

**Effects of past grazing management on songbirds and plants in rested
pastures: the potential for grazing management to influence habitat in
the landscape following livestock exclusion**

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ABSTRACT

Grasslands are the most threatened terrestrial ecosystem in the world, and as they decline the species that depend on them also decline. Variable stocking rates and resting rangeland could be used by range managers to manipulate plant cover and create wildlife habitat. I used generalized linear mixed-models to evaluate how effects of rest on vegetation and songbirds varied based stocking rates previously applied from 2006-2014 in Grasslands National Park, Canada. My results indicate, in the mixed-grass prairie, succession is retrogressive following rest, and both vegetation and songbirds are resilient to grazing. Recovery of songbirds was linked to the recovery of habitat structure. Songbirds with flexible habitat requirements, such as Savannah and grasshopper sparrows, responded rapidly to livestock exclusion. The retrogressive nature of succession in mixed-grass prairie offers managers an opportunity to take chances when attempting to create wildlife habitat with livestock grazing, as risk of irreversible change is relatively low.

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CHAPTER 1: INTRODUCTION

Background

The mixed-grass prairie ecosystem and the songbirds that depend on it for habitat have been experiencing serious declines since European settlement (eg. Samson et al. 2004; Brennan and Kuvlesky 2005; Askins et al. 2007). Cultivation, modifications of grazing patterns, and fire suppression have all been identified as contributors to these massive declines (Askins et al. 2007). The loss of differentiated ecotypes has also led to a loss of landscape level heterogeneity, and this may amplify the effects that declining mixed-grass prairie has on birds (Risser 1988).

Current grazing management practices promote the extensive use of moderate grazing intensity (Fuhlendorf and Engle 2001), and may contribute to loss of landscape level heterogeneity by creating an underrepresentation of heavily disturbed and undisturbed plant communities (Saab et al. 1995). The existence of vegetation communities at different successional stages is what has allowed the mixed-grass prairie to provide habitat for species that prefer ungrazed or lightly grazed prairies, such as Sprague's pipits (Saab et al. 1995), and species that prefer heavily grazed prairies, such as chestnut-collared longspurs (Davis et al. 1999).

Bison grazing and fire, which were historical disturbances in the mixed-grass prairie, created a mosaic of shifting plant communities at different successional stages (Fuhlendorf and Engle 2001). Grazing may be managed to mimic historical disturbances, and thereby increase habitat heterogeneity on the mixed-grass prairie (Fuhlendorf and Engle 2001). Applying variable stocking rates and resting rangeland are possible tools that range managers may use to mimic historical disturbances (Bock et al. 1993).

Stocking rate is defined as the number of animals on a given area for a set amount of time [Animal Unit Months per hectare (AUM/ha)] (Holechek et al. 2011). An AUM is equivalent to the amount of forage that a 1000 pound cow and her calf will consume over the course of a month (Holechek et al. 2011). A stocking rate of zero implies that domesticated grazers were excluded from a pasture and is called resting rangeland (Holechek et al. 2011). Grazing tends to shift communities to earlier successional stages, while resting rangeland leads to later successional stages (Holechek et al. 2011). Higher stocking rates produce earlier successional communities than lower grazing intensities (Ash et al. 2011). Therefore, applying variable stocking rates and excluding grazers from some areas, might increase landscape heterogeneity.

Project significance

Using variable stocking rates to mimic historical disturbance requires a thorough understanding of its effects on both vegetation and birds. At present, studies examining the effects of rest on vegetation have produced mixed results (Holechek 1991; Ash et al. 2011); although several studies agree rest can be used to improve rangeland health (Yeo 2005; Müller et al. 2007; Ash et al. 2011). Furthermore, only a few studies have explored how rest periods affect birds (eg. Dobkin et al. 1998; Garcia et al. 2008). Often studies have not isolated the effects of resting rangeland, but instead have examined the effects of grazing management strategies, such as rotational grazing and deferred grazing, that incorporate rest periods on plants (eg. Rolger 1951; Heady 1961) and birds (e.g. Rice et al. 1982; Temple et al. 1999; Ranellucci et al. 2012). In the mixed-grass prairie in particular there is a lack of research exploring the effects that rest periods have on birds and lowland plant communities.

Parks Canada established the Biodiversity And Grazing Management Area (BAGMA) in the East Block of Grasslands National Park in an area that had never been cultivated or heavily grazed by domestic livestock, which provided an excellent opportunity to explore the effects of resting rangeland (Koper et al. 2008). In 2008, Parks Canada introduced cattle grazing to an area that had been rested for two decades, and in 2012 cattle were again excluded from the experimental treatment area (see Koper et al. 2008 for further details). Analyzing a combination of pre-grazing, grazing, and post-grazing data provided a unique opportunity to explore how the effects of resting rangeland varied based on prior stocking rates applied between 2008 and 2012.

Previous studies conducted at my study site have focused on the effects of stocking rate on songbirds and vegetation, but my study was the first to evaluate effects of livestock removal and rest. Similarly, to the best of my knowledge, this is the first study conducted in the mixed-grass prairie that compares multi-year pre-grazing, grazing, and post-grazing data to evaluate the effects of stocking rates and rest periods. The large spatial scale and gradient of stocking rate treatments also made the study design unique and statistically powerful (Koper et al. 2008).

Research objectives

My project was part of a larger grazing experiment, the BAGMA project, and focused on the effects that resting rangeland had on vegetation structure, plant species cover, and songbird abundances in the mixed-grass prairie. The research objectives were:

- 1) To determine if vegetation response to rest was influenced by stocking rate applied prior to the exclusion of cattle from pastures.

- 2) To determine if songbird abundances response to rest was influenced by stocking rate applied prior to the exclusion of cattle from pastures.
- 3) To determine if changes in vegetation structure and cover produced by applying a gradient of stocking rates for four years were reversible, or if at certain stocking rates a threshold was crossed that made changes irreversible.
- 4) To determine if and how resting rangeland could be used to manage native mixed-grass prairie, and the avian species associated with it.

Hypotheses

Habitat structure— If impacts of grazing on habitat structure, which I define in this thesis as the vegetation structure and physical characteristics of a site, increased with stocking rate, I predicted the largest change in vegetation structure would be observed in pastures treated with the highest stocking rates. Based on results from previous studies, I predicted that grazing would negatively influence litter depth, litter cover, and vegetation-height density, but increase bare ground (Biondini et al. 1998; Bai et al. 2001; Derner and Hart 2007). If the changes in vegetation structure caused by the application of a gradient of stocking rates were reversible, I predicted that vegetation structure during rest years would transition from the state observed in grazing years towards the state observed in pre-grazing years.

Plant species cover —If changes in plant species cover caused by grazing were reversible, I predicted that cover would return to pre-grazing levels across all pastures following exclusion of cattle from BAGMA. However, if stocking rate applied was high enough to cross a threshold for a specific plant species (Biondini and Manske 1996; Hart 2001), I predicted a non-linear trend would emerge during rest years where cover in

pastures treated with light stocking rates would return to pre-grazing levels but cover in pastures treated with highest stocking rates would not.

Songbird abundance –Songbirds have been observed to select for particular habitat structure (Davis et al. 1999; Wheelright and Rising 2008; Sliwinski 2015), and both grazing and rest have been shown to change habitat structure (Cid et al. 1991; Milchunas et al. 1994; Cassels et al. 1995). Therefore, I predicted that songbirds would respond to livestock grazing and rest based on preference for specific habitat structure. If effects of stocking rate on habitat structure persisted in rested pastures, then I predicted stocking rate would continue to influence abundances of songbird species that displayed significant preferences for the habitat characteristic in question. For example, if effects of stocking rate on bare ground and vegetation-height density persisted in rested pastures, then I predicted effects of stocking rate on chestnut-collared longspur, which select for habitat with bare ground and short sparse vegetation (Anstey et al. 1995, Owens and Myres 1973), would also persist.

CHAPTER 2: LITERATURE REVIEW

The mixed-grass prairie

The Great Plains of North America are designated as short-grass prairie, mixed-grass prairie, and tall-grass prairie by ecologists based on vegetation height and composition (Anderson 2006). Common features of all three prairie types have historically included: presence of grazing animals in large numbers, level to gently rolling topography, frequent fires, and occurrence of periodic droughts (Risser et al. 1981; Anderson 1982; Anderson 1990). The shift between these prairie types occurs gradually, and boundaries are not sharply demarcated (Anderson 2006). The mixed-grass prairie receives between 375-625 millimeters (mm) of precipitation per year, and this creates a prairie dominated by species ranging in height from 0.8-1.2 metres (m) (Anderson 2006). Common species of the mixed-grass prairie include blue grama (*Bouteloua gracilis*), northern wheatgrass (*Elymus lanceolatus*), western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Hesperostipa comata*), June grass (*Koeleria macrantha*), moss phlox (*Phlox hoodii*), pasture sage (*Artemisia frigida*), scarlet mallow (*Sphaeralcea coccinea*), little clubmoss (*Selaginella densa*), western snowberry (*Symphoricarpos occidentalis*), wild prickly rose (*Rosa acicularis*) and silver sagebrush (*Artemisia cana*) (Coupland 1950; Lwiwski et al. 2015).

Grazing on the Great Plains of North America

Before the European settlement of North America, the primary grazer of the Great Plains was the plains bison (*Bison bison bison*). The disturbances of grazing and fire varied both temporally and spatially, thereby creating a heterogeneous landscape of shifting plant communities (Fuhlendorf and Engle 2001). In mixed-grass prairie, bison

preferentially grazed recently burned areas, amplifying the effects of burns and creating even more landscape heterogeneity (Fuhlendorf and Engle 2001). This benefited wildlife by meeting the needs of a wide range of species with different habitat requirements (Brennan & Kuvlesky, 2005). However, the widespread slaughter of bison following European settlement drove the species, which was estimated to once number as high as 60 million individuals, to the brink of extinction (Samson and Knopf 1994; Knapp et al. 1999). The loss of bison and fire suppression led to the loss of landscape heterogeneity (Fuhlendorf and Engle 2001). As bison populations were dwindling, prairie dog populations were also decimated (Marsh 1984), and this led to further homogenization of the landscape.

Cattle, which are currently the primary grazer on the North American Great Plains, may be managed to produce disturbance patterns that imitate those created by historic grazers (Bock et al. 1993). There are some noticeable differences between bison and cattle behavior, bison wallow (Hartnett et al. 1997), spend less time foraging (eg. Plumb and Dodd 1993; Hartnett et al. 1997; Knapp et al. 1999), and more selectively graze. Generally, however, cattle and bison are ecologically analogous (Hartnett et al. 1997). The preferential selection for grasses by both species has been shown to increase species diversity (eg. Plumb and Dodd 1993; Hartnett et al. 1997; Towne et al. 2005), and has led to the conclusion that grazing management strategies, rather than inherent differences between the two species, may determine their effect on the prairie landscape (Towne et al. 2005). Managing cattle to fill the ecological niche vacated by bison will require manipulation of both intensity and frequency of cattle grazing in the form of stocking density, rest periods, and grazing periods.

Mixed-grass prairie and grassland songbird conservation challenges

Grasslands are one of North America's most endangered resources (Samson et al. 2004). Estimates suggest that, since the time of European settlement, mixed-grass prairie has declined so severely that only 29% of its historic extent remains (Samson et al. 2004). In Saskatchewan, mixed-grass prairie has been reduced by an estimated 83.1%, from 13,400,000 hectares (ha) to 2,500,000 ha, but less than 0.1% of the mixed-grass prairie that still exists is protected (Samson and Knopf 1994). Furthermore, numbers describing the overall loss of prairie do not touch on the total loss of differentiated ecotypes, and therefore habitat heterogeneity (Risser 1988). The loss of large tracts of native-mixed grass prairie and habitat heterogeneity has had far reaching negative effects on both plants and animals (Samson et al. 2004). Severe population declines of grassland songbird species have been noted across the mixed-grass prairie (Askins et al. 2007), likely reflecting the impacts of declining prairie on grassland obligate songbirds. COSEWIC (2015) has listed Sprague's pipit and chestnut-collared longspur as threatened species, and both Baird's sparrow and McCown's longspur as species of special concern. In the eastern and central United States, 60% of all North American grassland songbirds species experienced significant declines (averaging 1.1% per year) from 1980 to 1990 (Murphy 2003). In Saskatchewan, McCown's longspur, Sprague's pipit, horned lark, grasshopper sparrow, and chestnut-collared longspur have experienced the largest declines while Savannah and vesper sparrow have experienced the smallest (Sauer et al. 2014). While a large portion of grassland songbird declines can be attributed to habitat loss, both fire suppression and changing grazing patterns may be contributing factors (Askins et al. 2007).

