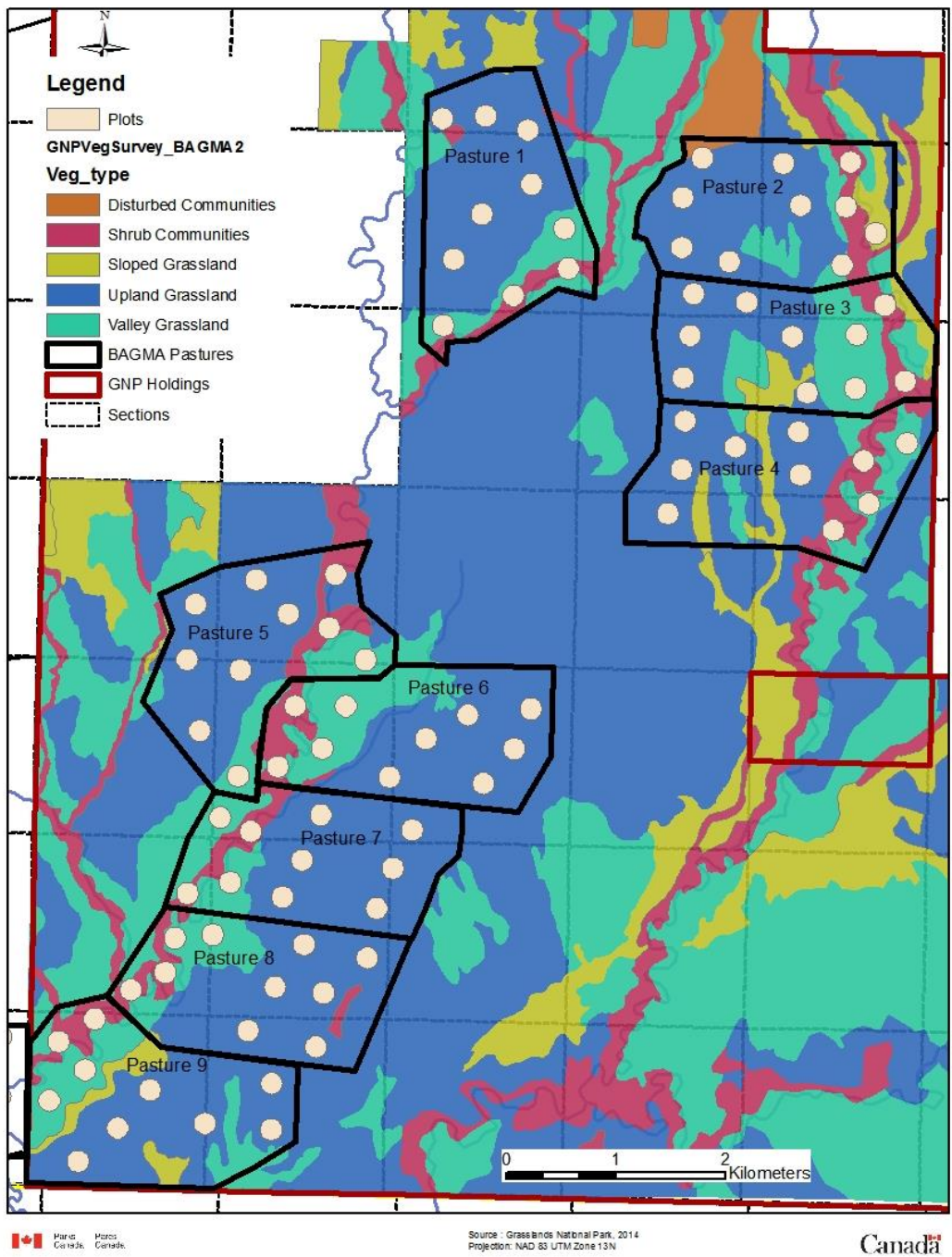
Figure 2. Vegetation communities in the East Block of Grasslands National Park, Saskatchewan,

Canada. Lowland points are found in shrub communities and valley grasslands.

Avian surveys

Avian surveys were conducted each year between mid-May and June 30. Protocols for these surveys were adapted from Hutto (1986). At each survey point a 6-minute point count was performed. All birds heard or seen within 100 meters of the point were recorded. Surveys were not conducted when wind exceeded 20 km/ hr or in the case of precipitation. All points were surveyed three times in the season and by different observers to control for observer bias. Each round of surveying was separated by at least three days. Bias in surveys due to weather differences was avoided as much as possible by surveying pastures with different stocking rates on the same day. Additionally, pastures in geographically different areas of the study site were surveyed on the same day.

Vegetation surveys

Vegetation surveys occurred between June 1 and July 31, following protocols established by Koper et al. (2008). Each fixed avian survey point had a 20 x 50m modified Whittaker plot 25 m to its south, where all plant species were identified and recorded. Vegetation characteristics were measured at 10, 1 x 0.5m frames within the larger Whittaker plot. Visual estimates of foliar coverage of each plant species within the frame was recorded, along with estimates of litter, bare ground, lichen, and algae cover.

In 2012 an additional vegetation survey was conducted at each avian survey point to determine the overall cover of bare ground and shrub cover throughout each plot. Four transects of 100 m were run in four directions radiating out from the point with a meter tape. The length of shrub cover, grass cover and bare-ground cover below the meter tape was recorded. These lengths were averaged over the four transects to create a relative estimate of shrub cover, grass cover and bare ground cover for each plot's 100-m radius survey area.

Statistical analyses

Bird data collected from 2006 to 2012 and vegetation data from 2006 to 2011 were used for analysis. The first 5 minutes of bird count data were used for statistical analysis, to be consistent with other literature (e.g. Davis et al. 1999). The most appropriate distribution (e.g. normal, negative binomial, Poisson) for the residuals of relative songbird abundances was determined using Proc Genmod in SAS 9.3. In order to determine the most suitable distribution, diagnostic plots (Q-Q plots and box plots) were used to determine normality; suitability of Poisson or negative binomial distributions were assessed using the deviance to degrees of freedom ratio, where 1:1 suggests a better fit. Analyses were then run with the selected distribution within generalized linear mixed models (GLMMs) using the Proc Glimmix procedure in SAS. GLMMs allow for the spatial clustering of plots within pastures and non-normal distribution of data (Quinn and Keough 2002). Abundances of each songbird species at each plot were summed over the three rounds of surveys, rather than averaged, as dependent variables cannot have decimals with Poisson or negative binomial distributions when used in Proc Glimmix. I ran all analyses for upland and lowland habitats separately as the two habitats differ substantially in terms of vegetation composition, topography, and heterogeneity.

Three rounds of bird surveys were conducted from late May to mid-June each year (Table 2). The study species return to the area from their wintering grounds in late April/ early May. Thus, the habitat conditions that birds were responding to were primarily reflective of conditions caused by cattle grazing in the previous year. Therefore, the vegetation and grazing conditions of the previous year were used as the indices of habitat conditions for birds (e.g. 2009 bird abundances were compared with 2008 vegetation and stocking rates).

Table 2. Dates of grazing and avian surveys in BAGMA, in Grasslands National Park, Saskatchewan, Canada, 2008-2012.

Year	Grazing start date	Grazing end date	Avian survey start date
2008	June 5	September 28	May 27
2009	May 15	September 9	May 30
2010	May 26	September 22	May 28
2011	May 30	September 27	June 5
2012	N/A	N/A	May 25

Models were run with stocking rate as an independent variable and individual bird species abundances and bird community diversity indices as response variables. I used an interaction term with year to determine if effects of stocking rate changed over time compared to pre-grazing years. A polynomial term and associated interactions were used to allow for a nonlinear relationship between stocking rate and the response variables each year. However, if interaction or polynomial terms were not significant I concluded that the data suggested that there was no non-linear trend in the data, and these variables were removed and the model was run again, to minimize problems with colinearity (Quinn and Keough 2002).

To determine if grassland songbirds were affected by plant composition variables additional models were created with forb and grass richness, forb cover, plant Shannon-Wiener diversity, and bare ground and shrub cover as independent variables and individual bird species abundances as response variables. I also evaluated responses of grassland songbirds to abundance of grasses (*Bouteloua gracilis, Calamagrostis montanensis, Elymus lanceolatus, Hesperostipa comata, Hesperostipa curtiseta, Koeleria macrantha,* and *Pascopyrum smithii)* and

forb species *(Achillea millefolium, Artemisia frigida, Pediomelum agrophyllum, Phlox hoodii,* and *Taraxacum officinale)* as independent variables. For the lowland analyses *Calamagrostis montanensis*, *Hesperostipa curtiseta*, *Pediomelum agrophyllum*, *Phlox hoodii* and *Taraxacum officinale* were removed as these species were very uncommon in that habitat. All models included year as a categorical variable.

I also tested for effects of habitat characteristics throughout the point-count plots (shrub cover and bare ground cover) on relative abundance of the avian study species using the vegetation transect data collected in 2012. These data were more reflective of site cover at the scale of the 3.2-ha point-count plot than the values collected at the Whittaker plots were These models were run with generalized estimating equations as there was only one year of data.

An alpha value of 0.10 was set before the analyses were performed. This alpha value was chosen because the possibility of a Type II error, rather than a Type I error, is of greater concern in conservation biology (Taylor and Gerrodette 1993).

Sorensen's index values (Bray-Curtis similarity index) in each pasture from pre-grazing years were compared to values in that pasture from each successive year to evaluate whether avian communities in grazed pastures changed more over time than ungrazed pastures. The equation is:

$$S = 2c/ (a + b)$$

where *a* is the sum of all individuals in sample 1, *b* is the sum of all individuals in sample 2, and *c* is the sum of all shared individuals by species between the two pastures (Chao et al. 2006). This index provides a percentage similarity between two communities. Plot counts in each pasture were combined to increase sample size and ensure equal sample sizes as required for this index (Chao et al. 2006). Blackbird species (including cowbirds), swallows, raptors and

shorebirds were all removed from the data set as these species are not effectively measured with my protocols. In order to determine if differences between avian communities increased over time and at different grazing intensities I determined whether Sorensen's index values were influenced by year, stocking rate, and an interaction term as independent variables using GLMM. For these analyses comparisons to both pre-grazing years (averaged) were used in the data set.

CHAPTER 4: RESULTS

Stocking rate

Relative abundance of grassland birds varied by species between lowland and upland habitat (Table 3). Abundances of individual grassland birds varied with grazing intensity (Table 4). Sorensen's quantitative index suggested that upland avian communities differed from their pre-grazing condition more at higher stocking rates, but surprisingly, this effect was significant only in the first year of grazing (Figure 6). In lowlands, similarity in songbird communities did not vary with grazing intensity (p > 0.1244). Overall, in the same pastures, lowland communities were less similar than upland communities from year to year (Table 5).

Upland

Cattle grazing had no effect on avian richness, abundance, or Shannon-Wiener diversity ($p > 0.1194$). Relative abundance of Brewer's sparrow, western meadowlark, and clay-colored sparrow were all independent of stocking rate in the upland sites (Appendix A), although abundances varied with year.

Both Baird's sparrow and Sprague's pipit showed negative responses to grazing after the first and second year of grazing (Figure 3) intensity in some years. Abundances in the years with significant interactions with grazing were highest at the lowest grazing intensities. Baird's sparrow showed a non-linear trend and declined between 0 and 0.3 AUM/ha. Sprague's pipit however showed a simple linear trend ranging from 2.7 down to 1.4 mean birds per point at the highest grazing intensity, in parallel trends among years (Figure 3), showing that any increase in stocking rate resulted in a decline in their relative abundance.

Grasshopper sparrow and Savannah sparrow showed significant responses to grazing in all years (Figure 3). Grasshopper sparrow abundances primarily decreased with grazing, though

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they appeared to be tolerant of grazing up to 0.4 AUM/ha. Savannah sparrow abundances began declining between 0.2 and 0.5 AUM/ ha depending on year. Vesper sparrow showed a weak positive effect of grazing overall (Figure 3).

Chestnut-collared longspur responded positively to grazing in all years (Figure 3). Abundances began to increase around 0.3 AUM/ ha, with a minimum of 0.5 birds per point to 3 birds per point at 0.8 AUM/ha. The effect of grazing decreased with time. Horned lark also had a positive response to grazing, although this effect was only significant after 4 years of grazing (Figure 3).