Natural history and habitat requirements of grassland songbirds

Most grassland songbirds found in the mixed-grass prairie of Saskatchewan, where BAGMA is located, are migratory (eg. Robins and Dale 1999; Jones and Cornely 2002; Wheelwright and Rising 2008), with the exception of horned larks, which have some small populations that at times remain year-round in southern Saskatchewan (Beason 1995). Migrant grassland species return to southern Saskatchewan in the spring of each year from as early as late February, e.g. migrant horned lark populations (Beason 1995), to the end of May, e.g. grasshopper sparrow (personal observation). Site fidelity, defined as the tendency of an individual to return to a previous breeding site following migration, is quite low in some grassland songbirds (Jones et al. 2007). This can result in local population densities fluctuating greatly between years (Cody 1985). Many grassland songbirds construct open-cup nests on or near the ground (Vickery et al. 1999), and therefore look for specific vegetation cues when selecting sites. However, vegetation structure and composition may vary widely between years due to differences in precipitation (Winter et al. 2005). Consequently, site fidelity might not benefit grassland songbirds, though reselection every year based on breeding habitat condition may (Jones et al. 2007).

When managing grasslands for particular habitat types it is important to take into account the habitat preferences of each species, and the ability of each species to use sub-optimal habitat. Mixed-grass prairie plant communities with limited visual obstruction, moderate litter depths, and intermediate grass height are more likely to contain Sprague's pipit and Baird's sparrow (Owens and Myres 1973; Green et al. 2002). Plant communities in the mixed-grass prairie that contain low to moderate shrub cover have higher

abundances of vesper sparrow, grasshopper sparrow, and Savannah sparrow (Wiens 1973; Dechant et al. 2000; Wheelwright and Rising 2008). Plant communities that contain shorter grass, sparser vegetation, and bare ground are more likely to contain chestnut-collared longspur (Owens and Myres 1973; Anstey et al. 1995), while plant communities with even sparser vegetation, barer ground, and minimal litter are more likely to contain horned lark and McCown's longspur (Wiens et al. 1987; Beason 1995; Kimberly 2010).

Habitat size may also be an important factor to consider when managing rangeland to create habitat for specific species. In Saskatchewan, Baird's sparrow occurrence was positively correlated with area of seeded fields (McMaster and Davis 2001). Baird's sparrow abundance and occurrence are positively correlated with native prairie patch size with 50% of maximum occurrence found to be reached in 58 ha prairie fragments in Saskatchewan (Green et al. 2002). Similarly, Grasshopper sparrows occupy larger habitat areas versus smaller fragments (Herkert 1994; Vickery et al. 1994). In Illinois, the minimum habitat area required by grasshopper sparrows was 30 ha (Herkert 1994), and in Maine, the minimum area was 100 ha (Vickery et al. 1994). These two examples illustrate that for some species it may be necessary to consider habitat area as well as the vegetation structure to effectively create appropriate habitat.

Detectability of songbirds

Standardized criteria, such as performing songbird surveys at set intervals in the day with minimal wind and no precipitation, are intended to reduce potential sources of bias in detectability (Ralph et al. 1990). However, some authors have suggested that simply standardizing data collection methods is insufficient for detecting differences in

abundances among sites as it fails to take into account differences in the probability of detection among these different sites (Anderson 2001). In addition, differences in the ability of observers and the likelihood of species to be detected are important potential sources of bias in naïve abundance estimates that could render them inappropriate indices for relative abundance (Sauer et al. 1994).

Several methods have been developed to address this concern, including distance sampling (Buckland et al. 1993), double-observer sampling (Nichols et al. 2000; Allredge et al. 2006), removal sampling (Fransworth et al. 2002), and mixture models (Royle and Nichols 2003). Each method includes assumptions that can be challenging to meet. For instance, it can be difficult to verify location of singing or displaying birds for distance sampling (Buckland et al. 1993). Population closure is difficult to achieve for removal sampling in the field (Fransworth et al. 2002), and even population closure within a breeding season is difficult to achieve for mixture models because grassland songbirds often re-nest at new sites following nest failure (Royle and Nichols 2003). The necessary information and assumptions of the dependent-double-observer method for determining detectability, which allow for the rejection of observer or species bias within the data, are achievable within a field setting. Furthermore, some studies have suggested using statistical adjustments to compensate for imperfect perception create less precise parameter estimates because they produce much larger confidence intervals than when unadjusted counts are used (Efford and Dawson 2009). Therefore, in this study no statistical adjustments were made to unadjusted point count data to compensate for imperfection perception.

Grazing management strategies

Current grazing practices usually use moderate stocking rates to maximize cattle weight gain while preventing damage to rangeland (eg. Briske et al. 2008). The excessive use of moderate stocking rates has led to homogenization of the landscape and resulted in an underrepresentation of heavily disturbed and undisturbed plant communities (Saab et al. 1995). The loss of plant communities at different successional stages may have contributed to the decline of species at risk with divergent habitat requirements, such as Sprague's pipits, which prefer ungrazed or lightly grazed prairies (Saab et al. 1995), and chestnut-collared longspurs, which prefer heavily grazed pastures (Davis et al. 1999). Greater landscape heterogeneity could be created by managing livestock grazing to mimic historical disturbances patterns (Fuhlendorf and Engle, 2001). Applying different grazing intensities and resting rangeland are possible methods for achieving landscape heterogeneity (Bock et al. 1993; Hart 2001).

Stocking Rates

Adjusting stocking rates is one way that managers can manipulate the grazing intensity in a pasture, but setting stocking rates too high for too long can negatively impact vegetation health and forage availability. Since grazing removes and damages the plant tissue necessary for photosynthesis it has the potential to affect the productive capacity of plants. Net primary productivity is greatest in a system with light grazing and is severely reduced as grazing intensity increases (Dyer et al. 1993). Other studies have also suggested that biomass is reduced under heavy grazing (Bement 1969; Milchunas and Lauenroth 1993). Studies have found that stocking rate can affect vegetation structure (eg. Milchunas et al. 1994; Gillen et al. 2000; Lwiwski et al. 2015), the amount of bare

ground (Hart et al. 1988; Lwiwski et al. 2015), and vegetation composition (Hart 2001; Biondini and Manske 1996). In contrast, Gillen et al. (2000) found that grazing did not change vegetation community composition or biomass. It is possible that stocking at a higher rate for a few years might not greatly change the composition of the plant community, but sustained grazing for many years at high intensity could potentially degrade rangeland (Manley et al. 1997). Sustained heavy grazing may impact rangeland productivity potential (Biondini et al. 1998) or reduce soil stability by increasing bare ground (Hart et al. 1988), and overgrazing could make plant communities more vulnerable to invasive species (Ellison 1960).

Grazing regime, the manipulation of a given number of livestock within 2 or more pastures using specific periods of reoccurring grazing, rest, and deferment (Heitschmidt and Taylor 1991), has been suggested as a method for manipulating livestock carrying capacity. However, many other factors apart from grazing regime may play an equal or greater role in determining livestock carrying capacity. Pasture size (Semmartin and Oosterheld 1996) and the distance cattle must travel to reach water (Hart et al. 1993) affect the stocking rate rangeland can safely sustain. In contrast, some grazing systems, such as rotational grazing, which have been suggested as means to facilitate the use of higher stocking rates (Savory 1983), may not actually achieve this goal (e.g. Hart et al. 1988; Derner and Hart 2007; Brisk et al. 2008). In fact, studies have suggested that climatic variation is more important than grazing intensity and grazing system in determining species composition and productivity (eg. Biondini and Manske 1996; Biondini et al. 1998).

The response of avian abundance and community composition to stocking rate appears to vary by species. At BAGMA chestnut-collared longspur abundances increased at stocking rates of 0.40 AUM/ha or greater (Sliwinski 2015), which is consistent with chestnut-collared longspur preference for early seral stages of grasslands and sparser vegetation (Owens and Myres 1973; Fritcher et al. 2004). However, another study found chestnut-collared longspur were not influenced by grazing intensity (Davis et al. 1999). Horned lark and McCown's longspur are 2 species that have also been associated with heavily grazed areas (eg. Creighton and Baldwin 1974; Kantrud and Kologiski 1983; Kimberly 2010). Grasshopper sparrows decrease at higher grazing intensities but not at lower grazing intensities (Walk and Warner 2000; Fritcher et al. 2004). In BAGMA, grasshopper and Savannah sparrows increased in abundance under moderate grazing but declined when cattle were stocked at rates above 0.40 AUM/ha (Sliwinski 2015). This finding is consistent with the habitat requirements for both these species (Vickery 1996; Wheelright and Rising 2008). Baird's sparrow and Sprague's pipit declined with increasing stocking rates at BAGMA (Sliwinski 2015); this result contradicts previous studies that found these two species were relatively insensitive to moderate grazing intensities (Davis et al. 1999; Koper and Schmiegelow 2006). Review of the literature reveals that songbird responses to stocking rates are variable just as songbird habitat preferences are; therefore, to create habitat for a broad range of grassland songbird species it may be necessary to apply variable stocking rates.

Resting rangeland

Another strategy available to rangeland managers to manipulate range condition is excluding grazers from pastures for periods of time. Several studies have found that

resting rangeland can improve range condition and shift plant community composition (Jones 1992; Müller et al. 2007; Ash et al. 2011). Conversely, some regional studies have suggested that resting rangeland has little effect on rangeland condition (Holechek 1991). However, several studies that examined the effects of excluding domestic grazers have often not isolated the effects of resting rangeland but instead examined grazing management strategies, such as rotational grazing and deferred grazing, that incorporate relatively short rest periods with other livestock management strategies (eg. Heady 1961; Rogler 1951). It can be difficult to determine what effects can be attributed to rest when it is used in conjunction with other grazing strategies.

The stocking rate applied prior to the exclusion of grazing may be important when determining appropriate rest lengths to shift vegetation community or structure. Cid et al. (1991) examined the impact of excluding native grazers, both bison and prairie dogs, on vegetation, and found that biomass recovered relatively quickly following exclusion of grazers while plant species diversity, equitability, and dominance remained similar to pre-exclusion levels. They suggested that prior intensity and duration of grazing, prior plant species composition, and weather conditions could play a large role in determining vegetation changes following exclusion of native grazers (Cid et al. 1991). Several other studies considering the effects of removing domesticated grazers agreed with this conclusion (eg. Holechek 1991; Fuhlendorf et al. 2001; Müller et al. 2007).

The length of rest necessary for a plant community to transition to pre-disturbance state varies based on the severity of the disturbance and soil conditions. When applying grazing management strategies on larger pastures with larger herds longer rest periods are required to effect transition to later successional plant communities (Corfield and Nelson

2008). Fertility and structure of the soil are also important in determining plant community recovery following drought or over-grazing (Ash et al. 2011). Furthermore, the length of time a grazing treatment is applied may increase the length of rest necessary to return plant communities to their original state, and if a grazing treatment is applied too long it may not be possible for plant communities to return to their pre-grazing state (Westoby et al. 1989; Jones 1992).

While several studies have examined the impact of resting rangeland on plants (eg. Jones 1992; Hickman et al. 2004; Ash et al. 2011) few studies have explored the effects of resting rangeland on birds. Greater diversity and abundance of avian communities were found in long-term grazing exclosures (>15 years) versus short term exclosures (≤ 4 years) in riparian meadows of Oregon (Dobkin et al. 1998). Also, in Saskatchewan, Sprague's pipit preferentially selected ungrazed pastures (Dale 1984, Sliwinski 2015); in contrast, Sprague's pipit occurred less frequently in idle fields (where grazing had been excluded for at least 5 years) compared to grazed fields in the mixed-grass prairie of southwestern Manitoba (Ranellucci et al. 2012). Conversely, in some regions grazing made habitat more attractive to some bird species (e.g. Frank and McNaughton 1993, Brisk et al. 2008). In southwestern Manitoba, idle sites had lower diversity of grassland obligate songbirds, which are dependent entirely on grassland habitats, and higher abundances of facultative songbirds, which use but are not entirely dependent on grassland habitats, possibly due to the increased woody vegetation cover (Ranellucci et al. 2012). In the Argentinian mountains, bird richness and density were greater in grazed areas compared to areas where livestock had been excluded for 4 years (Garcia et al. 2008). Although these studies attempted to evaluate the effects of excluding

livestock, rest period length, or different management strategies on birds, none evaluated interactions between resting rangeland and prior stocking rate.

Invasive Plant Species

Exotic species can alter ecosystems (Sudding et al. 2004), change vegetation structure and species composition (Pritekel et al. 2005), and make habitat unsuitable for some native plants or animals (Vitousek 1986). Exotic species invading an area can also reduce biodiversity (West 1993), forage quantity or quality (DiTomaso 2000), and transition a native plant community to a new irreversible state (Sudding et al. 2004). However, not all exotic species are of equal management concern; rather, the way these species fit into an ecosystem should determine if they are a threat (West 1993). Similarly, an increase in the proportion of certain native plant species, such as *Gutierrezia* spp. or *Juniperus* spp., can reduce forage quality or quantity (DiTomaso 2000), and therefore also be of management concern.