Lowland

There were less consistent effects of grazing in the lowlands. Cattle grazing reversed a pre-existing (spurious) negative trend of future stocking rate on bird richness and Shannon-Wiener diversity in the second year of grazing (Figure 4) , suggesting that grazing intensity increased species diversity. Stocking rate had a negative effect on songbird abundance after one year of grazing, but not in subsequent years (Figure 4).

Occupancy of habitat was too low to test for grasshopper sparrow responses to grazing in lowland. Western meadowlark showed no response to grazing in lowland habitat ($p > 0.1325$). Baird's sparrow exhibited a negative effect of grazing in the lowland habitat after each of the first two years of grazing (Figure 5), with abundances decreasing by up to 1 bird per point from the ungrazed pastures to 0.8 AUM/ha. Sprague's pipit abundances peaked at slightly higher stocking rates during each of the first three years of grazing.

Savannah sparrow exhibited a significant response to grazing in all four years in both lowland and upland habitat (Figure 5). Over four years of grazing Savannah sparrow abundances showed a shift in peak abundances, with highest abundances at lower stocking rates

with each successive year of. In most years Savannah sparrow abundance began to decline after 0.3 AUM/ha. Chestnut-collared longspur appeared to show a cumulative effect of grazing, as the slope of the relationship between grazing intensity and abundance increased with year. As in uplands, this species was positively affected by increased stocking rate, in the last two years (Figure 5). In the last year of grazing this positive effect was not seen until stocking rate reached 0.5 AUM/ha.

Relative abundances of vesper sparrow were generally independent of grazing, although a trend during a single intermediate year of grazing was found. Brewer's sparrow, clay-colored sparrow and horned lark were relatively insensitive to stocking rate in lowlands, responding to grazing in two non-consecutive years (Figure 5).

Effects of grazing on bare ground and shrub cover

Upland

Increasing stocking rates led to a significant increase in bare ground ($\beta = 3.4228$, $p <0.0001$). Shrub cover was independent of stocking rate ($\beta = 0.3849$, $p = 0.2452$). Mean cover of shrub and bare ground was low in the upland points; on average, they represented 2.5 % and 0.5% of cover respectively and did not exceed 11 % cover in any of the plots.

Savannah sparrow, Sprague's pipit, clay-colored sparrow, Baird's sparrow and grasshopper sparrow responded negatively to bare ground cover (Table 6), while horned lark and Brewer's sparrow responded positively to bare ground cover (Table 6). Clay-colored sparrow and grasshopper sparrow responded positively to shrub cover in the uplands while Baird's sparrow responded negatively (Table 6).

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Lowland

Stocking rate had no significant relationship with either the amount of bare ground (β = -0.4127; p = 0.5140) or shrub cover (β = 0.7788; p = 0.1146). The lowland survey points had higher average shrub and bare ground cover than upland points (16 % and 5 % cover, respectively). In the lowland areas more species responded to shrub cover and fewer responded to bare ground cover than in upland habitat. Clay-colored sparrows were the only species to respond positively to shrub cover (Table 7). Three species, including Baird's sparrow, Sprague's pipit, and Savannah sparrow, responded negatively to increased shrub cover in lowlands (Table 7). There did not appear to be a strong threshold at which Sprague's pipit and Baird's sparrow abundances began to decline. However, Savannah sparrow abundances declined sharply when shrub cover was above 30%. Clay-colored sparrows and western meadowlarks responded negatively to bare ground in the lowland habitat (Table 7).

Vegetation composition

Upland

Chestnut-collared longspur and Sprague's pipit had significant positive relationships with forb cover (β = 0.0150, p = 0.0586; β = 0.0497, p = 0.0405, respectively), while vesper sparrow was negatively correlated with increased forb cover (β = -0.0343, p = 0.0946). No other species showed a significant relationship with forb cover (p > 0.1505). Savannah sparrow showed a small decrease with increased forb richness (β = -0.0291, p = 0.0745). Western meadowlarks showed a positive correlation with graminoid richness (β = 0.1021, p = 0.0402). No other songbird species exhibited responses to forb or graminoid richness (p > 0.1086).

Avian richness, but not avian abundance, was positively correlated with forb cover (β = 0.0328, p = 0.0285; β = 0.0087, p = 0.5236 respectively). Avian abundance showed no

significant correlations with forb richness or graminoid richness (β = -0.0138 p = 0.2839; β = -0.0051 p = 0.9259 respectively). Shannon-Wiener diversity of birds had a small positive correlation with forb cover (β = 0.0054, p = 0.0279). Five species showed correlations with plant Shannon-Wiener diversity including Baird's sparrow, chestnut-collared longspur, grasshopper sparrow, horned lark, and Sprague pipit (Table 8).

Grass species

Clay-colored sparrow and western meadowlark showed no significant relationship with any of the plant species tested in upland habitat (Table 8). Chestnut-collared longspur abundance was negatively correlated with all grass species except prairie reedgrass (*Calamagrostis montanensis)* and prairie junegrass (*Koeleria macrantha)* (Table 8). Horned lark abundance was negatively correlated with cover of both *Hesperostipa* species (Table 8). Conversely, Sprague's pipit abundance was positively correlated with individual grass species, including northern wheatgrass (*Elymus lanceolatus)*, needle and thread grass (*Hesperostipa comata)*, and western wheatgrass (*Pascopyrum smithii)* (Table 8).

Forb species

Sprague's pipit abundance was correlated positively with three forb species, pasture sage (*Artemisia frigida)*, common dandelion (*Taraxacum officinale)*, and silverleaf scurfpea (*Pediomelum agrophyllum)* (Table 9). Responses by other bird species to forbs were variable. Sprague's pipit and chestnut-collared longspur were both associated with cover of more individual plant species than any other bird species.

Lowland

  Grass species

Specific plant and bird species associations varied considerably between the upland and lowland habitat. Baird's sparrow, Savannah sparrow, and western meadowlark showed no significant correlations with any of the plant species tested in the lowlands (Table 9). Unlike in the upland habitat, Sprague's pipit abundance was negatively correlated with grass species cover (Table 9). Chestnut-collared longspur abundance was positively correlated with prairie junegrass (*Koeleria macrantha)* in the lowland habitat (Table 9). Horned lark abundance again was negatively correlated with two grass species, northern wheatgrass (*Elymus lanceolatus)* and needle and thread grass (*Hesperostipa comata)* (Table 9). Clay-colored sparrow abundance, which showed no response to any plant species in the upland, was positively correlated with cover of three grass species, blue grama grass (*Bouteloua gracilis)*, needle and thread grass (*Hesperostipa comata)*, and northern wheatgrass (*Elymus lanceolatus)* in the lowland habitat (Table 9).

  Forbs

Sprague's pipit abundance did not show correlations with either forb in the lowlands (Table 9). Brewer's sparrow abundance was positively correlated with common yarrow (*Achillea millefolium*) in the lowland, the reverse of the trend it showed in the upland (Table 9).

Precipitation data

In the springs of 2010, 2011, and 2012, above average levels of precipitation occurred in the study region, with May and June of these years having between 100 % to over 250% of the normal amount of precipitation (Western Regional Climate Center 2012; Figure 7; Appendix B).

Table 3. Mean plot abundances of grassland songbird species, averaged over three point count surveys, in upland and lowland habitat by year in Grasslands National Park, Saskatchewan, Canada, from 2009 to 2012.

	2009		2010		2011		2012	
	Upland	Lowland	Upland	Lowland	Upland	Lowland	Upland	Lowland
Baird's sparrow	1.66	1.15	2.43	1.58	2.19	1.28	2.08	1.13
Brewer's sparrow	0.10	0.11	0.19	0.20	0.15	0.18	0.27	0.31
Chestnut-collared longspur	1.29	0.23	1.90	0.40	1.39	0.21	1.06	0.19
Clay-colored sparrow	0.15	0.88	0.28	1.48	0.28	1.55	0.23	1.53
Grasshopper sparrow	0.31	0.009	0.55	0.03	0.78	0.03	1.33	0.26
Horned lark	0.35	0.49	0.38	0.81	0.44	0.74	0.25	0.74
Savannah sparrow	0.61	0.76	0.98	1.00	1.30	0.85	1.23	1
Sprague's pipit	1.72	0.90	2.38	1.06	1.74	0.71	1.58	0.64
Vesper sparrow	0.07	0.26	0.42	0.86	0.26	0.74	0.26	0.61
Western meadowlark	0.18	0.31	0.50	0.56	0.32	0.45	0.08	0.14

Table 4. Overall responses of individual songbird responses to increased grazing intensity in Grasslands National Park, Saskatchewan, Canada, from 2009 to 2012. "+" indicates a positive response, "-" indicates a negative response, "none" indicates no significant response, and "NL" indicates a non-linear response.

Species	Upland	Lowland
Baird's sparrow	-	-
Brewer's sparrow	0	NL
Clay-colored sparrow	0	NL
Chestnut-collared longspur	+	+
Grasshopper sparrow	- / NL	N/A
Horned lark	+	+
Savannah sparrow	NL	NL
Sprague's pipit	-	-
Vesper sparrow	+	0 / +
Western meadowlark	0	0

Table 5. Comparison of variability in Sorensen's quantitative index between upland and lowland habitat by year, comparing pre-grazing years (2006 and 2007) to grazing years (2008-2011) in Grasslands National Park, Saskatchewan, Canada, 2009-2012.   The first row compares 2006 to 2007 (both ungrazed). Other rows show comparison of grazing years to the average of both pre-grazing years (e.g. year 2: average of the differences between 2006 and 2010, and 2007 and 2010).

Year(s) since grazing began	Upland		Lowland	
	Mean difference	Standard deviation	Mean difference	Standard deviation
Pre-grazing	0.791	0.038	0.691	0.071
1	0.733	0.055	0.667	0.056
2	0.722	0.051	0.649	0.097
3	0.764	0.050	0.658	0.076
4	0.740	0.058	0.632	0.063

Table 6. Effects of percent bare ground and shrub cover on grassland songbird species abundances in upland habitat in Grasslands National Park, Saskatchewan, Canada, from 2012.

	Shrub cover			Bare cover		
	β	*p*	*SE*	β	*P*	*SE*
Baird's sparrow	-0.2844	**<0.0001**	**0.0691**	-0.2754	**0.0006**	**0.0801**
Brewer's sparrow	-0.0907	0.3265	0.0924	0.1034	**0.0742**	**0.0579**
Chestnut-collared longspur	-0.0207	0.7239	0.0587	-0.0207	0.7515	0.0658
Clay-colored sparrow	0.3281	**<0.0001**	**0.0493**	-0.1166	**0.0017**	**0.0371**
Grasshopper sparrow	0.1599	**0.0653**	**0.0867**	-0.5519	**<0.0001**	0.0948
Horned lark	0.0201	0.8053	0.08	-0.1922	**0.0157**	0.0795
Savannah sparrow	0.0272	0.6497	0.0599	-0.3182	**0.0005**	**0.0909**
Sprague's pipit	-0.0933	0.3708	0.1403	-0.2476	**0.0724**	**0.1378**
Vesper sparrow	0.1027	0.1169	0.0655	0.0297	0.4379	0.0382
Western meadowlark	-0.0846	0.2963	0.0810	0.1591	0.1379	0.1072

*Bold font indicates a significant *p*-value

Table 7. Effects of percent bare ground and shrub cover on grassland songbird species in lowland habitat in Grasslands National Park, Saskatchewan, Canada, 2012.

	Shrub cover			Bare cover		
	β	*p*	*SE*	β	*P*	*SE*
Baird's sparrow	-0.551	**0.0064**	**0.0202**	-0.0214	0.5036	0.0320
Brewer's sparrow	-0.0103	0.5485	0.0172	-0.0455	0.2531	0.0398
Chestnut-collared longspur	-0.0545	0.3026	0.0529	-0.0303	0.4332	0.0386
Clay-colored sparrow	0.0847	**0.0006**	**0.0247**	-0.1363	**<0.0001**	**0.0296**
Grasshopper sparrow	0.0001	0.9931	0.0112	-0.0167	0.4567	0.0224
Horned lark	-0.0046	0.6258	0.0094	0.0432	0.4846	0.0618
Savannah sparrow	-0.0199	**0.0030**	**0.0067**	0.0041	0.6022	0.0079
Sprague's pipit	-0.0276	**0.0431**	**0.0136**	0.0108	0.4945	0.0158
Vesper sparrow	-0.0042	0.4984	0.0062	-0.0009	0.9737	0.0270
Western meadowlark	-0.0110	0.2635	0.0098	-0.1756	**0.0360**	**0.0837**

*Bold font indicates a significant *p*-value

Table 8. Effects of cover of individual plant species and plant diversity on grassland songbird abundances in upland habitat in Grasslands National Park, Saskatchewan, Canada, 2009-2012.

		Baird's sparrow	Brewer's sparrow	Chestnut-collared longspur	Clay-colored sparrow	Grasshopper sparrow	Horned lark	Savannah sparrow	Sprague's pipit	Vesper sparrow	Western meadowlark
Achillea millefolium	β	0.0360	-0.3370	-0.0489	0.0602	-0.0180	-0.0401	0.0434	-0.0220	0.0238	0.0135
	p	0.7192	**0.0384**	0.1935	0.5032	0.8311	0.5582	0.6115	0.8020	0.7749	0.8739
Artemisia frigida	β	0.0784	-0.0785	0.0317	0.0475	-0.2489	0.0216	-0.2429	0.2036	-0.1192	-0.0628
	p	0.5041	0.5100	0.4197	0.6266	**0.0124**	0.7782	**0.0135**	**0.0519**	0.2678	0.5865
Bouteloua gracilis	β	0.1596	0.0334	-0.0600	-0.0601	-0.1353	-0.0600	-0.0153	0.0238	0.0377	0.0361
	p	**0.0433**	0.6534	**0.0695**	0.3921	**0.0458**	0.2861	0.8170	0.7279	0.5791	0.5825
Calamagrostis montanensis	β	-0.0600	0.0469	-0.0324	-0.0224	0.0200	-0.0605	-0.0686	-0.0520	0.0774	-0.0024
	p	0.1974	**0.0950**	0.1757	0.5316	0.6082	0.2285	**0.0771**	0.2026	**0.0069**	0.9609
Elymus lanceolatus	β	0.0107	-0.0136	-0.0229	0.02048	0.0195	-0.0127	0.0192	0.0519	-0.0088	0.0185
	p	0.5544	0.4068	**0.0097**	0.1566	0.2252	0.3409	0.2137	**0.0014**	0.5387	0.1605
Hesperostipa comata	β	-0.0037	-0.0112	-0.0424	-0.0259	0.0512	-0.0522	-0.0231	0.0452	-0.0322	0.0137
	p	0.8828	0.6348	**0.0021**	0.2348	**0.0177**	**0.0101**	0.2934	**0.0379**	0.1115	0.4384
Hesperostipa curtiseta	β	0.0309	-0.0134	-0.0323	0.00180	-0.0145	-0.0481	0.0217	0.0264	-0.0141	0.0206
	p	0.2361	0.5996	**0.0105**	0.9296	0.5238	**0.0248**	0.3213	0.2461	0.5130	0.2702
Koeleria macrantha	β	-0.0050	-0.0857	-0.0094	0.0076	0.0345	-0.0361	0.0066	-0.0009	-0.0570	0.0279
	p	0.9068	**0.0708**	0.5244	0.8374	0.3408	0.2517	0.8534	0.9799	0.1232	0.5135
Pascopyrum smithii	β	-0.0068	-0.0071	-0.0362	-0.0227	0.0108	-0.0072	0.0005	0.0421	-0.0236	0.0025
	p	0.7652	0.6826	**0.0008**	0.3476	0.5749	0.6517	0.9805	**0.0326**	0.2160	0.8844
Pediomelum agrophyllum	β	0.0761	-0.1468	-0.0310	-0.0518	0.0582	-0.0208	-0.1640	0.3296	-0.0749	-0.0815
	p	0.4984	0.2118	0.3793	0.6508	0.5406	0.7523	0.0814	**0.0009**	0.4154	0.4936
Phlox hoodii	β	-0.1258	-0.0311	-0.0891	0.0717	0.0146	0.0851	-0.0808	0.1350	0.0638	0.0745

	p	**0.0601**	0.6514	**0.0034**	0.1870	0.7960	**0.0308**	0.1468	0.0224	0.2851	0.1677
Taraxacum officinale	β	0.0158	-0.0717	0.0133	-0.0915	0.0834	0.0140	-0.0391	0.2112	-0.0361	-0.0017
	p	0.8419	0.3160	0.6588	0.2298	0.2123	0.8096	0.5562	**0.0024**	0.5676	0.9775
Plant Shannon-wiener diversity	β	-0.8044	-0.02152	0.8415	-0.2834	-0.7859	1.1417	-0.4113	-0.9658	0.5076	-0.1142
	p	**0.0525**	0.9571	**<0.0001**	0.4099	**0.0032**	**0.0007**	0.2054	**0.0073**	0.1292	0.6761

*Bold font indicates a significant *p*-value

Table 9. Effects of cover of individual plant species and plant diversity on grassland songbird abundances in lowland habitat in

Grasslands National Park, Saskatchewan, Canada, 2009-2012.

		Baird's sparrow	Brewer's sparrow	Chestnut-collared longspur	Clay-colored sparrow	Horned lark	Savannah sparrow	Sprague's pipit	Vesper sparrow	Western meadowlark
Achillea millefolium	β	-0.0743	0.7093	-0.0489	0.0545	0.0682	-0.0009	0.1117	0.4137	0.2145
	p	0.4859	**0.0313**	0.8507	0.6089	0.5860	0.9947	0.3475	**0.0471**	0.1833
Artemisia frigida	β	0.0358	-0.0799	0.3366	-0.1003	0.0405	-0.0391	0.0964	0.1048	0.0794
	p	0.5219	**0.0129**	**0.0019**	0.1118	0.6178	0.6429	0.1581	0.4123	0.4792
Bouteloua gracilis	β	-0.0258	0.0334	0.0769	0.0786	0.0051	-0.0360	-0.0901	0.0158	0.0177
	p	0.4508	0.6041	0.2169	**0.0406**	0.9030	0.4259	**0.0413**	0.8225	0.7437
Elymus lanceolatus	β	0.0014	0.0408	-0.0144	0.0156	-0.0174	-0.0037	-0.0046	-0.0195	0.0044
	p	0.7963	**0.0412**	0.3356	**0.0332**	**0.0342**	0.6017	0.4712	**0.0957**	0.6632
Hesperostipa comata	β	0.0047	-0.0995	-0.0240	0.0437	-0.0930	-0.0105	-0.0267	-0.0295	0.0049
	p	0.6762	0.1944	0.4454	**0.0118**	**0.0004**	0.5250	**0.0815**	0.2445	0.8127
Koeleria macrantha	β	0.0434	0.1674	0.4658	-0.0964	0.1784	-0.0321	0.0732	0.3868	0.1741
	p	0.5284	0.3665	**0.0004**	0.2096	**0.0146**	0.7173	0.4475	**0.0047**	0.1251
Pascopyrum smithii	β	-0.0061	0.0233	-0.0428	0.0188	0.0019	0.0115	-0.0380	-0.0078	-0.0219
	p	0.6333	0.6616	0.2456	0.2370	0.9177	0.4355	**0.0205**	0.7773	0.3750

*Bold font indicates a significant *p*-value

A   B

C   D
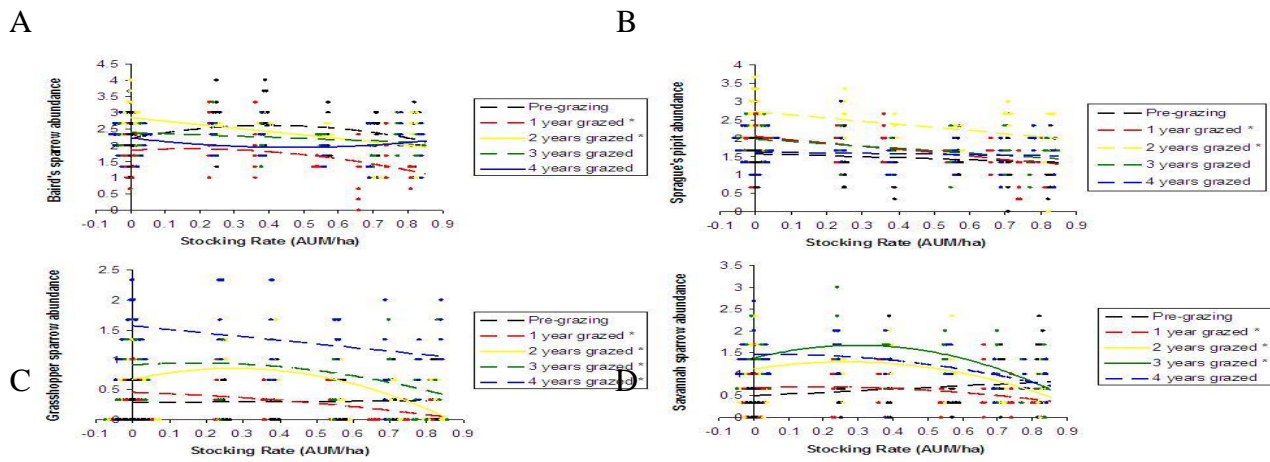
Figure 3 A-D. Effects of cattle stocking rates on individual bird species abundances in upland

habitat in Grasslands National Park, Saskatchewan, Canada, 2009-2012. Years with significant

interaction terms are indicated by asterisks in legend. Years with shape significantly different

from pre-grazing trends indicated with solid lines.
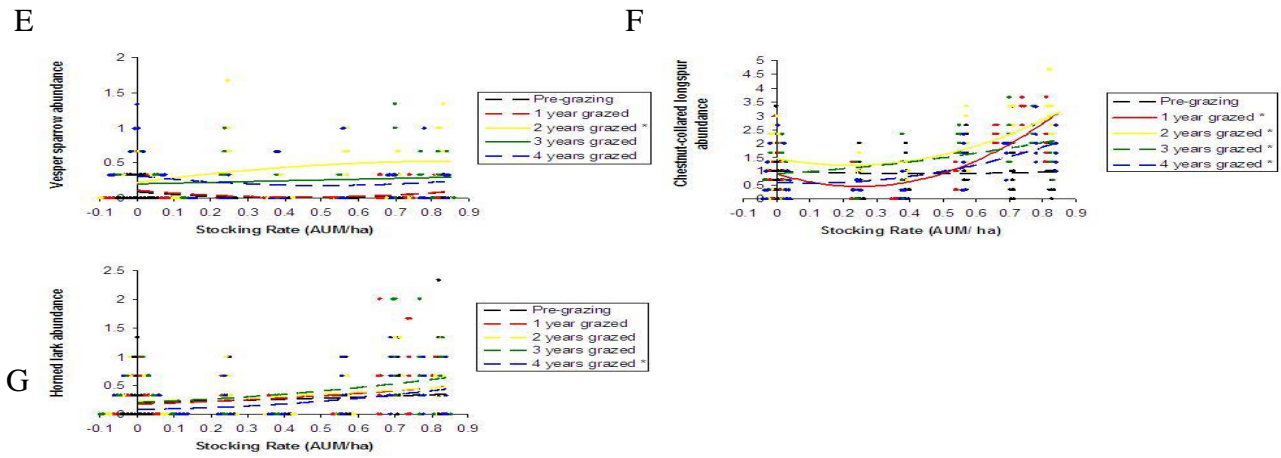
Figure 3 E-G. Effects of cattle stocking rates on individual bird species abundances in upland habitat in Grasslands National Park, Saskatchewan, Canada, 2009-2012. Years with significant interaction terms are indicated by asterisks in legend. Years with shape significantly different from pre-grazing trends indicated with solid lines.
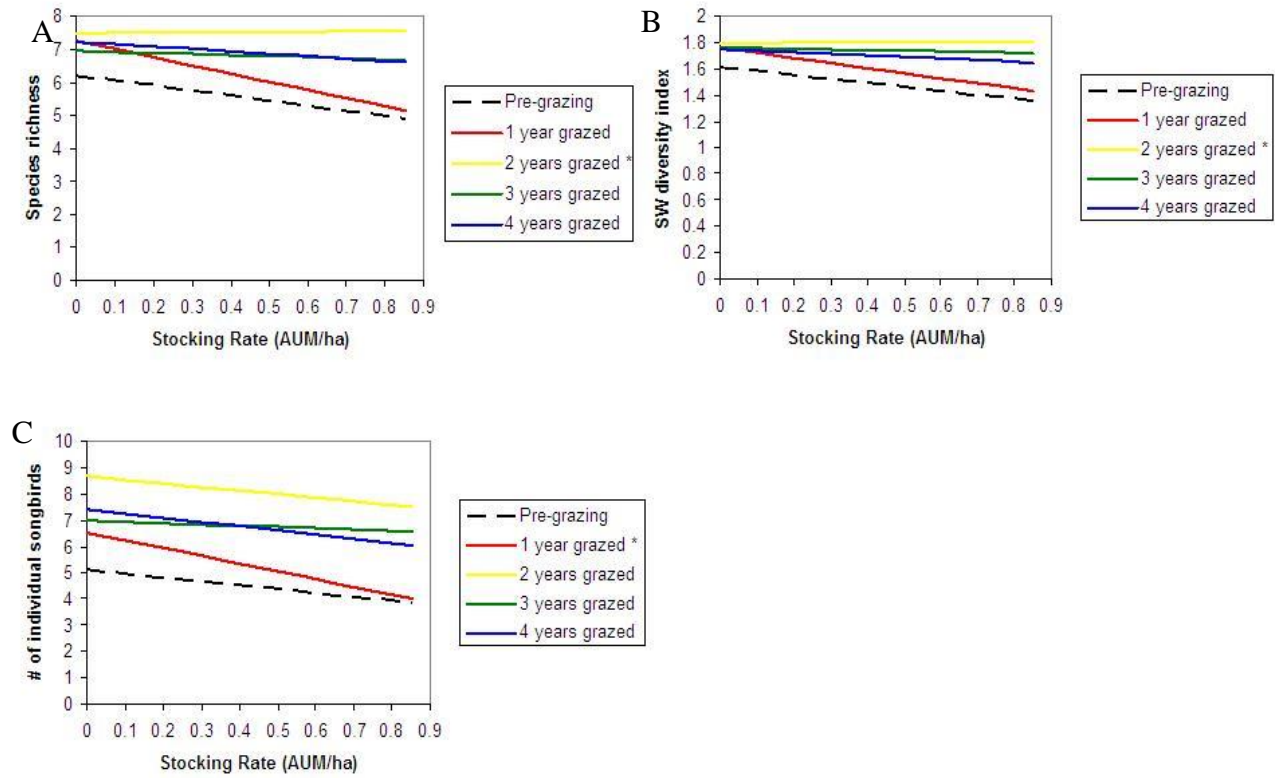
Figure 4 A-C. Effects of cattle stocking rates on songbird diversity in lowland habitat in