Grazing can enable problem species to invade plant communities and facilitate competitive release. Furthermore, overgrazing has been linked to habitat degradation, and degraded landscapes can become more vulnerable to exotic species invasion (Ellison 1960). Domestic livestock can facilitate the invasion and expansion of exotic species through forage selection or seed dispersal via adhesion to hair or digestion and deposition in fecal matter ((Hobbs and Huenneke 1992; Pettit 1995; DiTomaso 2000). Some invasive species, such as diffuse knapweed (*Centaurea. diffusa*) require competitive release to allow them to invade mixed-grass prairie (LeJuen et al. 2006). Once established, the presence of invasive species can facilitate invasion by other species (Pritekel et al. 2005).

Excluding livestock from pastures is one possible method to reduce exotic invasive plants and lower the potential for these plants to invade. Resting rangeland can maximize the competition in a plant community (Sheley and Petroff 1999), which reduces the space and resources available for invader species. Some studies found more exotic invasive plants in grazed sites compared to sites where grazing was excluded (Turner 1969; Pettit 1995). For instance, dandelion (*Taraxacum officinale*) was more abundant in grazed pastures versus ungrazed pastures (Turner 1969). The ability of invasive plant species to persist is partly dependent on the amount of viable seed in the seed bank (Panetta 1985). Excluding cattle from pastures for 12 months has reduced seed density of *Mentha pulegium*, a problem species in Australia that landowners are currently obligated to control, because cattle improve seed viability through trampling action, which buries seeds deeper in the ground and enforce dormancy (Panetta 1985). In montane regions, removal of grazing pressure resulted in plant communities shifting from forb or non-native grass communities to native grass and sedge communities (eg. Green and Kauffman 1995; Schulz and Leininger 1990).

The use of grazing exclusion as a strategy for controlling invasive species should be weighed carefully prior to implementation as grazing does fulfill an important role in maintaining the mixed-grass prairie ecosystem and not all studies agree that exclusion reduces invaders. For instance, excluding cattle from a riparian area surrounding a stream increased invasive plant cover in one study (Miller et al. 2010). The mixed results in the literature regarding the potential for resting rangeland as a management method to control invasive species suggests that the effectiveness of this strategy may vary regionally, or between habitats.

Furthermore, while grazing has been identified as a cause for exotic plant invasions, it has also been suggested as a strategy to manage exotic plants. Some studies have found that exotic species may be more vulnerable to grazing than native species, which are adapted to local grazers, and have suggested grazing could be used as a biological control method (eg. Hayes and Holes 2003; del Pozo et al. 2006; Kemp et al. 2010). The effectiveness of grazing as a biological control for exotic species may depend on the particular plant species that is the target for management. Some species appear to respond to grazing in one direction consistently, for example *Bromus japonicus* (Stohlgren et al. 1999) and *Bromus tectorum* (Mack 1981). Other plant species, including exotic or native problem species, have failed to show consistent directional responses to grazing (Stohlgren et al. 1999). Furthermore, systems that have been exposed to grazing over time may be more resilient and able to avoid invasion by exotic species in the aftermath of disturbance (Davies et al. 2009). Both timing of grazing and stocking rates could be used to manage rangeland for more desirable species and to help control exotic species (Kemp et al. 2010).

Responses of grassland songbird species to the presence of exotic plant species are variable. Introduced plants might change the species composition of avian communities by changing the habitat structure and food availability for birds (Cody 1985). Some grassland songbird species, such as horned lark and vesper sparrow, appear insensitive to non-native vegetation (Beason 1995; Davis and Duncan 1999). Chestnut-collared longspurs can also be found in pastures containing exotic species, although they preferentially select native grassland (Anstey et al. 1995). Sprague's pipit, in contrast, respond negatively to non-native vegetation (Wilson and Belcher 1989; Davis et al.

2013). The abundance of Baird's sparrow and Sprague's pipit may be influenced by the native grassland present at the landscape level, rather than just the immediate habitat (Davis et al. 2013).

Interestingly, some grassland songbird species appear to be sensitive to certain exotic vegetation species, and not others. Savannah sparrows are able to use a relatively broad range of habitat, but they are sensitive to the presence of leafy spurge (Davis et al. 1999). Baird's sparrows were less abundant in pastures that contain broad leaved exotic grasses, such as smooth brome (Grant et al. 2010), but were insensitive to exotic vegetation whose structure and function more closely resembled native prairie grasses (Green et al. 2002). In Oregon, Baird's sparrow nest density, clutch size, productivity, nest survival, and nestling size were not correlated with non-native vegetation cover (Kennedy et al. 2009). However, it remains unclear whether the reproductive success of Baird's sparrow is impacted by the presence of exotic plant species in the mixed-grass prairie (Green et al. 2002).

Controlling non-native vegetation expansion, or removing such vegetation altogether, may be necessary to create good habitat for Sprague's pipit or other species sensitive to non-native vegetation. Possible strategies for doing so may include resting rangeland or conversely, using a variety of grazing strategies including relatively high stocking rates. The strategy required will vary depending on both the habitat requirements of bird species under management and the exotic plant species being targeted. Additional studies are required to explore the potential of resting rangeland as a tool for managing exotic species. To date, studies have produced mixed results when evaluating effects of resting rangeland on exotic plant species.

CHAPTER 3: METHODS

Study area

The study site was located in the Biodiversity And Grazing Management Area (BAGMA) established by Parks Canada within the East Block of Grasslands National Park in southwestern Saskatchewan (lat 49°01'00"N and long 106°49'00"W) (Koper et al. 2008). BAGMA covers 26.5 km², and consists of 9, approximately 300-ha, pastures (Koper et al. 2008). Historically, the experimental area was never cultivated or heavily grazed by livestock, and the land was purchased by Parks Canada in 1987 for the purpose of establishing Grasslands National Park, after which livestock were excluded entirely from the area (Henderson 2006).

This region has a mean annual precipitation of approximately 350 mm (Henderson 2006). The temperatures can vary from extremes of -49°C in January to +41°C in August, but mean annual temperature is 3.8°C (Henderson 2006). Differences in elevation between upland and lowland areas within individual pastures vary between 15-46 m. Among pastures, the maximum elevation of upland areas is approximately 890 m and the minimum elevation of lowland areas 785 m.

BAGMA is located within the mixed-grass prairie, and is dominated by native vegetation typical of this ecoregion. Upland areas are dominated by pasture sage (*Artemisia frigida*), blue grama (*Bouteloua gracilis*), northern wheatgrass (*Elymus lanceolatus*), needle-and-thread (*Hesperostipa comata*), June grass (*Koeleria macrantha*), western wheatgrass (*Pascopyrum smithii*), moss phlox (*Phlox hoodii*), lesser spikemoss (*Selaginella densa*) and scarlet mallow (*Sphaeralcea coccinea*) (Lwiwski et al. 2015). The shrub species western snowberry (*Symphoricarpos occidentalis*) and prickly rose

(*Rosa acicularis*) and the forbs Canada goldenrod (*Solidago canadensis*) and wild licorice (*Glycyrrhiza lepidota*) are dominant vegetation typically found in lowland areas, but not in upland areas (Lwiwski et al. 2015).

Experimental Treatment

From 2008-2011, 6 pastures were grazed using stocking rates varying between 0.25 AUM/ha, which was intended to removed 20% of the biomass in the pasture, to 0.88 AUMs/ha, which was intended to remove 70% of the biomass; 3 pastures were left ungrazed as controls. The typical stocking rate for this area is approximately 0.40 AUM/ha; therefore, treatments represented low to high stocking rates. To ensure dispersion of treatments across the study area, treatments were distributed randomly within a stratified design, with higher stocking rates applied to pastures located downstream compared to upstream (Figure 1). Vegetation and avian surveys were conducted during the pre-grazing years of 2006 and 2007, the 4 years when the grazing treatment was applied from 2008-2011, and for 3 years following livestock removal from 2012-2014.

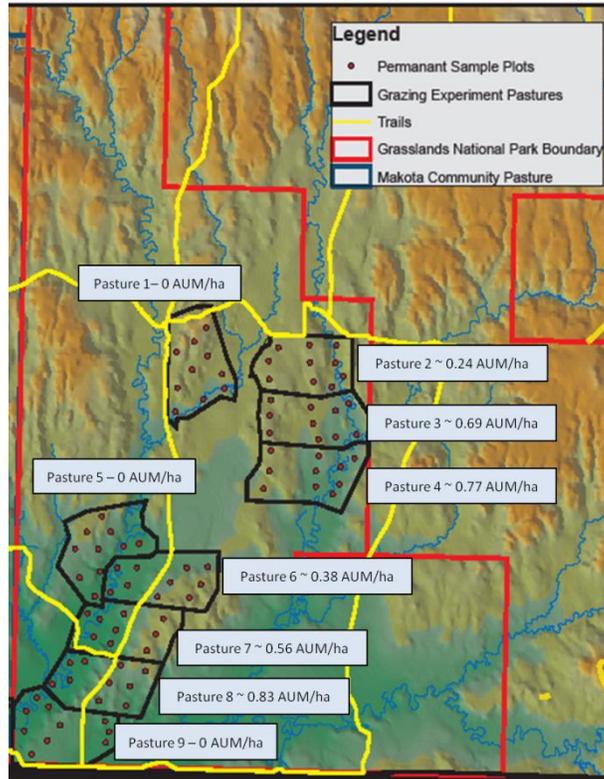


Figure 1: Experimental pastures, treatments, and outline of Biodiversity And Grazing Management Area in Grasslands National Park, Saskatchewan (Lwiwski 2013).

Vegetation surveys

In 2006, 2 years before the grazing treatment was applied, 10 permanent 50-m x 20-m modified Whittaker sampling plots were established in each pasture (see Koper et al. 2008 for further information). The vegetation plots were located 25 m south of the centre of the avian point count location, and were thus encompassed by the 3.2-ha point-count plot. Following the protocol established in 2006, colleagues and I conducted walkthrough surveys within each modified Whittaker sampling plot to determine presence or absence of every plant species (Koper et al. 2008). Walkthrough surveys consisted of an observer visually scanning 1 m on either side of themselves for plant species while systematically moving through the entire plot.

We then positioned 10 0.5-m by 1-m quadrats at predetermined intervals within the larger modified Whittaker sampling plot (Stohlgren et al. 1995), and estimated the cover of all plant species, litter, and bare ground, within each frame by assigning them to a cover class modified from Daubenmire (1959) [0 (0%), 1 (>0 to 0.1%) 2 (0.1 to 1%), 3 (1 to 3%), 4 (3 to 10%), 5 (10 to 25%), 6 (25 to 50%), 7 (50 to 75%), 8 (75 to 95%), and 9 (95 to 100%)]. Midpoint percent of the cover classes, for example 2% for cover class 3 and 6% for cover class 4, were used during statistical analysis. In the upland, I analyzed the effects of prior stocking rates and rest on frequency of bare ground occurrence, instead of cover, within frames. Litter depth was measured at the uppermost point of the litter layer at the center of the Daubenmire frames using a meter stick, using data from 2007-2013 in the uplands and 2006-2014 in the lowlands. I also measured vegetation height-density at the center of the frame using the Robel pole visual obstruction method (Robel et al. 1970). To analyze my vegetation variables at the scale of the plot, I averaged vegetation measurements among 10 quadrats in each plot.

Avian surveys

Three rounds of 6-minute, 100-m radius point count surveys were conducted in 10 locations within each pasture between the middle of May and the end of June from 2006-2014. Only the data collected during the first 5 minutes of the point count were used in the statistical analysis, to be consistent with the method followed in previous BAGMA studies (Molloy 2014; Sliwinski 2015). All point count centres were located a minimum of 250-m apart to ensure that songbirds were not recorded twice at different locations. Six of the 10 points counts were in upland habitat, and the other 4 were in lowland habitat. I conducted point counts between dawn and 0950 hours in conditions of low precipitation

and when winds speeds were below 15 km/h. To minimize the effects of observer bias, each year every point count location was surveyed by at least 2 different observers, and I summed the results across the 3 rounds before using them in my analysis to allow for analyses using Poisson or negative binomial distributions.

During our last survey year, 2014, we also completed one round of dependent-double-observer point counts at each point count location in our experiment to assess detectability (Nichols et al. 2000). To conduct the dependent-double-observer point count surveys 2 observers, labeled as the primary and the secondary observer, conducted the point count simultaneously. The secondary observer stood directly behind the primary observer, and moved as the primary observer moved so that they remained out of site and did not give cues to the primary observer. The primary observer called out and recorded the species, direction, and distance of all birds that they observed. The secondary observer recorded these observations on their own point-count sheet and added any additional birds they detected that the primary observer did not. All technicians that performed point count surveys in 2014 also participated in the dependent-double-observer point counts as both primary and secondary observers. Each technician participated in 30 to 40 dependent-double observer point counts, with three different observers.

Statistical analyses

To determine songbird perceptibility, I compared number of species and individuals detected by primary and secondary observers during the 2014 point counts using DOBSERV (Hines 2000). I considered naïve abundance estimates as an appropriate index of relative abundance when perceptibility values were greater than 0.85.

Next I selected the most appropriate distribution (for example normal, negative binomial, or Poisson) for model residuals using diagnostic graphs, including box plots, quantile-quantile graphs, and histograms, and the measure of deviance divided by degrees of freedom (Proc Genmod, Proc Univariate, SAS 9.4). I then analyzed the data using generalized linear mixed models (GLMM) with the Proc Glimmix procedure at the plot scale. Using GLMM allowed me to analyze non-normally distributed data (Quinn and Keough 2002), to include the random variables to account for the nesting of plots within pastures and repeated surveys of the same plots at different times, and to analyze both categorical and continuous variables within the same model (Quinn and Keough 2002).

To assess the cumulative effects of 4 years of grazing and 3 years of rest on vegetation species cover (including blue grama, June grass, northern wheatgrass, needle-and-thread, western porcupine grass (*Hesperostipa curtiseta*), western wheatgrass, dandelion, common yarrow (*Achillea millefolium*), goat's beard (*Tragopogon dubius*), lesser spikemoss, milkvetch (*Astragalus*), purple milkvetch (*Astragalus agrestis*), and silver sagebrush (*Artemisia cana*)) and habitat structure (including litter depth, litter cover, bare ground, and vegetation height-density), I included stocking rate, year, and an interaction term between the two as independent variables in my GLMMs. I also included plot and/or pasture as random variables, which allowed me to account for spatial and temporal correlation of dependent variable responses. I determined whether to include pasture only or both pasture and plot as random variables in my GLMM by using AIC_c (Akaike 1973, Burnham and Anderson 2002) to compare models with and without each random variable and models with both. In a few cases, models that included both random variables failed to converge, probably because of over-parameterization, suggesting that

one of the random variables was unnecessary. In these cases, I included only pasture as a random variable. I included an interaction term between stocking rate and year, which compared the slope of the response in the pre-grazing years to responses in last grazing year and rest years, to determine if effects of stocking rate were influenced by year or vice versa. I also included both a quadratic term and associated interaction term to detect non-linear responses to stocking rate. For example:

$$\text{Blue grama cover} = \text{Year} + \text{Stocking Rate} + \text{Year} * \text{Stocking Rate} + \text{Stocking Rate} * \text{Stocking Rate} + \text{Year} * \text{Stocking Rate} * \text{Stocking Rate}$$

where year was treated as a categorical variable and stocking rate as a continuous variable. However, if the quadratic term or associated interaction term was not significant, then they were removed to reduce problems of collinearity (Quinn and Keough 2002).

I compared individual plant species cover and habitat structure following 4 years of grazing (2011), 1 year of rest (2012), 2 years of rest (2013), and 3 years of rest (2014) to the baseline pre-grazing year (2006). I interpreted significant parameter estimates for the main effect of stocking rate in my models to mean that a pre-grazing trends existed based on future stocking rates prior to the introduction of livestock. I interpreted significant parameter estimates for the main effect of year to mean that effects of temporal variability or environmental conditions were present that were independent of stocking rate. I interpreted livestock introduction to pastures and stocking rate as having positive effects on response variables when the slope of the interaction term in 2011 (after 4 years of grazing) was positive, and assumed a negative effect when the slope was

negative. If I detected no effect of livestock grazing or stocking rate after 4 years of grazing, I concluded that abundance or cover was independent of grazing, and thus the impacts of rest were not analyzed. I interpreted differences between the 2006 interaction term slope compared to the slopes of 2012-2014 to mean effects of grazing remained during rest years, and no significant difference to mean a return to pre-grazing conditions. I also examined differences between the 2011 interaction term slope compared to the slopes of 2012-2014 to assess whether partial recovery to pre-grazing levels occurred. I used an alpha value of 0.1 for my study because I was more concerned with committing a Type II error versus a Type I error (Quinn and Keough 2002). Lowering the alpha values increases the uncertainty surrounding the rejection of a null hypothesis and acceptance of an alternative hypothesis, but in conservation problems failing to detect negative effects of environmental factors or human manipulations is riskier than assuming there is an effect.

To assess the effects of grazing and rest on songbird abundance, I followed the same method as for vegetation and habitat structure, except that I treated 2012 as the last year that songbirds were responding to livestock grazing and 2013 as the first year songbirds responded to rest. The effects of livestock grazing from the previous year were measured at the beginning of the growing season, when we conducted point count surveys, while later in the growing season, when we conducted vegetation surveys, the effects of livestock grazing during the current year were more influential. In addition, songbird species primarily responded to habitat conditions caused by grazing in the previous years because they have low site fidelity (Jones et al. 2007), are migratory, and select territories prior to the annual reintroduction of cattle for seasonal grazing (around

the end of May). For this reason, when I analyzed the response of songbird abundance, I treated vegetation and grazing conditions of the previous year as the independent variables. For instance, songbirds were assumed to respond to habitat conditions created by grazing in 2011 when selecting sites in May of 2012.

CHAPTER 4: RESULTS

Effects of stocking rate and rest on habitat structure

Upland

All vegetation structure variables were affected by stocking rate after four years of grazing, but responses to rest varied. Stocking rate had a negative linear effect on litter depth and litter cover in the uplands, and this effect remained during the 3 rest years (Figure 2, Appendix A). Interestingly, though stocking rate continued to affect litter depth during rest years, litter depth was greater during rest years. Stocking rate had a negative non-linear effect on vegetation height-density after 4 years of grazing, but 1 year of rest was adequate for this vegetation structure variable to return to pre-grazing levels.

Bare ground occurrence increased with higher stocking rates in uplands following 4 years of grazing. I detected an effect of rest during the second and third rest years though a positive effect of stocking rate remained apparent.

Lowland

Effects of stocking rate and rest on vegetation structure in the lowlands were more variable than in uplands. A spurious non-linear trend in litter depth existed in pastures prior to the introduction of livestock, with higher values occurring in pastures later treated with moderate stocking rates (Figure 3, Appendix A). A negative non-linear effect of stocking rate was detected after 4 years of grazing and this effect remained apparent during the first rest year. By the second rest year there were no residual effects of grazing on litter depth.

A spurious non-linear trend in vegetation height-density existed prior to the introduction of livestock, with higher values occurring in pastures later treated with moderate stocking rates. This spurious trend was reversed during the 4-year grazing period and a negative effect of stocking rate on vegetation height-density emerged. During the first rest year, pre-grazing trends

in vegetation height-density began to re-emerge but stocking rate continued to affect vegetation height-density during the 3 rest years.

Effects of stocking rate and rest on cover of plant species

Upland

A spurious trend in cover of western wheatgrass prior to the re-introduction of cattle grazing was evident, with lowest cover occurring in pastures later treated with moderate stocking rates (Figure 4, Appendix A). After 4 years of grazing this pattern seemed to be amplified and western wheatgrass cover increased significantly in control pastures and pastures later treated with highest stocking rates. Following livestock exclusion, western wheatgrass cover became relatively even among pastures, but by the third rest year the pre-grazing trend began to re-emerge.

Stocking rate had a non-linear effect on needle-and-thread cover, with highest cover occurring in pastures treated with moderate stocking rates, after 4 years of grazing. After pastures were rested 1 year, stocking rate no longer had an effect, but in 2014 the significant positive non-linear trend re-emerged. Percent cover of northern wheatgrass, blue grama, western porcupine grass, and June grass among pastures did not vary significantly from pre-grazing levels after 4 years of grazing, and no significant effect of stocking rate was detected.

A spurious trend in dandelion cover existed prior to the introduction of cattle grazing with higher cover occurring in pastures later grazed at lower stocking rates. After 4 years of grazing dandelion cover became relatively even among pastures treated at a variety of stocking rates. I detected a significant effect of rest after 2 years but even with 3 years of rest dandelion failed to return to pre-grazing levels. Interestingly, following the re-introduction of cattle grazing to BAGMA, dandelion cover increased within all test pastures, including the control pastures, and even after pastures were rested for 3 years, cover in control pastures remained significantly higher

than in pre-grazing years. In the uplands, lesser spikemoss cover was positively impacted by stocking rate after four years of grazing, and this effect remained until the third rest year.

No effect of stocking rate was detected on the percent cover of common yarrow or silver sagebrush, purple milk-vetch, the milk-vetch genus, or goat's beard.

Lowland

We did not detect an effect of stocking rate after 4 years of grazing on northern wheatgrass, western wheatgrass, June grass, or needle-and-thread. A spurious negative non-linear trend existed for blue grama cover prior to the re-introduction of cattle grazing. Following 4 years of grazing this non-linear trend was reversed, and greater blue grama cover occurred in pastures treated with moderate stocking rates. Even after only one year of rest there was no residual effect of stocking rate on blue grama cover.

A spurious negative trend in lesser spikemoss existed prior to the re-introduction of cattle grazing. Stocking rate had a non-linear effect on lesser spikemoss cover in the lowlands after 4 years of grazing, with the lowest lesser spikemoss cover occurring in pastures treated with moderate stocking rates. Stocking rate applied during grazing years continued to affect lesser spikemoss cover even after cattle had been excluded from pastures for 3 years. There was no effect of stocking rate on percent cover of dandelion, yarrow, silver sagebrush, purple milk-vetch, the milk-vetch genus, or goat's beard. The response of Western porcupine grass to grazing in the lowlands was not analyzed because of insufficient sample size.

Effects of stocking rate and rest on individual bird species

Dependent double-observer point counts

The probability of detecting songbirds was greater than 0.93 for all species. The songbird species with the lowest probability of detection was brown-headed cowbird ($p=0.9375$) and the songbird species with the highest probability of detection was bobolink ($p=1.0000$). Therefore, I used naïve counts as an index of relative abundance.

Upland

There were no pre-existing trends for Baird's sparrow or chestnut-collared longspur abundances prior to the reintroduction of livestock grazing (Figure 6, Appendix A). However, a spurious positive linear trend in Savannah sparrow abundances appeared to exist in pastures prior to the re-introduction of grazing.

After 4 years of grazing a negative effect of stocking rate was evident for Savannah sparrow. There was no residual effect of stocking rate on Savannah sparrow abundance following livestock exclusion. Stocking rate had a significant non-linear effect on Baird's sparrow abundances with highest abundances occurring in pastures used as controls or treated with the highest stocking rates. This effect declined after 1 year of rest but was again detectable after 2 years of rest.

Stocking rate had a significant positive effect on chestnut-collared longspur abundance. Effects of grazing on chestnut-collared longspur abundances persisted after 2 years of rest but this effect declined in the second year of rest.

Although effects of stocking rates persisted during rest years, chestnut-collared longspur abundances decreased by 25-85% during rest years with larger decreases in abundance occurring following 2 years of rest compared to 1 year of rest. As this decrease occurred across all treatments, it may have been driven by environmental conditions such as high precipitation.

Lowland

There were no pre-existing trends in Baird's sparrow, Savannah sparrow, or grasshopper sparrow abundances prior to the reintroduction of livestock grazing. Stocking rate had a significant negative linear effect on Baird's sparrow abundances and non-linear negative effect on Savannah sparrow abundances in lowlands (Figure 7, Appendix A). I detected a significant effect of rest on Baird's sparrow and no residual effect of grazing. In contrast, stocking rate continued to influence the distribution of Savannah sparrow abundance during the first rest year but by the

second rest year abundances returned to pre-grazing levels. Stocking rate had a significant non-linear effect on grasshopper sparrow abundances with the highest abundances occurring in pastures treated with moderate stocking rates. After one year of rest, stocking rate no longer had an effect on grasshopper sparrow abundances. Chestnut-collared longspur responses to grazing in the lowlands were not analyzed because of insufficient sample size.

Precipitation

Annual precipitation in 2013 and 2014 was approximately 120% of the long term average precipitation levels for this region (Environment Canada 2015, The Weather Network 2015). At least 2 months of above average precipitation occurred from 2011-2014 between April and June in the study region, ranging between 100-250% of the long term average precipitation levels (Environment Canada 2015, Figure 8).

Table 1. Summary of responses of individual plant species to stocking rate following 4 years of livestock grazing (2011), and following grazing exclusion (2012-2014) at Grasslands National Park, Saskatchewan, Canada (see also Appendix A). Positive response indicated by “+”, negative response indicated by “-”, non-linear response indicated by “NL”, “none” indicates no significant response, and N/A indicates not applicable. There was no effect of grazing in the uplands or lowlands after 4 years of grazing on sliver sagebrush, common yarrow, silver sagebrush, purple milkvetch, the milkvetch genus, northern wheatgrass, western porcupine grass, June grass, or goat’s beard.