Grasslands National Park, Saskatchewan, Canada, 2009-2012. Years with significant

interaction terms are indicated by asterisks in legend.
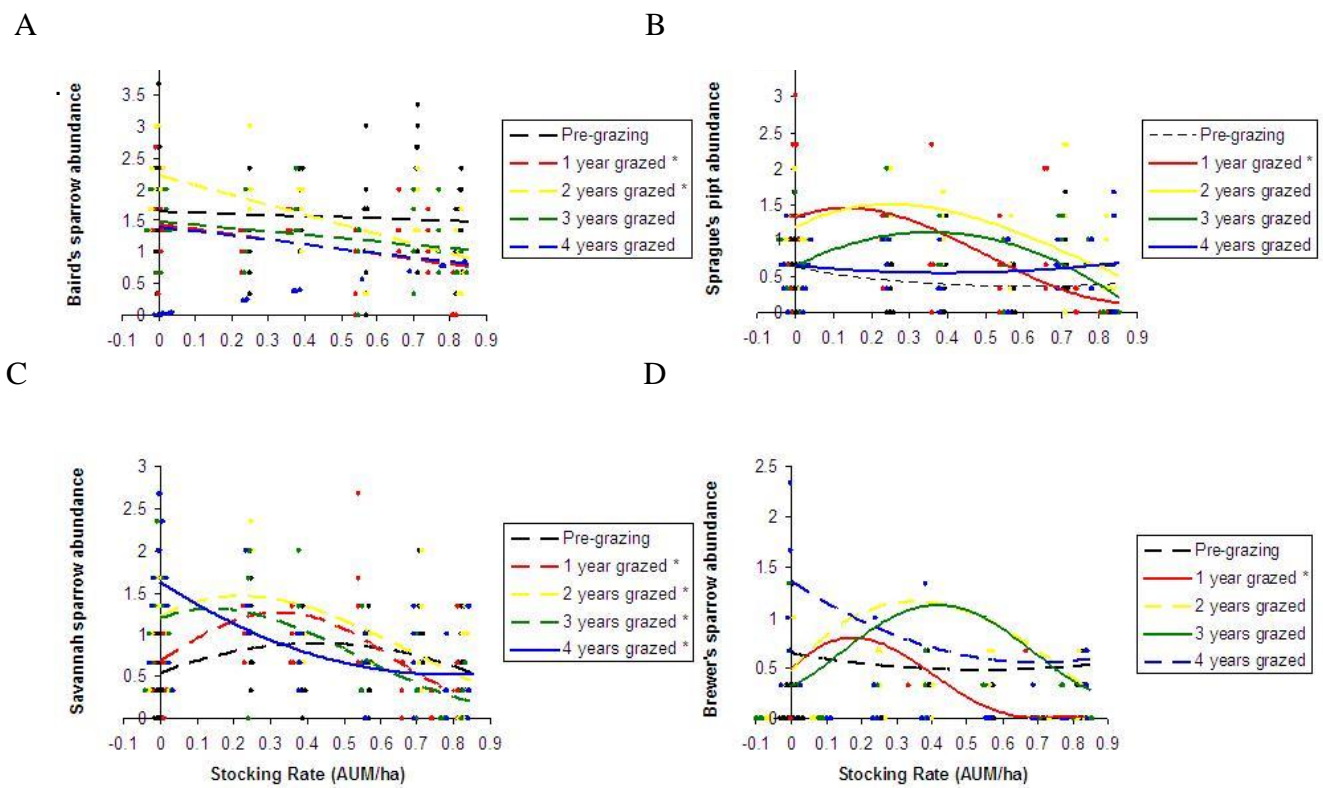
Figure 5 A-D. Effects of cattle stocking rates on individual bird species abundances in lowland habitat in Grasslands National Park, Saskatchewan, Canada, 2009-2012. Years with significant interaction terms are indicated by asterisks in legend. Years with shape significantly different from pre-grazing trends indicated with solid lines.
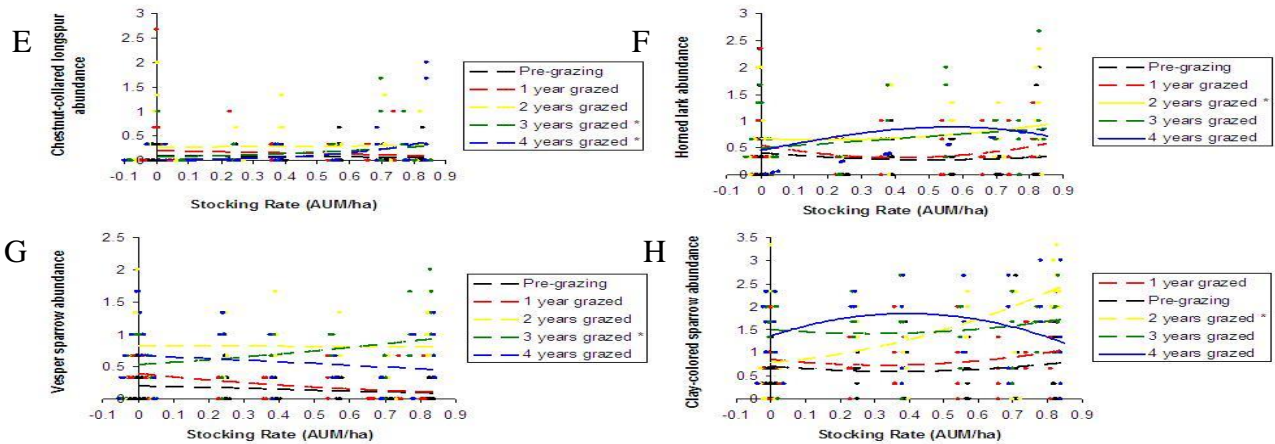
Figure 5 E-H. Effects of cattle stocking rates on individual bird species abundances in lowland habitat in Grasslands National Park, Saskatchewan, Canada, 2009-2012. Years with significant interaction terms are indicated by asterisks in legend. Years with shape significantly different from pre-grazing trends indicated with solid lines.
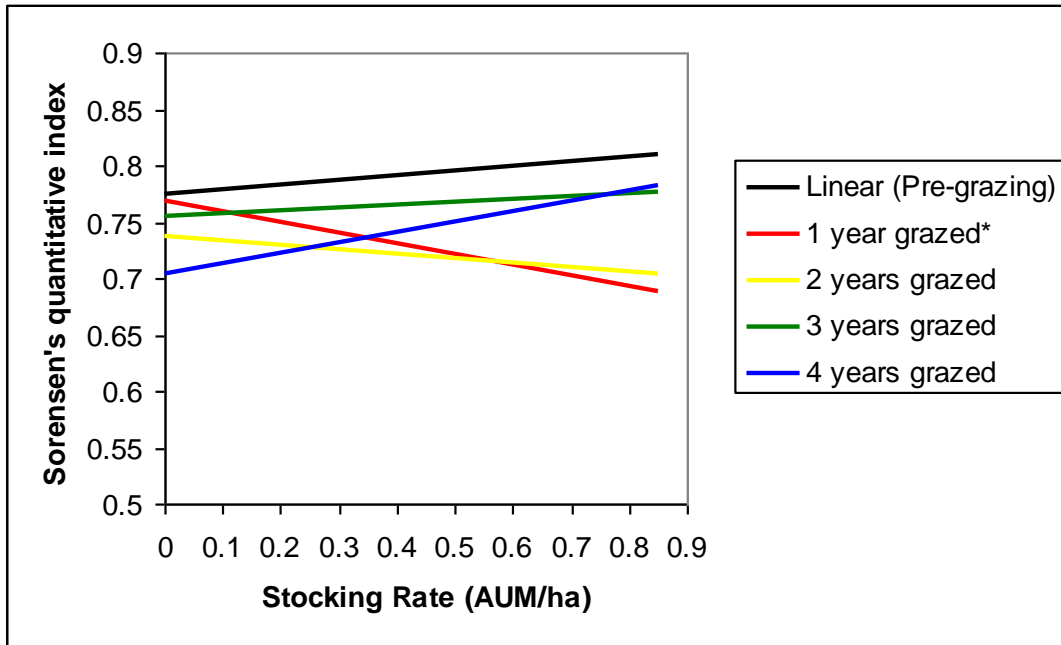
Figure 6. Effects of stocking rate on Sorensen's quantitative index values comparing pasture communities to a pre-grazing state in Grasslands National Park, Saskatchewan, Canada, 2009-2012. Asterisk indicates a trend significantly different from pre-grazing.
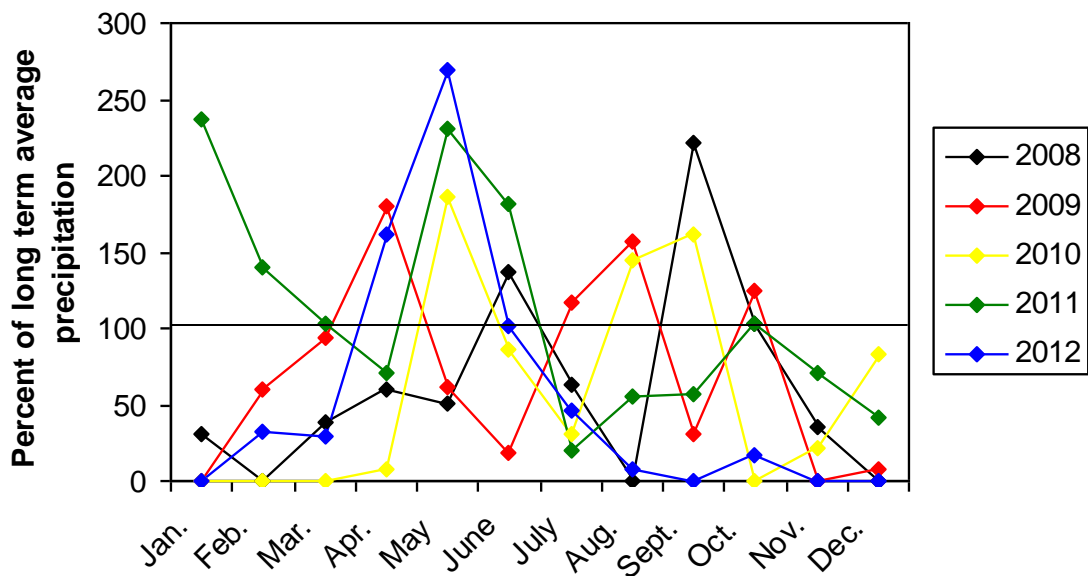
Figure 7. Percent of long-term average (since 1956) of monthly precipitation in Opheim, MT from 2008-2012. Data from Western Regional Climate Center (2013).