Species	Upland			Lowland		
	Stocking Rate	Grazing Exclusion	Rest Required to return to pre-grazing condition	Stocking rate	Grazing Exclusion	Rest Required to return to pre-grazing condition
Blue Grama (<i>Bouteloua gracilis</i>)	None	N/A	N/A	NL	NL	1 year
Needle-and-thread (<i>Hesperostipa comata</i>)	NL	None	>3 years	None	N/A	N/A
Western Wheatgrass (<i>Pascopyrum smithii</i>)	NL	NL	3 years	None	N/A	N/A
Little-spike clubmoss (<i>Selaginella densa</i>)	+	-	3 years	NL	None	>3 years
Dandelion (<i>Taraxacum officinale</i>)	+	-	>3 years	None	N/A	N/A

Table 2. Summary of responses of individual songbird species to cattle grazing following 4 years of livestock grazing (2012), and following grazing exclusion (2013-2014) at Grasslands National Park, SK, Canada (see also Appendix A). Positive response indicated by “+”, negative response indicated by “-”, non-linear response indicated by “NL”, and “none” indicates no significant response. There was no effect of grazing in the uplands or lowlands after 4 years of grazing on brown-headed cowbird, horned lark, Sprague’s pipit, vesper sparrow, or western meadowlark.

Species	Upland			Lowland		
	Stocking Rate	Grazing Exclusion	Rest Required to return to pre-grazing condition	Stocking Rate	Grazing Exclusion	Rest Required to return to pre-grazing condition
Baird’s sparrow	NL	NL	> 2 years	-	+	1 year
Chestnut-collared longspur	+	-	>2 years	N/A	N/A	N/A
Grasshopper sparrow	None	None	N/A	NL	NL	1 year
Savannah sparrow	-	+	1 year	NL	NL	1 year

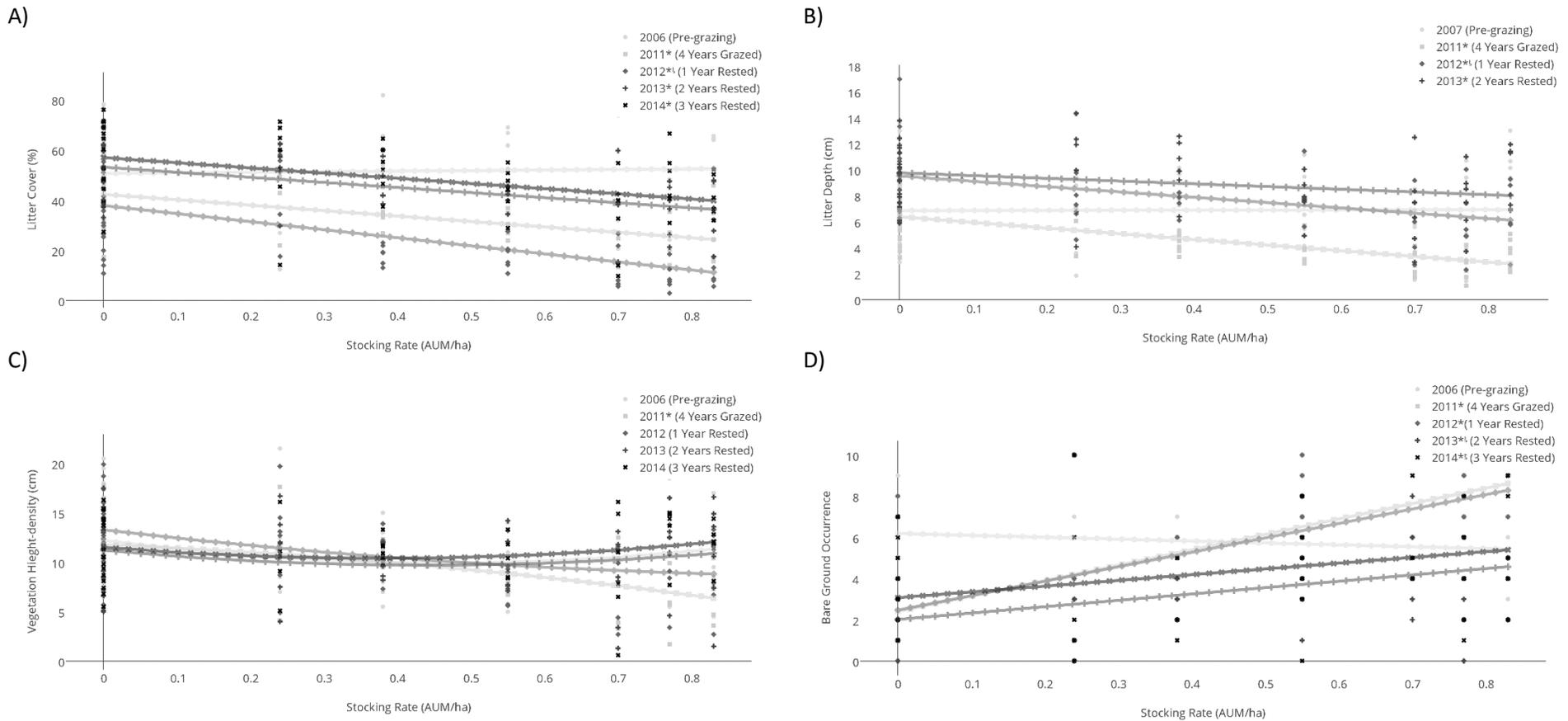
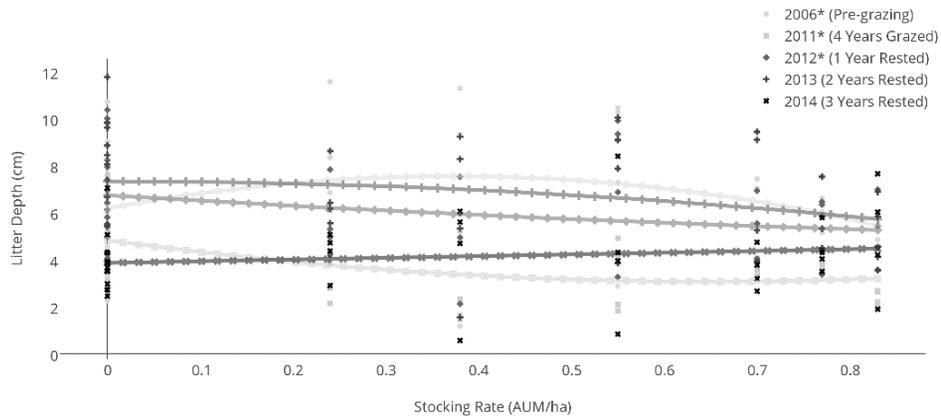
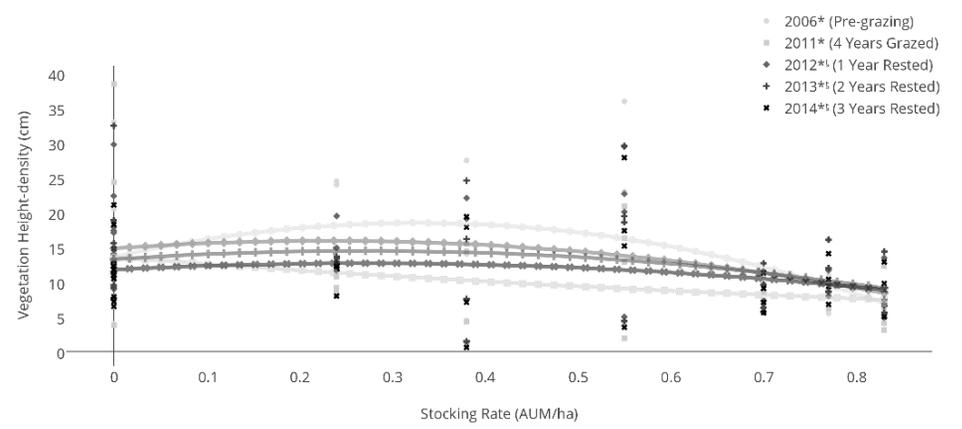


Figure 2: Effects of cattle stocking rate on vegetation variables (A) litter cover, (B) litter depth, (C) vegetation height-density, and (D) frequency of bare ground occurrence within frames in upland habitat before cattle grazing was re-introduced (2006), after 4 years of livestock grazing (2011), after 1 year of rest (2012), 2 years of rest (2013), and 3 years of rest (2014) at Grasslands National Park, Saskatchewan, Canada (see also Appendix A). * next to the pre-grazing year 2006 indicates a spurious pattern existed prior to the re-introduction of grazing. * next to years 2011-2014 indicates a significant effect of stocking rate compared to what was observed in pre-grazing year (2006). † next to years 2012-2014 indicates the effect of stocking rate in rest year was significantly different from last year of grazing (2011).

A)



B)



C)

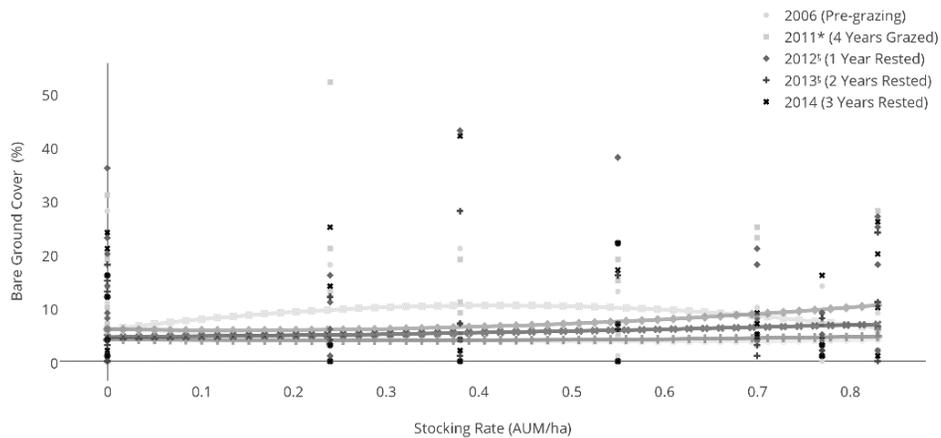


Figure 3: Effects of cattle stocking rate on vegetation variables (A) litter depth, (B) vegetation height-density, and (C) bare ground cover in lowland habitat before cattle grazing was re-introduced (2006), after 4 years of livestock grazing (2011), after 1 year of rest (2012), 2 years of rest (2013), and 3 years of rest (2014) at Grasslands National Park, Saskatchewan, Canada (see also Appendix A). * next to pre-grazing year 2006 indicates a spurious pattern existed prior to the re-introduction of grazing. * next to years 2011-2014 indicates a significant effect of stocking rate compared to what was observed in pre-grazing year (2006). † next to years 2012-2014 indicates the effect of stocking rate in rest year was significantly different from last year of grazing (2011).