CHAPTER 5: DISCUSSION

Grazing and songbird communities

Grazing effects on structure (e.g. Biondini et al. 1998) may have driven avian responses to stocking rate. Sprague's pipit and Baird's sparrow showed declines with increased grazing in both upland and lowland habitats likely due to their habitat requirements for moderate to tall litter depth and vegetation height (Sutter and Brigham 1998, Davis and Duncan 1999). As cattle grazing removes plant material, litter depth and biomass decrease (Gillen et al. 2000, Bai et al. 2001, Lwiwski 2013), making the habitat less suitable for these songbird species. Baird's sparrow may have more flexible habitat requirements than Sprague's pipit (Davis et al. 1999) as it tolerated some light grazing (up to 0.3 AUM/ha) before abundances begin to decline. In contrast, in the upland, Sprague's pipit abundances decreased with any amount of grazing.

Chestnut-collared longspur, horned lark, and vesper sparrow all showed overall positive trends associated with increased grazing. Chestnut-collared longspur is historically associated with grazing (Hill and Gould 1997) and my results support this association, in contrast to other studies (Davis et al. 1999). In the upland habitat horned lark only responded to grazing in the fourth year. Lwiwski (2013) found that the fourth years of grazing was the first year that grazing had a strong impact on bare ground cover within the study site; this may explain why horned lark responded to grazing in that year.

Grazing impacts on songbird diversity indices varied with habitat. In the upland habitat stocking rate had no effect on songbird diversity, although the community composition shifted with stocking rate. Surprisingly, in many cases this effect became less evident as number of years grazed increased, perhaps because extensive precipitation in later years of the study compensated for biomass removed through livestock grazing (Oesterheld et al. 2001). In contrast, in the lowland habitat, species diversity increased, while overall songbird abundance

decreased, at higher stocking rates. Grazing may have increased songbird diversity in these habitats because of an increase in heterogeneity, leading to more habitat niches (Fuhlendorf and Engle 2001). In both habitats it appeared that grazing had the greatest effect on individual bird species and not community and diversity indices, suggesting that species composition shifted at the plot level, but not the pasture level.

This research highlights the importance of using non-linear models to detect effects of grazing. Models that allow for non-linear trends and the identification of thresholds provide important information for adaptive management (Groffman et al. 2006). For example, with a non-linear model it was possible to see that in the lowland Sprague's pipit tolerated some light grazing before it began to experience declines. Information like this can be especially useful for managers in determining an acceptable range of stocking rates to manage for specific songbird species. Relying on simplified categories of grazing intensity means that some trends might be missed.

Most studies in the literature on ecosystem effects of grazing use categories of grazing intensity (ungrazed, light, moderate, heavy) and rarely report actual stocking rates used (e.g. Davis et al. 1999, Bai et al. 2001). Although relative grazing intensity created by stocking rates may vary regionally (e.g. a lower stocking rate can create the same effects in a more arid climate as a higher stocking rate elsewhere), reporting actual stocking rates would be useful for study replication, as well as for managers. This research help fills the knowledge gap on the effects of a complete range of stocking rates (Symstad and Jonas 2011). I recommend that future studies, whether they use grazing intensity as a continuous or categorical variable, report the range of stocking rates used.

Intermediate levels of grazing disturbance can have several ecological effects. Moderate grazing may lead to greater structural heterogeneity at the pasture scale as cattle select and avoid

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areas within the pasture, creating a patchy effect (Fuhlendorf and Smeins 1999, Fuhlendorf and Engle 2001). Some studies have also found increased plant diversity at moderate grazing intensities (Hart et al. 2001). This corresponds with range theory, which holds that patchiness created by moderate grazing should allow the presence of both grazing resistant plants and plants less tolerant of grazing (Milchunas et al 1988, Cingolani et al 2005). Grasshopper sparrows require both areas of cover and areas of bare ground for foraging (Vickery 1996). Areas of moderate grazing may create the mix of habitats this species needs within one pasture.

Savannah and grasshopper sparrow may also simply be selecting for moderate levels of vegetation cover, litter, etc. Savannah sparrow was found at highest abundances at light to moderate stocking rates which corresponds with other studies (Kantrud and Kologiski 1983). Savannah sparrow, similar to some other grassland species, requires areas of dense vegetation for cover (Davis and Duncan 1999). For this species the heaviest grazing intensities likely remove too much biomass. Grasshopper sparrow requires moderate vegetation height (Patterson and Best 1996), and this habitat is likely found in ungrazed to moderately grazed pastures, depending on the amount of annual primary production.

Changes in shape of the response curve over time may reflect yearly shifts in precipitation and vegetation as well as cumulative effects of grazing or precipitation. The lack of simple relationships demonstrates the complexity of ecological interactions between precipitation and stocking rate, which would be missed in linear models. Not only the magnitude of grazing effects but also the shape of these effects varied annually for some species in this study. Management actions may not always have the desired results for species with more variable annual trends. In addition, the number of years management actions are applied may alter the effect of management.

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I found little evidence of cumulative effects of grazing on songbird abundances, with the exception of chestnut-collared longspur in lowland habitat, and horned lark in the upland habitat. Savannah sparrow abundances peaked at lower stocking rates each year, implying that less grazing was having equivalent effects each year. This may have been due to a cumulative impact of grazing on a structural characteristic such as bare ground. Surprisingly, effects of grazing on some species (e.g. Sprague's pipit, chestnut-collared longspur in upland habitat) decreased with time. Research on long term effects of grazing is limited (Biondini et al. 1998, Hart et al. 2001), especially research on grazing effects on songbirds. Some research has found grazing to have cumulative impacts on some structural variables (Lwiwski 2013) although other research has found precipitation, rather than grazing, drives vegetation trends (Biondini et al. 1998).

My results suggest that above average precipitation during the latter part of the study period may have reduced structural impacts of grazing. Within the study area canopy height increased overall over the course of the four years of grazing in both upland and lowland habitat (Bylo et al. 2014) suggesting that increased precipitation during the growing season in later years had ecologically significant consequences. Increased vegetation regrowth can reduce or compensate for effects of grazing on vegetation, and this effect can be increased by several consecutive wet years (Oesterheld et al. 2001, Chase et al. 2001). Total plant basal area and above ground net primary production is correlated with precipitation from the current year as well as previous years (Fuhlendorf et al. 2001, Oesterheld et al. 2001). One study found that a difference in precipitation between two years led to a 17 % percent difference in forage utilization at the same stocking rate (Ballard and Krueger 2005). Studies have found that spring precipitation (April-June) explains a majority of the variation in standing crop (Derner and Hart 2007, Vermeire et al. 2008). It is likely then that the above-average spring precipitation

observed in the study region contributed to primary production, both in those years and the following years, thereby reducing the proportion of biomass removed by cattle and reducing the structural impact of grazing (Oesterheld et al. 2001).

The increased vegetation growth due to precipitation and the accompanying decrease in forage utilization could account for the decreased effects of grazing on some songbird populations in the last two years of the study. Both Sprague's pipit and Baird's sparrow showed no effect of grazing in 2011 and 2012 in the uplands, even though they had shown a significant negative response to grazing in the first two years of the study (see also Davis et al. 1999, Madden et al. 2000). Increased vegetation growth may have effectively reduced the actual percent biomass removed meaning that even pastures grazed at higher intensities could have suitable habitat for these species.

By using four years of data I was able to see a range of songbird responses which varied by year. Yearly changes in the presence or magnitude of responses to grazing may explain conflicting results of short term studies (1-2 years) on songbird species' responses to grazing. For example, Davis et al. (1999) in a one year study found no effect of grazing on Baird's sparrow, whereas Kantrud and Kologiski (1983) found Baird's sparrow to respond positively to light grazing. This research also highlights the importance of using baseline data when determining grazing effects (Koper et al. 2008). Without pre-grazing trends it would have appeared that there was no effect of grazing on songbird richness and diversity.

Species that showed consistent responses to grazing among years may be responding to different vegetation characteristics than species that responded less consistently to grazing. Chestnut-collared longspur and grasshopper sparrow responded to grazing in all years in upland habitat and Savannah sparrow responded in all years in both habitats. Other species in this study showed responses to grazing in some years only, or no response. Species that only responded to

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grazing in some years may be less sensitive to grazing-induced changes in vegetation structure and are instead responding to precipitation induced changes in vegetation, such as overall increased biomass (Oesterheld et al. 2001). As chestnut-collared longspur, Savannah sparrow, and grasshopper sparrow responded to grazing in all years in upland habitat these species are presumably the most sensitive to stocking rate, regardless of environmental conditions. For chestnut-collared longspurs, grazing in wet years may be especially important to create habitat with low vegetation and low litter that they require (Davis et al. 1999).

An additional explanation for bird associations with grazing even in wet years may be that they are responding to grazing-caused changes not associated with structural changes, such as shifts in plant community composition. Davis (2005) found that both chestnut-collared longspur and Savannah sparrow nests were associated with nearby dung. This indicates that there may be an association with the presence, rather than the foraging behavior, of cattle. Grasshoppers and other invertebrates are a large part of grassland songbird diets (Wiens 1973, Wiens and Rotenberry 1979). Grazing intensity influences the presence and abundance of grasshopper species and this may account for some of the importance of cattle grazing for these bird species (Holmes et al. 1979, Quinn and Walgenbach 1990). Additionally, Holmes et al. (1979) found that overall abundance of grasshoppers increased with heavier grazing due to habitat changes (but see Fielding and Brusven 1995). This could explain chestnut-collared longspur preference for heavily grazed areas, as Orthoptera are a large part of grassland bird diets (Wiens and Rotenberry 1979). However, structural requirements may still deter other insectivorous species from using these areas.

It is important to note that this study examined songbird abundance only. Nesting success is also an important factor to consider for conservation of these songbird populations. Grazing has negligible direct effects on grassland songbird nests (Bleho et al. 2014); however it can

indirectly affect nesting success (Fondell and Ball 2004, Pipher 2010, Bleho et al. 2014).

Grazing intensity effects on nest success and survival vary with both species and year (Pipher 2010, Bleho et al. 2014). Sprague's pipits, for example, showed highest nesting success at ungrazed and moderate (0.4-0.5 AUM/ha) stocking rates in Grasslands National Park, Saskatchewan and surrounding areas in one of two years (Pipher 2010). When study species were grouped together for analysis, highest nest success was found at the highest grazing intensity (0.8 AUM/ha).

Weather may also influence nest outcomes. Severe weather was the second highest cause of nest failure, following predation in a Montana study (Jones et al. 2010). Although increased precipitation can have a positive effect on grassland songbird abundances (Niemuth et al. 2008), if this comes in the form of severe weather (hail, storms) then nesting success may decrease.