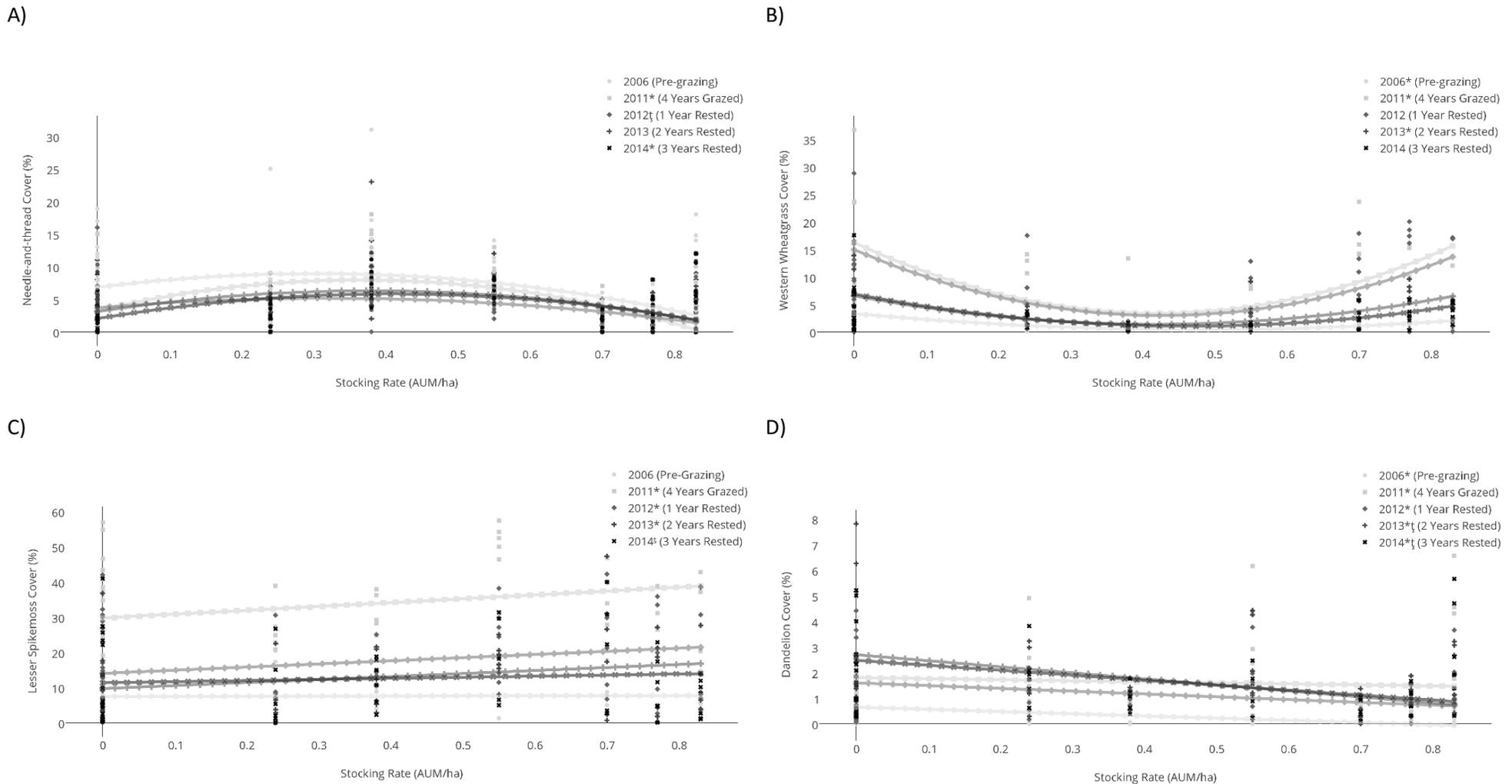
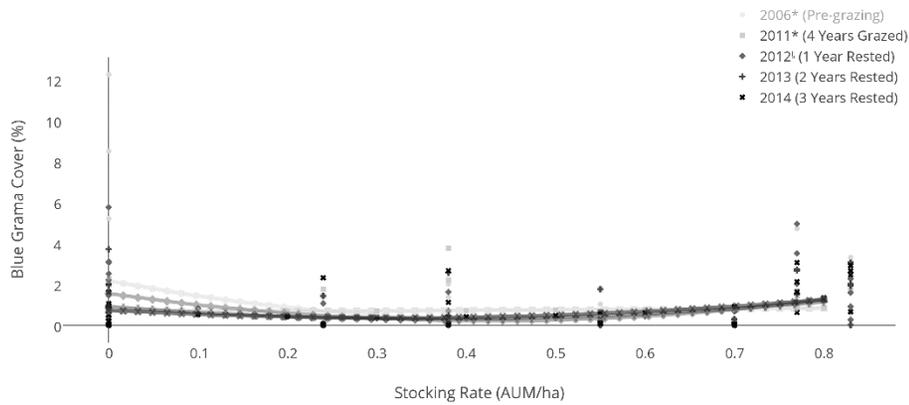


Figure 4: Effects of cattle stocking rate on (A) needle-and-thread grass, (B) western wheatgrass, (C) lesser spikemoss, and (D) dandelion in upland habitat before cattle grazing was re-introduced (2006), after 4 years of livestock grazing (2011), after 1 year of rest (2012), 2 years of rest (2013), and 3 years of rest (2014) at Grasslands National Park, Saskatchewan, Canada (see also Appendix A). * next to pre-grazing year 2006 indicates a spurious pattern existed prior to the re-introduction of grazing. * next to 2011-2014 indicates a significant effect of stocking rate compared to what was observed in pre-grazing year (2006). † next to 2012-2014 indicates effect of stocking rate in rest year was significantly different from last year of grazing (2011).

A)



B)

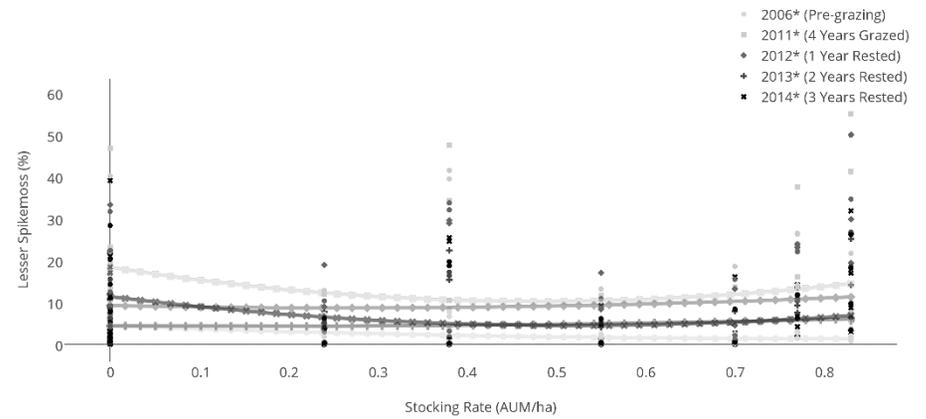
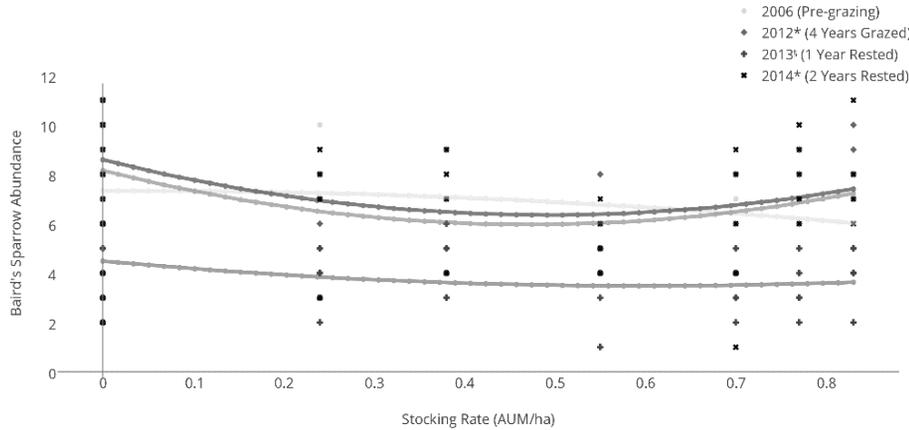
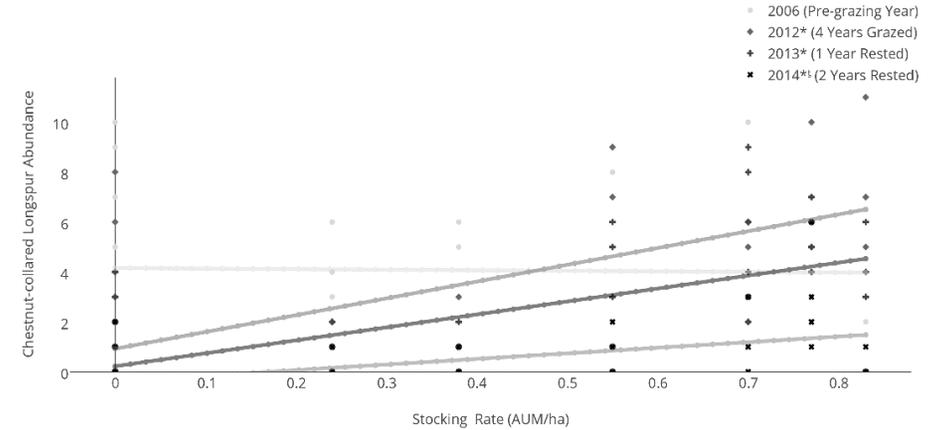


Figure 5: Effects of cattle stocking rate on (A) blue grama and (B) lesser spikemoss in lowland habitat before cattle grazing was re-introduced (2006), following 4 years of livestock grazing (2011), following 1 year of rest (2012), 2 years of rest (2013), and 3 years of rest (2014) at Grasslands National Park, Saskatchewan, Canada (see also Appendix A). * next to pre-grazing year 2006 indicates a spurious pattern based existed prior to the re-introduction of grazing. * next to years 2011-2014 indicates a significant effect of stocking rate compared to what was observed in pre-grazing year (2006). † next to the years 2012-2014 indicates effect of stocking rate in rest year was significantly different from last year of grazing (2011).

A)



B)



C)

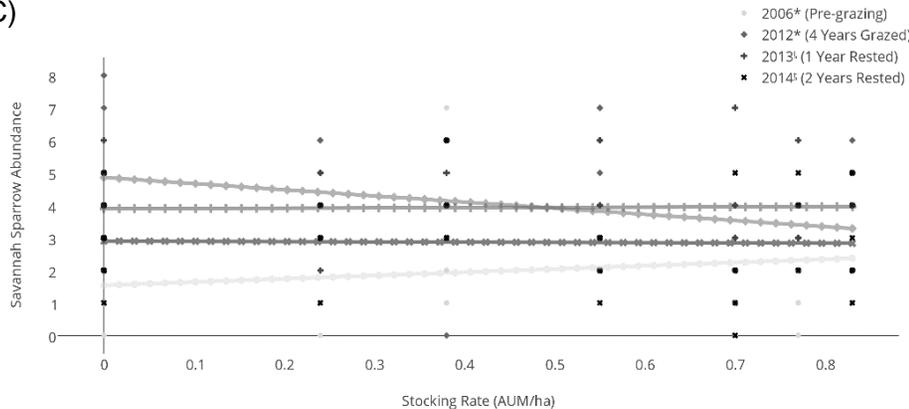


Figure 6: Effects of cattle stocking rate on (A) Baird's sparrow, (B) chestnut-collared longspur, and (C) Savannah sparrow in upland habitat before cattle grazing was re-introduced (2006), after 4 years of livestock grazing (2012), after 1 year of rest (2013), and 2 years of rest (2014) at Grasslands National Park, Saskatchewan, Canada (see also Appendix A). * next to pre-grazing year 2006 indicates a spurious pattern existed prior to the re-introduction of grazing. * next to 2012-2014 indicates a significant effect of stocking rate compared to what was observed in pre-grazing year (2006). † next to 2013-2014 indicates effect of stocking rate in rest year was significantly different from last year of grazing (2012).

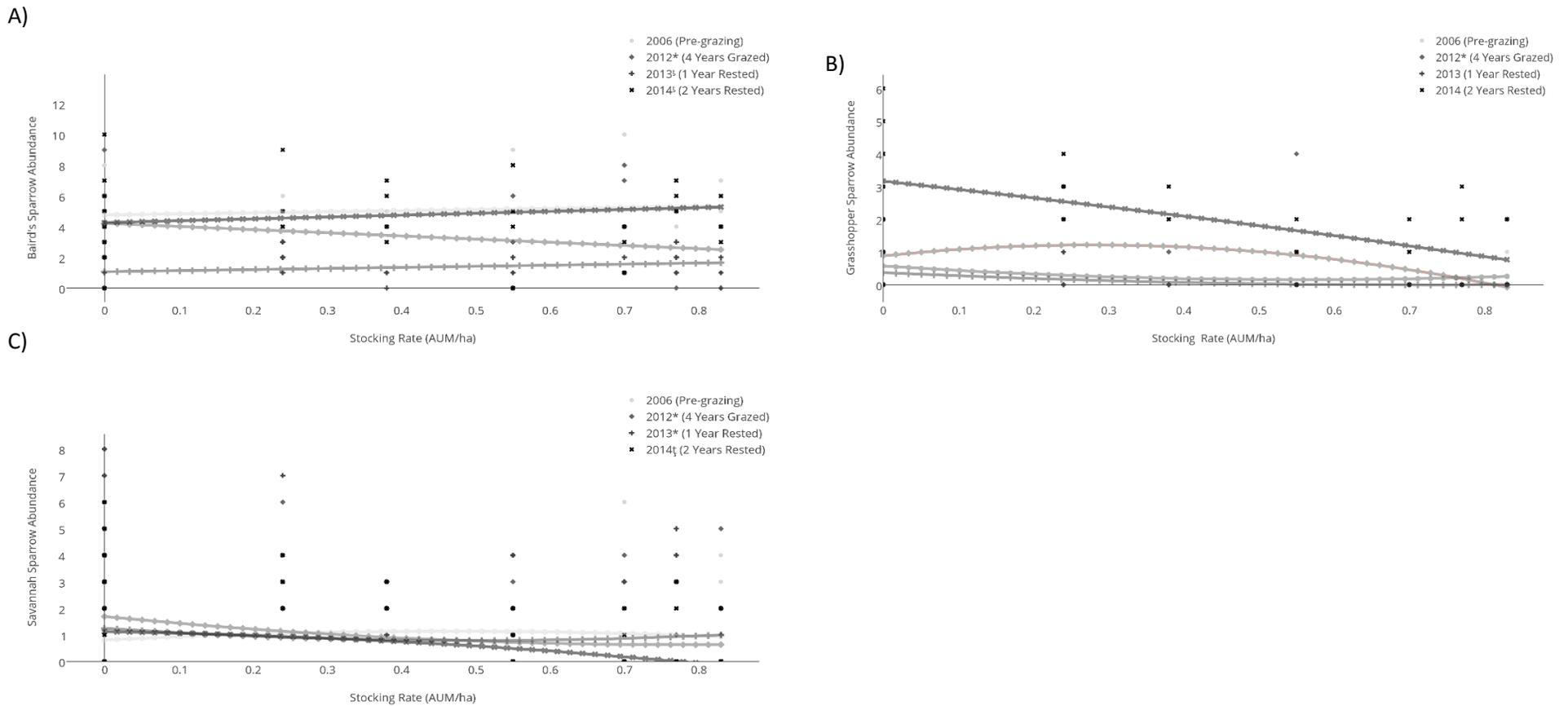


Figure 7: Effects of cattle stocking rate on (A) Baird's sparrow, (B) grasshopper sparrow, and (C) Savannah sparrow in lowland habitat before cattle grazing was introduced (2006), after 4 years of livestock grazing (2012), after 1 year of rest (2013), and 2 years of rest (2014) at Grasslands National Park, Saskatchewan, Canada (see also Appendix A). * next to pre-grazing year 2006 indicates a spurious pattern prior to the re-introduction of grazing. * next to years 2012-2014 indicates effect of stocking rate was significantly different from pre-grazing year (2006). † next to the years 2013-2014 indicates effect of stocking rate in rest year was significantly different from last year of grazing (2012).

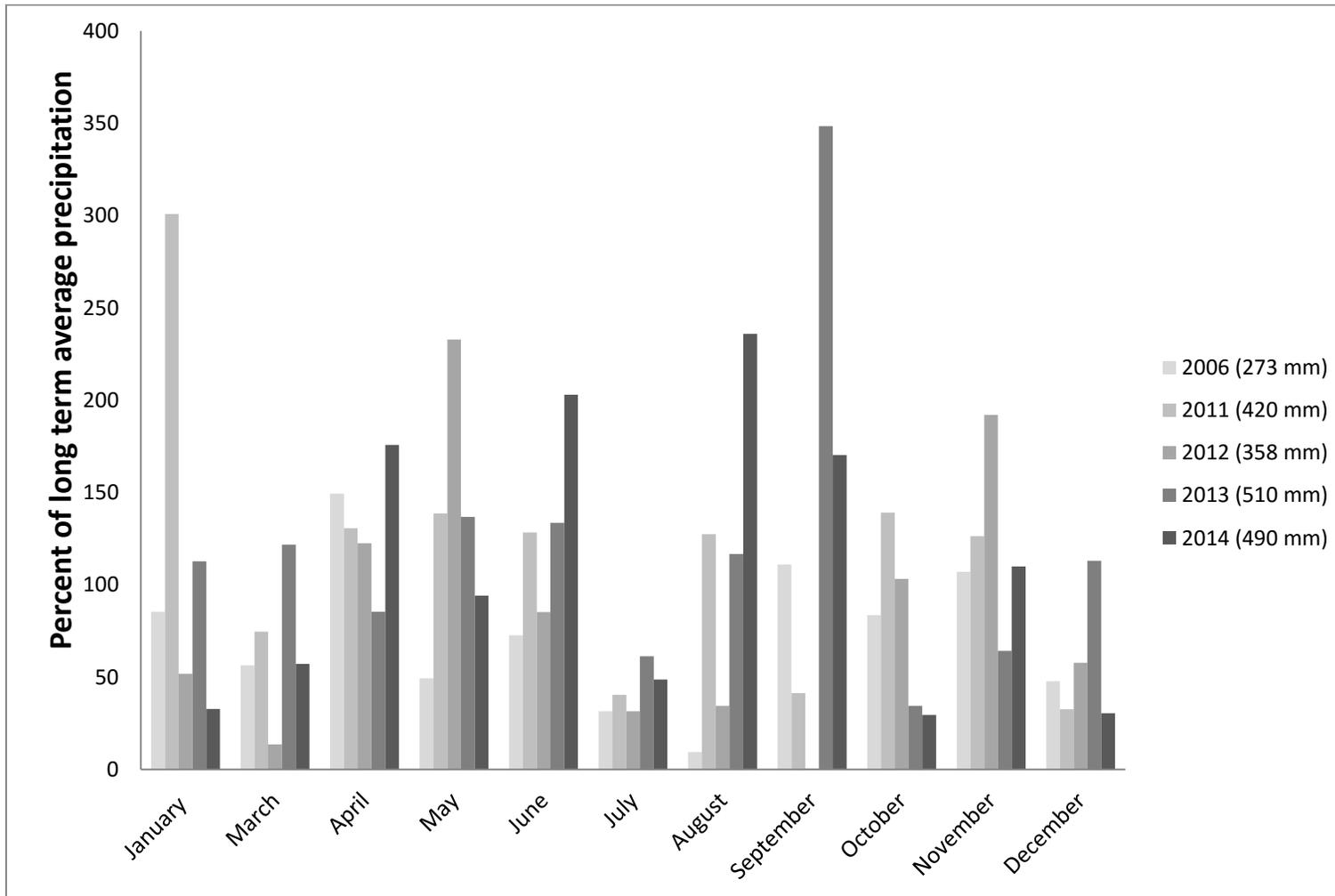


Figure 8: Percent of long-term average monthly precipitation before cattle grazing was introduced (2006), after 4 years of grazing (2011), and during rest years (2012-2014) in Rockglen, SK, Canada. Data from Environment Canada and the Weather Network (2015).

CHAPTER 5: DISCUSSION

The mixed-grass prairie is an ecosystem defined by disturbance. Its very existence hinges on the presence of grazers, fire, drought, and rain. As a result, species native to the Great Plains of North America have evolved to be resilient to these natural disturbances (Milchunas et al. 1988; Fuhlendorf et al. 2001). My results indicate that mixed-grass vegetation and songbirds are resilient to grazing and suggest that succession is retrogressive (ie. Dyksterhuis 1948) rather than following a state-and-transition model (ie. Westoby et al. 1989). The majority of songbird species, plant species, and vegetation structure variables altered by 4 years of grazing returned to pre-grazing levels following 3 years of rest. This suggests changes created by grazing at stocking rates up to 0.83 AUM/ha, which is considered a high grazing intensity in the mixed-grass prairie, remain reversible for up to 4 years, and possibly even longer. Therefore, range managers can afford to take risks in the mixed-grass prairie and apply higher stocking rates to create habitat for songbirds and other organisms.

Retrogressive succession in the mixed grass prairie is likely the result of the evolutionary history of the North American Great Plains (Milchunas et al. 1988). The mixed-grass prairie evolved with large herds of grazing animals, and this might explain the resilience of the ecosystem to grazing pressure (Fuhlendorf and Engle 2001). This resilience to grazing from native herbivores is still apparent today. For instance, studies have found changes created by the presence of bison or prairie dogs were reversed within 2 years once these species were excluded (Osborn and Allan 1949, Klatt and Hein 1978, Cid et al. 1991). The results of my study suggest that the resilience of the ecosystem extends to grazing by introduced livestock species such as cattle.

However, the goals of producing healthy rangeland for livestock production and healthy habitat for wildlife are not always the same. Some wildlife species co-exist well with cattle grazing, for example chestnut-collared longspur and cattle (Davis et al. 1999), and others do not, but it varies with grazing intensity. Later seral plant communities can sustain maximum cattle

production and long term forage productivity, which insures continued production, but a complete wildlife community requires plant communities at a wide variety of seral stages. For instance, focusing on range health to prevent soil erosion or provide adequate forage to sustain long-term cattle ranching operations will provide habitat for some wildlife while decreasing habitat for species that require early seral plant communities, such as chestnut-collared longspur or McCown's longspur. Also, the climax community, which has been viewed subjectively as the pinnacle of succession, has been challenged as an abstraction of reality (Pickett and McDonnell 1989). The concepts of climax community and rangeland health have meant that later seral plant communities have historically been viewed as the healthiest state a system can be maintained at. However, the reality is that the mixed-grass prairie is a system continually undergoing disturbance, and therefore continually in flux (Fuhlendorf and Engle 2001). Each seral stage in the mixed-grass prairie, created through the processes of disturbance and succession, is vital for supporting the many diverse organisms that have evolved to depend on them (Brennan & Kuvlesky, 2005).

Previous studies examining the effects of rest from livestock grazing conducted in the mixed-grass prairie focused on comparing differences in diversity or plant biomass production between grazed sites and long-term exclusion sites (Yeo 2005, Ranellucci et al. 2012). However, my study assessed the potential of rest to revert changes created by grazing over several years and examined whether this potential varied with stocking rate prior to rest. To the best of my knowledge, only one other study, conducted in the tropical savanna of Kenya, has examined the impacts of rest in this way (Mworia et al. 1997). The Kenyan study found that changes created by grazing intensities above 4 heifers per hectare were irreversible though changes below this threshold were reversible (Mworia et al. 1997). Four important differences between the Kenyan study and this study might explain these contrasting results: Mworia et al. (1997) applied a higher maximum stocking rate (3.2 AUM/ha versus 0.83 AUM/ha), included fewer rest years (2 versus 3), used smaller experimental pastures (2 ha versus 300 ha), and conducted the experiment

partially in drought years. This might imply that irreversible changes in the mixed-grass prairie could still occur at stocking rates greater than those applied in my study or with different climatic conditions. Alternatively, differences in the resilience of tropical savannah versus mixed-grass plant communities to grazing may be due to differences in evolutionary history. For example, grasslands in North America are thought to have expanded in the Miocene when carbon dioxide levels were low, which reduced the quality of C3 grasses that existed in that time period, resulting in the expansion of hindgut fermenters (Janis et al. 2002). In contrast, African grasslands expanded in the Plio-Pleistocene, which coincided with lower carbon dioxide levels and therefore higher quality C3 grasses but also the proliferation of C4 grasses, resulting in the evolution of a wide variety of bovid species (Janis et al. 2002).

Grazing, rest, and habitat structure

Livestock grazing and resting rangeland both change habitat structure, and are therefore effective tools to create habitat for a variety of grassland-obligate animal species. In my study, grazing reduced vegetation height-density, litter depth, and litter cover and increased bare ground. Additionally, the impacts observed were greater at higher stocking rates, consistent with results of other studies (e.g., Biondini et al. 1998, Gillen et al. 2000, Bai et al. 2001; Molloy 2014). Cattle decrease vegetation height-density and increase bare ground directly through their consumption of plant biomass during the growing season (Gillen et al. 2000, Hart 2001) and indirectly by trampling (Dunne et al. 2011). Cattle can influence litter in multiple ways including direct consumption of litter while consuming fresh forage (personal observation), reduction of the live plant matter added to the litter layer at the end of the growing season, and by altering decomposition rates via trampling and fecal deposition (Dubeux et al. 2006, Semmartin et al. 2008, Dunne et al 2011). In addition, environmental factors, such as soil moisture content, can alter the impacts of grazing by changing the biomass produced during a growing season (Chase et al. 2000); therefore, greater water availability in lowlands may explain the reduced effect of grazing on habitat structure in lowland areas (Western et al. 2002).

Resting rangeland increased litter depth, litter cover, and vegetation height-density and reduced bare ground at BAGMA. In Australia, biomass, grass basal area, and ground cover increased when strategic rest periods or low utilization rates were applied as parts of management strategies (Ash et al. 2011). In east central Idaho, bare ground cover was significantly higher in grazed sites (Yeo 2005). The required rest period length varied depending on the structure variable, and between upland and lowland habitat. Vegetation height-density responded immediately to the exclusion of livestock in both upland and lowland areas, but recovered far more rapidly in upland areas. Greater shrub presence in lowland areas (Molloy 2014) might account for the difference in recovery time of vegetation height-density. For shrubs, unlike grasses or annual forbs, size is the cumulative result of multiple growing seasons rather than the current growing season; therefore, several years may be necessary to produce vegetation height-density lost due to consumption or trampling of shrubs (Schlesinger et al. 1990, Dunne et al. 2011). In contrast, litter in both upland and lowland areas did not respond to rest until the second year but recovered more quickly in lowland versus upland areas. Similarly, bare ground recovered more quickly in lowland versus upland areas. Greater biomass production in lowland areas may be due to higher moisture availability (Chase et al. 2000, Western et al. 2002) and may explain the faster return of litter and bare ground to pre-grazing conditions.