Lowland responses to grazing

Although studies have examined cattle grazing impacts around riparian pastures and meadows in the Great Basin and a Wisconsin agricultural landscape (Renfrew and Ribic 2001, Dobkin et al. 2008), few previous studies have examined grassland bird use of riparian or lowland areas in mixed-grass prairie habitats. These studies of grazing in riparian areas have found an overall benefit of grazing in riparian zones to grassland and upland shrub birds (Renfrew and Ribic 2001, Dobkin et al. 2008), but these results may not be directly relatable to mixed-grass prairie riparian zones. My study suggests a more complex picture in which individual songbird species are benefited from areas rested from grazing (e.g. Baird's sparrow) or areas with varying intensities of grazing. My study suggests that the benefits of grazing in lowland habitat at my study site are species-specific

Increased shrub cover in the lowland habitat may shape both songbird responses and cattle use of these areas. Several songbird species responded negatively to increased shrub area

in the lowland habitat, but not in upland habitat, likely because shrub cover was so much greater in the lowland habitat. Many grassland species will avoid areas dominated by shrub (Grant et al. 2004, Coppedge et al. 2001). It is likely that these grassland species avoid dense areas of shrub in lowlands, leading to reduced abundances. There is also evidence that cattle avoid these shrubby areas in lowlands, instead showing a preference for meadow type habitats (Ballard and Krueger 2005). It is possible that cattle use of lowlands could increase with climate change as they seek out these areas as thermal refuge at high temperatures (Allred et al. 2010), which might increase cattle grazing impacts in these areas.

Because cattle congregate around water sources and can have negative ecological impacts on hydrology, soil, and plant communities in riparian areas, (Kaufmann and Krueger 1984) it is important to monitor impacts in these areas carefully. It is important to note that there was one water trough located in the upland and one in the lowland upland habitat of each grazed pasture as well as mineral blocks. This may have helped reduce the impact of concentrated use of grazing in the lowlands (Stillings et al. 2003) and may explain why most species did not show stronger responses to grazing in the lowlands.

Response to plant community

Several songbird species were sensitive to plant community composition. When birds are responding to specific plants it is difficult to know what the specific causal mechanism is behind these responses. Plant community composition may affect songbird habitat selection by influencing habitat structure (e.g. heterogeneity, height, density) or food availability (seeds or insects). Rotenberry (1985) suggested that composition matters because of its link with food sources. Vegetative diversity and composition influence grassland insects (Craig et al. 1999, Stoner and Joern 2004, Kearns and Oliveras 2009). Several species of mixed-grass associated grasshoppers (Melanoplinae) are positively associated with forb cover (Craig et al. 1999).

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Grasshoppers are an important part of grassland songbird diets (Wiens 1973, Wiens and Rotenberry 1979). Similarly, Lepidopteran larvae have strong associations with specific host plants (Swengel and Swengel 1999) and are also a common food source for grassland songbirds (Wiens and Rotenberry 1979). These connections could explain the positive responses of chestnut-collared longspur and Sprague's pipit to both overall forb cover and cover of specific forb species.

Songbirds may show relationships with specific plant species because of their influence on habitat structure. A species with enough cover may have the ability to influence habitat structure and heterogeneity. Rotenberry (1985) suggested that structural requirements are selected for at a larger scale, and that composition is important at a smaller scale, perhaps because of its relationship with food availability. Similarly, Haire et al. (2000) found avian associations with specific plant communities at the local scale that were not seen at the landscape scale. Conversely, such patterns may reflect dietary or niche breadth, as Rotenberry (1985) noted, more generalist species may respond to plant communities rather than individual plant species (Rotenberry 1985).

My results indicate increased cover of specific grasses may influence some grassland bird species, presumable due to the effect of grasses on habitat structure. Skinner (1975) found that foraging songbirds did not select for single species stands of grass versus mixed species stands of grass. Chestnut-collared longspur and horned lark showed negative responses to most grass species that they had associations with. The exception to this was *Koeleria macrantha*, which both species showed positive responses to in the lowland. Both of these songbird species require low vegetation cover and this is likely why they showed a negative response to taller grasses (Davis et al. 1999, Davis and Duncan 1999).

Sprague's pipit showed mostly positive or neutral associations with grass species cover in the upland, reflecting its need for structural cover. Interestingly, Baird's sparrow showed no responses to grasses, which may be because it has more flexible habitat requirements (Davis et al. 1999). Similarly western meadowlark showed no response to any plant species (in either habitat) consistent with its characterization as a generalist. This is consistent with Haire et al.'s (2000) finding that western meadowlarks were not as sensitive to grass cover-type as other songbird species.

Bouteloua gracilis is the only short grass of abundance in the area (Coupland 1950), but it substantially influences vertical and horizontal structure. *B. gracilis* may fill in gaps in the understory, and patches of *B. gracilis* mixed in with other taller grasses can create variation in vegetation height and density. Skinner (1975) pointed out that the height and densities of individual grass species contribute to the structure of mixed-grass prairie. Species responding positively (e.g. Baird's sparrow, clay-colored sparrow) to *Bouteloua gracilis* may be showing these responses due to shifts in response to vertical and horizontal heterogeneity and cover.

Some songbird correlations with plant species may be due to associations with specific habitats. For example, *Phlox hoodii* is a low forb, most abundant on bare hilltops in the region (Coupland 1950). Horned lark showed a positive response and Sprague's pipit a negative response to *P. hoodii*. For these species the response to *P. hoodii* may actually be a response to habitat features of the areas it is commonly found in.

Overall there is very little existing research on specific plant-grassland songbird associations and further research may be needed to see if my results are applicable in other regions. Within the study response varied by habitat, for example, Sprague's pipit showed a positive response to *Pascopyrum smithii* in the upland and a negative response in the lowland. Another study found results that contrast mine for Brewer's sparrow, vesper sparrow, Western

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meadowlark and grasshopper sparrow (Paczek and Krannitz 2005). The differences between our two studies and the differences between upland and lowland habitat in our study suggest that bird responses to individual plants likely vary regionally and with habitat.

Soil types between the pastures were fairly similar at a landscape scale, with more variation within the pastures (Saskatchewan Soil Survey 1992). It is therefore unlikely that differences in soil and potential vegetation communities among pastures were responsible for the results seen in this study. However, differences in upland and lowland soils may have influences the difference in responses to plants in the two habitats.

CHAPTER 6: MANAGEMENT IMPLICATIONS

Overview

In order to manage for a complete songbird community a range of stocking rates will be required. A range of stocking rates will provide habitat for different songbird species, even with shifts in precipitation. Managing for different species, including wildlife not studied in this project, requires balancing the needs of different species and acknowledging that grazing to benefit one species may negatively affect another species (Vavra 2005). It may be harder to consistently manage for songbird responses in the lowland habitat, as songbird responses to grazing were less consistent among years in this habitat. It appears that plant community composition is important for some of the study species, but this may be hard to manage for directly.

Ecosystem management using livestock

In some cases, multiple songbird species can benefit from a single management regime as they show similar responses to stocking rate (e.g. Baird's sparrow and Sprague's pipit). However, to manage for the songbird community, or even just the two threatened songbird species present in the park (Sprague's pipit and chestnut-collared longspur), will require multiple stocking rates. A range of stocking rates in several pastures from no grazing to heavy grazing (e.g. approx. 0.85 AUM/ ha) can provide habitat for a complete grassland bird community. Since much of the land surrounding the park is managed for livestock production, the park should use stocking rates to complement the surrounding area, thereby contributing to a heterogeneous landscape (Fuhlendorf et al. 2012). For example, since the adjacent Mankota Community Pasture is managed with moderate stocking rates (0.34-0.56 AUM/ ha), the park could therefore have ungrazed areas, lightly grazed areas, and heavily grazed areas to create a range of habitats on the landscape. By creating a mosaic of habitats management will also benefit grassland

species such as long-billed curlew which require a mix of structural habitats for different life stages (Derner et al. 2009). Many ranchers are concerned about over-grazing and are careful to avoid high stocking rates. It may therefore be especially important for the park to have areas of heavy grazing that might otherwise be absent from the landscape. These areas of heavy grazing will provide habitat for a suite of species such as chestnut-collared longspur and horned lark, as well as McCown's longspur, and long-billed curlew (Derner et al. 2009). Additionally, the park is federal land, and so must manage for listed species such as chestnut-collared longspur. Other land owners are not legally required to manage for listed species, creating an additional impediment to conserving species that need light or heavy stocking rates.

Upland grazing

From this study, it appears that actions taken to manage for Sprague's pipit will benefit Baird's sparrow as well. Both species have similar habitat requirements (Davis et al. 1999) and exhibited similar responses to stocking rate and year. Habitat for these species can be managed for with ungrazed or very lightly grazed pastures. Grasshopper sparrow and Savannah sparrow can be best managed for with ungrazed pastures or pastures grazed below 0.3 AUM/ ha. Vesper sparrows are best managed with stocking rates above 0.5 AUM/ha. Chestnut-collared longspurs and horned larks should be managed for with the highest grazing intensities (e.g. 0.8 AUM/ha). Stocking rates need to be at least above 0.3 AUM/ha to be useful in managing these two species. It is important to keep in mind the possible effects of cattle grazing on nesting success, even for species which showed no response of abundance to grazing (Fondell and Ball 2004, Pipher 2011).

Clay-colored sparrow presence in an area is driven by shrub cover, so to preserve these populations, shrubby areas should be maintained for this species, especially snowberry (Knapton

1994). Similarly, Brewer's sparrow requires sagebrush shrub cover (Rotenberry et al. 1999) and should be managed for in naturally occurring shrubby areas.

Lowland grazing

Heavy grazing can be used in lowlands to create small increases in songbird diversity and richness, although it may also lead to a decrease in songbird abundance. However, because these effects were only seen in one year, it appears that livestock grazing is unlikely to consistently alter these diversity measures.

Sprague's pipit and Baird's sparrow populations may respond positively in lowlands by leaving some pastures ungrazed, or grazed lightly (up to 0.3 AUM/ha), as they showed negative effects of grazing in this habitat. Brewer's sparrow may respond positively to light grazing as they showed a response to grazing their abundances peaked at 0.2 AUM/ha. Savannah sparrow abundance may be maximized at low stocking rates (0.2-0.4 AUM/ ha). Grasshopper sparrows were present at low abundances in lowland habitat and efforts to increase their numbers should be focused in upland habitat. Western meadowlark populations, as in upland habitats, did not respond to differences in grazing management.

Similar to upland, chestnut-collared longspur and horned lark abundances can be best managed with high stocking rates above 0.3-0.4 AUM/ha in lowland. For maximum abundances, I recommend stocking rates of about 0.8 AUM/ha during wet years. For species with variable responses to grazing in non-consecutive years such as Brewer's sparrow, clay-colored sparrow, and vesper sparrow, managing for them consistently with grazing may be difficult.

Management in lowlands and uplands

I recommend using the same stocking rate in one pasture that includes upland and lowland habitat, but being aware of the different effects stocking rate may have on species of

interest in the two habitats. Fencing off lowland habitat could create problems associated with additional fencing (e.g. avian predators, fence collisions of wildlife, brown-headed cowbirds). I believe maintaining the current set up of the BAGMA pastures would be ideal. Water troughs should be maintained in the upland to reduce negative effects of disproportionate cattle use of lowlands (e.g. soil compaction, water quality concerns) (Kauffman and Krueger 1984). Maintaining the proportion of lowland to upland may also prevent concentration of cattle in a smaller area, reducing negative impacts. My results apply to grassland songbirds; however there are numerous documented negative environmental effects of long-term livestock grazing in riparian areas (Belsky et al 1999, Kauffman and Krueger 1984). It will therefore be important to keep monitoring effects of long-term grazing in riparian areas, especially in dry years.

Some species had much lower abundances in the lowland (e.g. chestnut-collared longspur, grasshopper sparrow), and for these species management actions should focus on upland habitat. Lowland areas should be managed for songbirds such as clay-colored sparrow and horned lark which had higher abundances in this habitat. Additionally, species such as greater sage-grouse and waterfowl are found in lowlands and management actions could focus on these species in the lowland habitat. Other studies have found that grazing in riparian zones led to a shift in avian species composition, with increased upland species and decreased specialist wetland species (e.g. Wilson's phalarope, duck species) (Dobkin et al. 2008). It is therefore important to keep in mind effects of grazing on other wildlife in the lowlands (Vavra 2005).

Management priorities should be based on intrinsic habitat qualities. In the upland habitat, shrub cover is of little management concern, as only Baird's sparrow responded negatively to the amount of shrub cover at a plot (0-10 % shrub cover). However, in the lowland plots, which overall had more shrubby areas, four species responded negatively to increased

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shrub cover. These lowland plots with high shrub cover are not suitable for some grassland birds because of high patchiness and shrub cover and should instead be managed for other species (e.g. clay colored sparrow, greater sage-grouse, and waterfowl species). This also suggests that there may be a threshold where shrub cover begins to affect grassland birds. Management actions should be focused on upland habitat for grassland dependent species as the habitat has less bare ground and shrub cover. Additionally, intrinsic features of particular lowlands should be considered when deciding which pastures to manage with high or low stocking rates. A pasture with extensive shrubby lowland areas in semi-arid mixed-grass prairies could be managed with higher stocking rates for clay-colored sparrows in the lowland, while at the same time benefiting chestnut-collared longspurs in the upland habitat. Similarly, a pasture with higher grass cover in the lowland could be managed for species that prefer more grass or less bare ground cover.

Climate and grazing impacts

When multiple years of high spring precipitation occur, the park should consider increasing stocking rates across all pastures to account for the extra biomass produced as there is additional forage for the cattle. Management decisions such as this need to be adaptive (e.g. ability to reduce stocking rates in the case of drought). Appropriate stocking rates may not be able to be determined until April/ May when spring rains occur. Having a range of stocking rates, means that as precipitation varies there will still be habitat for multiple species, although optimal habitat for a species may shift in location from year to year. It appeared that grazing had very little cumulative impacts on songbird abundances. Therefore it seems that bird community recovery from short periods of up to 4 years of grazing will occur quickly in wet years. This corresponds with another study that found that grassland bird abundances recovered just one year after a drought (George et al. 1992). This quick recovery time for bird abundances allow for flexible, adaptive management from year to year, meaning that management strategies can vary

in any particular pasture from year to year. My results are only applicable to periods of above-average moisture, and the park may require additional information to properly manage grazing in dry years. Management decisions should be based on multiple year datasets where possible, as a single year data set may provide misleading information. Several species did not respond to grazing in all years, so a limited data set might incorrectly conclude there was no sensitivity to stocking rate for these species.

Managing plant communities for songbirds

It would be difficult to manage for individual plant species in order to influence avian habitat use. However, the results of this study may provide useful information for prairie restoration and conservation. Plant community composition could help provide information when prioritizing lands for conservation or determining which areas to manage for which songbird species. The information on plant-songbird associations could help determine an appropriate mix of grass species for restoration. It is important to note that the two songbird species most sensitive to plant species composition were Sprague's pipit and chestnut-collared longspur, which are both listed as threatened in Canada. In areas where prairie restoration occurs the preferences of these songbird species should be taken into account in seeding mixes, especially because Sprague's pipit and chestnut-collared longspurs tend to avoid non-native grasslands, so native restored grasslands are all the more important (Davis and Duncan 1999).

Conclusion

Managing for multiple species can be complex, as different species show different responses to grazing, year, habitat, and vegetation composition. To manage for a complete songbird community in the park, different areas should be managed with different grazing intensities resulting in a range of habitat structures. Ideally, a range of habitats ranging from shrubby areas to sparsely vegetated bare hillsides to areas of tall grass cover would be present, to

provide habitat for a diverse suite of grassland birds. Some of these areas occur naturally, but can also be managed for by using grazing as a management tool. Lowland habitats contribute significantly to landscape heterogeneity, and have a key role to play in supporting grassland bird populations.

Grasslands National Park should use its unique position in the area as a conservation area to complement surrounding land uses to provide a complete range of habitats on the landscape. Much of the land surrounding the park is used for grazing, either in the provincial Mankota Community Pasture or by private landowners. The park can use stocking rates that are higher or lower, or rest pastures as needed, so that at a large landscape scale a range of stocking rates are used. This will provide habitat for a range of grassland species. Informing area residents of these reasons for using heavier and lighter stocking rates may help allay local concerns about park management of grazing.

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APPENDIX A

Effect of stocking rate and year on grassland songbirds in upland habitat in Grasslands National

Park, Saskatchewan, Canada, from 2008-2012. Year used as a categorical value. All models

compared to pre-grazing values. Models shown without AUM*AUM and AUM*AUM*year

terms had these terms removed from final model because they were not significant.

Upland models

Baird's sparrow

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		7.834	<.0001	7.0694	8.5986
AUM		0.2436	0.7174	-0.8661	1.3533
Year	**2009**	-2.3834	<.0001	-3.2076	-1.5593
Year	**2010**	-0.5801	0.2455	-1.4107	0.2505
Year	**2011**	-1.0169	0.0458	-1.8456	-0.1882
Year	**2012**	-2.0057	0.0003	-2.833	-1.1784
AUM*Year	**2009**	-2.5842	0.0024	-3.9746	-1.1938
AUM*Year	**2010**	-3.4895	<.0001	-4.8221	-2.1569
AUM*Year	**2011**	-0.6196	0.4504	-1.9725	0.7332
AUM*Year	**2012**	-0.8821	0.2817	-2.2318	0.4676
AUM*AUM		-7.4368	0.019	-12.64	-2.2338
AUM*AUM*Year	**2009**	2.2209	0.5847	-4.4762	8.918
AUM*AUM*Year	**2010**	8.3215	0.0285	2.0842	14.5587
AUM*AUM*Year	**2011**	5.1876	0.1847	-1.2499	11.6252
AUM*AUM*Year	**2012**	11.4738	0.0033	5.0757	17.872

Brewer's sparrow

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		-2.2924	0.003	-3.3055	-1.2792
AUM		0.4484	0.6594	-1.2283	2.125
Year	**2009**	0.5741	0.3314	-0.4118	1.56
Year	**2010**	0.9601	0.0798	0.06133	1.859
Year	**2011**	1.2048	0.0252	0.336	2.0735
Year	**2012**	1.9567	0.0002	1.1767	2.7367
AUM*Year	**2009**	0.3072	0.7772	-1.4826	2.0971
AUM*Year	**2010**	0.6555	0.4902	-0.9101	2.2212
AUM*Year	**2011**	-0.3894	0.6922	-2.0111	1.2322
AUM*Year	**2012**	-0.8278	0.3547	-2.3014	0.6457

Chestnut-collared longspur

Variable	**Year**	β	P-value	90% LCL	90% UCL
Intercept		2.7676	0.0107	1.2129	4.3223
AUM		-0.1525	0.9119	-2.4252	2.1201
Year	**2009**	-0.9708	0.0945	-1.925	-0.0166
Year	**2010**	1.2907	0.0294	0.3317	2.2497
Year	**2011**	1.1943	0.0425	0.2369	2.1516
Year	**2012**	-0.393	0.4911	-1.3486	0.5626
AUM*Year	**2009**	6.3854	<.0001	4.7191	8.0516
AUM*Year	**2010**	4.9972	<.0001	3.459	6.5353
AUM*Year	**2011**	4.2979	<.0001	2.7267	5.869
AUM*Year	**2012**	4.6718	<.0001	3.1079	6.2357
AUM*AUM		1.2839	0.841	-9.2651	11.8329
AUM*AUM*Year	**2009**	21.0724	<.0001	13.285	28.8598
AUM*AUM*Year	**2010**	13.3781	0.0024	6.1771	20.5792
AUM*AUM*Year	**2011**	1.2817	0.7765	-6.1604	8.7238
AUM*AUM*Year	**2012**	6.6804	0.1368	-0.7073	14.0681

Clay-colored sparrow

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		-1.0266	0.0537	-1.8713	-0.1818
AUM		-1.0135	0.2749	-2.5424	0.5154
Year	**2009**	0.3568	0.3158	-0.2362	0.9498
Year	**2010**	0.6677	0.0452	0.125	1.2104
Year	**2011**	0.4311	0.2045	-0.1327	0.9949
Year	**2012**	0.5739	0.0887	0.02023	1.1275
AUM*Year	**2010**	0.407	0.528	-2.0109	0.8972
AUM*Year	**2011**	1.0717	0.5644	-0.757	1.5711
AUM*Year	**2012**	0.06878	0.131	-0.09591	2.2393

Grasshopper sparrow

Variable	**Year**	β	P-value	90% LCL	90% UCL
Intercept		0.9621	0.0092	0.4378	1.4863
AUM		0.124	0.7869	-0.632	0.8799
Year	**2009**	0.04099	0.9177	-0.626	0.7079
Year	**2010**	1.5243	0.0005	0.852	2.1966
Year	**2011**	1.7206	0.0001	1.0499	2.3912
Year	**2012**	3.1057	<.0001	2.4362	3.7752
AUM*Year	**2009**	-1.4969	0.0281	-2.6163	-0.3775
AUM*Year	**2010**	-1.7591	0.0075	-2.8374	-0.6809
AUM*Year	**2011**	-1.6354	0.0142	-2.7289	-0.542
AUM*Year	**2012**	-1.8815	0.0048	-2.9728	-0.7902
AUM*AUM		-0.6757	0.7555	-4.2529	2.9015
AUM*AUM*Year	**2009**	-0.3502	0.9151	-5.7652	5.0648
AUM*AUM*Year	**2010**	-6.7164	0.0289	-11.765	-1.6683
AUM*AUM*Year	**2011**	-2.7914	0.3771	-7.9988	2.4159
AUM*AUM*Year	**2012**	-0.075	0.9809	-5.2502	5.1001

Horned lark

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		-0.4744	0.1992	-1.1047	0.1559
AUM		0.6328	0.3113	-0.3965	1.6621
Year	2009	-0.143	0.6348	-0.6479	0.362
Year	2010	0.08527	0.766	-0.396	0.5665
Year	2011	0.00392	0.989	-0.4762	0.4841
Year	2012	-0.903	0.0273	-1.5642	-0.2419
AUM*Year	2009	0.5486	0.2883	-0.3023	1.3995
AUM*Year	2010	0.2677	0.5727	-0.5144	1.0497
AUM*Year	2011	0.7004	0.1391	-0.0788	1.4796
AUM*Year	2012	1.3505	0.0303	0.3269	2.3741

Savannah sparrow

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		1.8827	0.0002	1.3451	2.4204
AUM		1.0574	0.0253	0.2811	1.8338
Year	2009	0.1457	0.7254	-0.5507	0.8422
Year	2010	1.8619	<.0001	1.1596	2.5642
Year	2011	3.0298	<.0001	2.3292	3.7303
Year	2012	2.0892	<.0001	1.3898	2.7886
AUM*Year	2009	-1.9814	0.0055	-3.1504	-0.8124
AUM*Year	2010	-2.7899	<.0001	-3.9166	-1.6631
AUM*Year	2011	-2.8552	<.0001	-3.998	-1.7125
AUM*Year	2012	-3.0682	<.0001	-4.2089	-1.9276
AUM*AUM		1.1486	0.6056	-2.5176	4.8148
AUM*AUM*Year	2009	-3.3099	0.335	-8.9648	2.3451
AUM*AUM*Year	2010	-8.1725	0.0111	-13.447	-2.8984
AUM*AUM*Year	2011	-11.157	0.0008	-16.596	-5.7173
AUM*AUM*Year	2012	-4.2089	0.2002	-9.6182	1.2004

Sprague's pipit

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		4.7662	<.0001	4.2573	5.2751
AUM		-0.8578	0.1062	-1.7313	0.01563
Year	**2009**	1.3946	0.0008	0.7579	2.0313
Year	**2010**	3.4075	<.0001	2.7589	4.056
Year	**2011**	1.1485	0.0046	0.5109	1.7862
Year	**2012**	0.1083	0.7754	-0.5293	0.746
AUM*Year	**2009**	-1.821	0.0172	-3.075	-0.567
AUM*Year	**2010**	-1.6701	0.0239	-2.8838	-0.4563
AUM*Year	**2011**	-1.0446	0.1642	-2.2806	0.1914
AUM*Year	**2012**	0.5132	0.493	-0.7204	1.7468

Vesper sparrow

Variable	**Year**	β	P-value	90% LCL	90% UCL
Intercept		-3.2985	0.0126	-5.2156	-1.3813
AUM		-0.7795	0.2103	-1.8039	0.245
Year	**2009**	0.7357	0.5692	-1.4312	2.9026
Year	**2010**	3.5596	0.0015	1.8268	5.2923
Year	**2011**	3.0086	0.007	1.2397	4.7775
Year	**2012**	2.7502	0.0126	0.9879	4.5124
AUM*Year	**2009**	-0.0253	0.9811	-1.7835	1.733
AUM*Year	**2010**	1.8179	0.0134	0.6122	3.0237
AUM*Year	**2011**	1.2064	0.1168	-0.0591	2.472
AUM*Year	**2012**	0.2769	0.7178	-0.9859	1.5396
AUM*AUM		11.9161	0.0589	1.5474	22.2848
AUM*AUM*Year	**2009**	-3.6531	0.6685	-17.714	10.4074
AUM*AUM*Year	**2010**	-13.299	0.0397	-23.918	-2.6788
AUM*AUM*Year	**2011**	-12.082	0.0689	-23	-1.1636
AUM*AUM*Year	**2012**	-9.745	0.1401	-20.613	1.1229

Western meadowlark

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		-0.9647	0.0061	-1.4498	-0.4796
AUM		0.6446	0.1612	-0.1127	1.402
Year	**2009**	0.1774	0.673	-0.5281	0.8829
Year	**2010**	1.3845	0.0002	0.8277	1.9413
Year	**2011**	1.0299	0.0055	0.4437	1.6161
Year	**2012**	-0.5427	0.3091	-1.4322	0.3467
AUM*Year	**2009**	-0.2486	0.7554	-1.5642	1.067
AUM*Year	**2010**	-0.7248	0.2332	-1.7261	0.2764
AUM*Year	**2011**	-0.9583	0.1565	-2.0713	0.1548
AUM*Year	**2012**	-0.4132	0.681	-2.07	1.2436

Lowland models

Effect of stocking rate and year on grassland songbirds in upland habitat in Grasslands National

Park, Saskatchewan, Canada, from 2008-2012. Year used as a categorical value. All models

compared to pre-grazing values. Models shown without AUM*AUM and AUM*AUM*year

terms had these terms removed from final model because they were not significant.

Baird's sparrow

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		4.9679	<.0001	4.107	5.8287
AUM		-0.6063	0.4932	-2.0655	0.853
Year	2009	-0.6137	0.2602	-1.5205	0.2932
Year	2010	1.6861	0.0037	0.7729	2.5993
Year	2011	-0.5072	0.351	-1.415	0.4006
Year	2012	-0.7376	0.1776	-1.6439	0.1686
AUM*Year	2009	-1.7939	0.0992	-3.5837	-0.0041
AUM*Year	2010	-4.0606	0.0001	-5.7706	-2.3506
AUM*Year	2011	-0.9715	0.3588	-2.7169	0.774
AUM*Year	2012	-1.508	0.1481	-3.2242	0.2082

Brewer's sparrow

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		-1.3851	0.5588	-5.6073	2.8371
AUM		-0.2939	0.8462	-2.7938	2.2061
Year	2009	-0.103	0.9481	-2.7586	2.5527
Year	2010	0.8844	0.6017	-1.9571	3.7259
Year	2011	0.8157	0.5484	-1.4622	3.0935
Year	2012	0.356	0.8366	-2.5442	3.2563
AUM*Year	2009	-5.4803	0.0821	-10.662	-0.2981
AUM*Year	2010	0.04723	0.9717	-2.1532	2.2476
AUM*Year	2011	0.6308	0.7024	-2.0938	3.3555
AUM*Year	2012	-0.8448	0.5266	-3.0462	1.3565
AUM*AUM		1.7879	<.0001	.	.
AUM*AUM*Year	2009	-15.076	<.0001	.	.
AUM*AUM*Year	2010	-7.2578	0.22	-17.007	2.4909
AUM*AUM*Year	2011	-8.299	0.0935	-16.436	-0.1618
AUM*AUM*Year	2012	0.4578	0.9344	-8.725	9.6407

Chestnut-collared longspur

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		-1.1345	0.0185	-1.8499	-0.419
AUM		-0.4489	0.5625	-1.7276	0.8298
Year	2009	0.6501	0.0852	0.03006	1.2702
Year	2010	0.9291	0.0104	0.3511	1.507
Year	2011	-0.3191	0.506	-1.1226	0.4845
Year	2012	-1.7671	0.0289	-3.0754	-0.4588
AUM*Year	2009	-0.2986	0.7374	-1.7682	1.1711
AUM*Year	2010	0.5866	0.4286	-0.6356	1.8088
AUM*Year	2011	2.0475	0.0233	0.5673	3.5278
AUM*Year	2012	4.0572	0.0009	2.0734	6.0411

Clay-colored sparrow

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		0.5951	0.0399	0.1435	1.0466
AUM		0.05375	0.8776	-0.5221	0.6296
Year	2009	0.2142	0.3984	-0.2097	0.638
Year	2010	0.7502	0.0024	0.3641	1.1363
Year	2011	0.8627	0.0003	0.5019	1.2236
Year	2012	1.1275	<.0001	0.7584	1.4966
AUM*Year	2009	0.1331	0.7492	-0.5542	0.8204
AUM*Year	2010	1.306	0.0051	0.5441	2.0679
AUM*Year	2011	0.07687	0.8239	-0.4932	0.6469
AUM*Year	2012	-0.0567	0.8684	-0.6213	0.5079
AUM*AUM		1.22	0.4889	-1.6879	4.1279
AUM*AUM*Year	2009	0.1195	0.9522	-3.1737	3.4127
AUM*AUM*Year	2010	-1.0233	0.5458	-3.8183	1.7717
AUM*AUM*Year	2011	-0.5743	0.724	-3.2578	2.1093
AUM*AUM*Year	2012	-3.2228	0.0539	-5.969	-0.4767

Horned lark

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		-0.1298	0.7677	-0.9192	0.6597
AUM		-0.3345	<.0001	.	.
Year	2009	0.1277	0.6531	-0.349	0.6044
Year	2010	0.8516	<.0001	0.554	1.1491
Year	2011	0.7148	0.0101	0.2723	1.1573
Year	2012	1.0617	<.0001	0.8015	1.3219
AUM*Year	2009	0.1963	0.7439	-0.7954	1.188
AUM*Year	2010	0.6799	0.0967	0.00661	1.3531
AUM*Year	2011	0.8257	0.1299	-0.0715	1.7229
AUM*Year	2012	1.0368	0.1023	-0.007	2.0806
AUM*AUM		1.469	0.7286	-5.5182	8.4563
AUM*AUM*Year	2009	1.5508	0.4996	-2.2389	5.3404
AUM*AUM*Year	2010	-0.6938	<.0001	.	.
AUM*AUM*Year	2011	-0.2343	0.9132	-3.7813	3.3128
AUM*AUM*Year	2012	-3.6783	<.0001	.	.

missing values occur where t-value is infinity / 0 standard error

Savannah sparrow

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		1.0016	0.001	0.6303	1.3729
AUM		0.1899	0.5903	-0.3921	0.7718
Year	2009	0.3089	0.1739	-0.0673	0.6851
Year	2010	0.3986	0.0813	0.0235	0.7736
Year	2011	0.1425	0.5448	-0.2518	0.5367
Year	2012	-0.1345	0.586	-0.5484	0.2795
AUM*Year	2009	-1.0154	0.0514	-1.8715	-0.1593
AUM*Year	2010	-1.1627	0.0063	-1.8592	-0.4663
AUM*Year	2011	-2.0269	<.0001	-2.8631	-1.1906
AUM*Year	2012	-1.6508	0.0001	-2.3431	-0.9584
AUM*AUM		-2.8339	0.0761	-5.4601	-0.2078
AUM*AUM*Year	2009	-3.1516	0.1403	-6.669	0.3658
AUM*AUM*Year	2010	-0.3293	0.8573	-3.3525	2.6938
AUM*AUM*Year	2011	-1.0046	0.6327	-4.4733	2.464
AUM*AUM*Year	2012	3.9374	0.0438	0.7303	7.1444

Sprague's pipit

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		0.1645	0.615	-0.42	0.7489
AUM		-0.6004	0.2088	-1.3872	0.1864
Year	2009	1.0164	0.0014	0.526	1.5068
Year	2010	1.2985	<.0001	0.8387	1.7582
Year	2011	1.0888	0.0006	0.6027	1.575
Year	2012	0.3534	0.2886	-0.2013	0.9081
AUM*Year	2009	-1.748	0.0055	-2.7775	-0.7184
AUM*Year	2010	-0.1577	0.7212	-0.887	0.5716
AUM*Year	2011	0.07864	0.8748	-0.7451	0.9023
AUM*Year	2012	0.6025	0.1924	-0.1588	1.3637
AUM*AUM		1.3768	0.5519	-2.4415	5.195
AUM*AUM*Year	2009	-6.1116	0.0265	-10.63	-1.5932
AUM*AUM*Year	2010	-4.5073	0.035	-8.0152	-0.9993
AUM*AUM*Year	2011	-6.8162	0.0055	-10.828	-2.8041
AUM*AUM*Year	2012	-0.3133	0.9001	-4.4333	3.8067

Vesper sparrow

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		-0.4357	0.1717	-0.9754	0.104
AUM		-0.944	0.131	-1.9727	0.08462
Year	2009	0.6153	0.0751	0.04882	1.1817
Year	2010	1.3435	<.0001	0.8704	1.8166
Year	2011	0.9061	0.0047	0.4008	1.4114
Year	2012	1.1679	0.0003	0.6817	1.6541
AUM*Year	2009	-0.5544	0.5153	-1.9603	0.8514
AUM*Year	2010	0.9322	0.1318	-0.0858	1.9502
AUM*Year	2011	1.6165	0.0114	0.5702	2.6629
AUM*Year	2012	0.4567	0.4794	-0.6083	1.5217

Western meadowlark

Variable	Year	β	P-value	90% LCL	90% UCL
Intercept		0.5885	0.0066	0.288	0.8889
AUM		-0.8673	0.0145	-1.4488	-0.2859
Year	2009	-0.6856	0.0394	-1.2262	-0.1449
Year	2010	-0.0616	0.8145	-0.5026	0.3794
Year	2011	-0.3112	0.2783	-0.7892	0.1667
Year	2012	-1.4027	0.0022	-2.1174	-0.688
AUM*Year	2009	0.9086	0.1745	-0.1932	2.0104
AUM*Year	2010	0.7691	0.1482	-0.1065	1.6447
AUM*Year	2011	0.8779	0.1325	-0.0826	1.8384
AUM*Year	2012	0.7304	0.3887	-0.6669	2.1278

Model distribution and shape for stocking rate models in upland habitat listed in Appendix A.

Species	Model used	Distribution
Baird's sparrow	non-linear	normal
Brewer's sparrow	linear	Poisson
Chestnut-collared longspur	non-linear	normal
Clay-colored sparrow	linear	Poisson
Grasshopper sparrow	non-linear	normal
Horned Lark	linear	negative binomial
Savannah sparrow	non-linear	normal
Sprague's pipit	linear	normal
Vesper sparrow	non-linear	Poisson
Western meadowlark	non-linear	negative binomial

Model distribution and shape for stocking rate models in lowland habitat listed in Appendix A.

Species	Model used	distribution
Baird's sparrow	linear	normal
Brewer's sparrow	non-linear	Poisson
Chestnut-collared longspur	linear	Poisson
Clay-colored sparrow	non-linear	negative binomial
Horned Lark	non-linear	negative binomial
Savannah sparrow	non-linear	negative binomial
Sprague's pipit	non-linear	negative binomial
Vesper sparrow	linear	negative binomial
Western meadowlark	linear	negative binomial

APPENDIX C

Precipitation data (mm) from Opheim, MT, USA (Opheim 10 N station) 2008-2013. Data from

Western Regional Climate Center (2013). N/A indicates data not available.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
2008	2.29	N/A	3.30	9.65	23.88	101.09	35.81	N/A	69.60	15.24	2.54	0.00	263.40
2009	N/A	3.81	8.13	28.70	29.46	13.72	66.55	50.80	9.65	18.29	0.00	0.51	229.62
2010	0.00	0.00	0.00	1.27	88.39	64.26	17.02	46.99	50.80	0.00	1.52	5.08	228.35
2011	18.03	8.89	8.89	11.43	109.98	134.11	11.43	17.78	18.03	15.24	5.08	2.54	361.44
2012	0.00	2.03	2.54	25.91	128.02	75.44	25.91	2.54	0.00	2.54	0.00	0.00	264.92
Average	7.62	6.35	8.64	16.00	47.50	74.17	56.64	32.51	31.50	14.73	7.11	6.10	309.12