Grazing, rest, precipitation, and plants

The mixed-grass prairie is characterized by a shifting mosaic of plant communities at different successional stages. As a result, some plant species hold a competitive advantage during early successional stages, while others do better in late succession environments. Blue grama has culmless vegetative shoots and therefore relatively low growth points, which allows the species to tolerate higher stocking rates (Branson 1953). In addition, blue grama benefited from moderate to high stocking in BAGMA because the species is relatively shade intolerant, and litter and vegetation-height levels were reduced at these intensities (Epstein et al. 1996). These benefits did not persist during rest years, as both litter and vegetation height density increased rapidly

following the exclusion of livestock grazing. In contrast, western wheatgrass is a species found in both late and early seral plant communities (Knapp 1991, Tirmenstein 1999). This species is particularly effective at competing for resources of light and moisture with other species because it reproduces via both rhizomes and seed (Hafenrichter et al. 1968 in Tirmenstein 1999).

Interestingly, rhizomes also allow this species to tolerate higher stocking rates by enabling regrowth of western wheatgrass in the summer and fall after clipping by grazing animals (Trlica and Menke 1977). Needle-and-thread grass generally occurs in early to mid-seral plant communities (Zlatnik 1999, Frederick and Klein 1994), which is consistent with the results of my study. Needle-and-thread flushes relatively early in the season, which gives the species a head start in securing horizontal and vertical space (Zlatnik 1999). This provides needle-and-thread a competitive advantage for capturing limited resources, such as sunlight and moisture, but also makes the species more susceptible to overgrazing in the spring, which might explain the decrease of needle-and-thread observed in pastures treated with the highest stocking rate (Goetz 1963, Hassell and Barker 1985). Needle-and-thread reproduces relatively slowly compared to other native grasses because the species does not have an extensive rhizome network (Weaver and Albertson 1956), and instead propagates via seed and tillers (Akinsoji 1988, Weaver and Albertson 1956); this might explain the residual influence of stocking rate on needle-and-thread after livestock were excluded.

The adaptations of exotic vegetation may allow such species to invade and persist at multiple seral stages within the mixed-grass prairie ecosystem. In BAGMA, dandelion cover increased in all pastures following cattle grazing re-introduction, possibly due to the species' ability to reproduce with seed over large distances via wind dispersal and by vegetative regeneration (Clements et al. 1999). Overgrazing is commonly cited as a disturbance that allows dandelion to establish (McLean and Marchand 1968, Bergen et al. 1990). The continued higher levels of dandelion following 3 years of rest might suggest that once introduced it has the ability to persist even in relatively undisturbed rangeland.

The response of plants to grazing and rest often vary across their range of occurrence depending on climate or site-specific conditions (ie. topography, plant communities, soil moisture, etc.) as the effectiveness of plant adaptations also vary across this range. For instance, the varied response of lesser spikemoss to grazing has often been attributed to confounding effects of drought or other weather variables (Crane 1990). I detected expansion of lesser spikemoss during grazing years, which is consistent with studies from Montana, Alberta, and Saskatchewan but not other areas (Clark et al. 1943; Van Dyne and Vogel 1967; Ross and Hunter 1976). Similarly, western wheatgrass decreases under grazing pressure when annual precipitation is below 500 mm in upland sites but increases with precipitation above this threshold (Tirmenstein 1999). Therefore, higher than normal levels of precipitation received from 2010-2012 might explain the non-linear response of this species to grazing and quickened recovery to pre-grazing levels (Molloy 2014). Changes in plant response to disturbance across their range of occurrence mean that the plant communities that can occur in the absence of grazing will also vary.

Relict sites, areas devoid of the disturbance of grazing, provide examples of potential vegetation communities that might exist in the absence of grazing (Clements 1936, Dyksterhuis 1958). Using relict sites as targets for recovery is one method to account for potential variation between regions. I considered BAGMA a relict site, as it was only lightly grazed during the winter prior being acquired by Parks Canada and then rested completely from 1987-2008, and therefore collecting pre-management data was sufficient for establishing potential vegetation communities in the absence of grazing. In addition, pre-management data acts as a spatial control as it establishes patterns that may exist in the landscape due to differences among pastures. For instance, I concluded there was no effect of stocking rate on goat's beard after 4 years of grazing in 2011, despite the fact that I detected a negative linear effect of stocking rate, as this pattern existed prior to the re-introduction of grazing. In other circumstances pre-management data can help better determine how extreme the effects of a management action are. For example, the non-

linear pre-grazing trend of western wheatgrass, with lowest cover occurring in pastures later treated at moderate stocking rates, suggested a weaker effect of stocking rate after 4 years of grazing than I would have interpreted without information regarding the pre-grazing trend.

Control pastures, which were left devoid of grazing throughout the study period, help to quantify effects caused by inter-annual variation rather than management actions. A variety of weather related variables, such as temperature, precipitation, and snow pack, could have effects on songbird and plant communities. The high levels of precipitation during a portion of the BAGMA experiment could have influenced site conditions in several ways. Increased precipitation has the potential to reduce or even offset impacts of grazing by increasing potential biomass production of plants (Chase et al. 2000, Oesterheld et al. 2001). Multiple consecutive wet years can amplify this effect (Oesterheld et al. 2001). As a result, biomass production may increase during high precipitation years despite consistent annual stocking rates (Ballard and Krueger 2005). This heightened productivity can alter vegetation structure by increasing canopy height (Bylo et al. 2014), and may alter species composition by increasing competition for space (Dunne et al. 2011) or by favoring plant species with higher water requirements or greater tolerance for flooding (Banach, et al. 2009). Because grazing and precipitation influence vegetation simultaneously it can be challenging to separate the effects of one from the other. Changes in vegetation structure and plant species cover in control pastures could provide clues as to the effects of precipitation in my study. The expansion of western wheatgrass cover in control pastures suggests effects of environmental variables such as precipitation. Western wheatgrass expands with greater precipitation levels because it is moderately flood tolerant and is able to take advantage of higher soil moisture levels (Tirmenstein 1999). In contrast, needle-and-thread and blue grama have relatively low tolerances for flooding, high water table levels, and/or high soil moisture content (Epstein et al. 1996, Coupland 1958), which may explain why their cover decreased in control pastures.

Grazing, rest, precipitation, and songbirds

Cattle grazing and stocking rate continued to impact some songbird species in BAGMA even after cattle were excluded from the area. However, the amount of time necessary for residual effects to disappear varied by species, and depended on recovery of habitat structure.

Given that effects of stocking rate on bare ground and litter in the uplands persisted in rest years, it is not surprising that residual benefits of higher stocking rate remained for chestnut-collared longspur. Several studies have shown chestnut-collared longspur prefer early seral stages of grasslands with shorter and sparser vegetation (Fritcher et al. 2004, Owens and Myres 1973) and pastures grazed with higher stocking rates (Sliwinski 2015 and Molloy 2014). However, to the best of my knowledge, this study is the first to demonstrate that the benefits of grazing at high stocking rates persist following grazing exclusion. This suggests that managers may use higher stocking rates to increase chestnut-collared longspur populations, and also intermittently rest pastures for up to 2 years without losing the positive benefits accrued to this species from grazing.

In contrast, Baird's sparrows have typically been associated with mixed-grass prairie plant communities that have limited visual obstruction, moderate litter depths, and intermediate grass height (Green et al. 2002, Owens and Myres 1973). Given that residual effects of stocking rate on bare ground and litter persisted in upland but not lowland areas, it is not surprising that residual effects of stocking rate on Baird's sparrow distribution persisted only in upland areas. Previous studies have suggested that Baird's sparrow are capable of tolerating moderate stocking rates (Davis et al. 1999, Koper and Schmiegelow 2006), although multiple studies at BAGMA have found that Baird' sparrow abundance declines with increasing stocking rate (Molloy 2014, Sliwinski 2015). This study suggests that the negative effects of grazing at moderate stocking rates persist following grazing exclusion for at least 2 rest years in upland but not lowland areas. Therefore, resting rangeland for even 1 year in lowland habitat can significantly benefit Baird's

sparrow abundances in pastures previously treated with moderate stocking rates, but more than 2 years of rest are needed to provide a similar benefit in upland habitats.

Species less sensitive to grazing, or capable of tolerating moderate grazing intensities, recovered more rapidly following grazing removal than species more sensitive to grazing. Several studies have suggested both grasshopper and Savannah sparrows are insensitive to lower grazing intensities (Walk and Warner 2000, Fritcher et al. 2004), or that their abundances may actually increase under moderate grazing conditions (Sliwinski 2015), but this study suggests both respond rapidly to the removal of livestock. Grasshopper sparrows typically require low to moderate litter depths and moderate vegetation height (Wiens 1973, Davis and Duncan 1999). Savannah sparrow are positively associated with litter depth, litter cover, and taller denser vegetation, but negatively associated with bare ground (Sutter and Brigham 1998, Davis and Duncan 1999, Molloy 2014). However, both species have been found to select habitats with structural characteristics outside of these typical preferences (Wiens 1973, Wheelwright and Rising 2008), and also have a higher tolerance for shrub cover than most grassland songbirds (Swanson 1996). These relatively flexible habitat requirements might explain why Savannah and grasshopper sparrows can tolerate low grazing intensities but respond negatively to higher stocking rates. Additionally, these flexible habitat requirements might explain why partial or full recovery of only some habitat structure variables are adequate to return both species distribution to pre-grazing levels. Therefore, managers can rest a pasture for as little as one year to quickly recover the populations of both grasshopper and Savannah sparrows.

The effects of precipitation on songbird abundance are indirect, and probably result from impacts on vegetation and insect populations. For instance, insect population crashes across North America have been linked to periods of drought (Hawkins and Holyoak 1998), which could have important implications on availability of food for songbirds. Greater biomass production due to precipitation could result in taller vegetation (Chase et al. 2000), which might benefit grassland songbird species, such as Sprague's pipit, that select for this type of habitat. Songbird distribution

on a landscape is fluid compared to plant distribution because of the mobile nature, yearly migrations, and low site fidelity of many prairie bird species (Jones et al. 2007). Consequently, evaluating temporal changes in control pastures does not necessarily offer the same information for songbirds as it does for plants. However, variability due to environmental factors still becomes apparent at times. For instance, the residual effects of stocking rate on Baird's sparrow were overwhelmed by an environmental condition that made all sites sufficient during the first rest year, though residual effects were apparent again by the second rest year. Alternatively, this trend could be the result of low survival on their wintering grounds. Also, higher than normal precipitation levels, which increase biomass production (Oosterheld et al. 2001), might have driven the decrease in chestnut collared-longspur abundance across all pastures given the species' habitat preference for short, sparser vegetation.

Detectability of songbirds

My study was the first at BAGMA to incorporate dependent-double-observer point counts into the study design, and my results suggest that unadjusted abundance estimates are an appropriate index for relative songbird abundance at BAGMA. The probability of detection for all songbird species was high, and did not vary between observers. Several other studies have suggested that naïve abundance estimates are appropriate indices for relative abundance, and that this is especially true in the mixed-grass prairie environment (Johnson 2008; Efford and Dawson 2009; Leston et al. 2015). In the mixed-grass prairie the probability of perceiving songbirds should be similar along a gradient of stocking rate treatments because the perceptibility of songbirds singing below grass canopy, perching on shrubs, or displaying aerially, is unlikely to be altered by site differences in the form of grass height and vegetation structure (Leston et al. 2015). Consequently, using naïve abundance as an index for relative songbird abundance should not result in the inflation of abundances estimated at this particular site and is therefore an appropriate measure.

Conclusion

The results of this study suggest that succession is retrogressive in the mixed-grass prairie. Retrogressive succession in the mixed-grass prairie is likely the result of the evolution of this ecosystem with large herds of grazing animals. Furthermore, the findings of this study imply that the plants and songbirds of the mixed-grass prairie are resilient to grazing, including livestock grazing by cattle. Range managers have applied many theories and practices, including the climax concept and rangeland health, to make decisions about how to graze livestock. However, when managing the mixed-grass prairie for wildlife these theories or approaches may not always be appropriate as some organisms require early seral plant communities that are viewed as less optimal. Therefore, using grazing to produce wildlife habitat requires a new mindset different from the old paradigms of climax as the pinnacle of a system, rangeland health, and maximum forage production. If succession in the mixed-grass prairie is truly retrogressive then managers have the opportunity to operate outside of the traditional grazing or range health paradigm when attempting to create wildlife habitat with livestock grazing as the risk of irreversible change is relatively low in the northern mixed grass prairie.

CHAPTER 6: MANAGEMENT IMPLICATIONS

Overview

Resting rangeland can be a useful tool for creating habitat for species that prefer later seral plant communities in the mixed-grass prairie. However, on its own, this tool cannot provide the range of habitat necessary to support the varied species that occur within the mixed-grass prairie biome. Resting rangeland from livestock grazing can help to create a greater diversity of habitat types when combined with spatially variable stocking rates, thereby improving ecological integrity within this system.

Using grazing to create habitat for Species at Risk

Parks Canada as an agency is committed to the protection of endangered species through the Species at Risk Act (SARA). Chestnut-collared longspur is listed as a threatened species under Schedule 1 of SARA. My results suggest that grazing is very beneficial for chestnut-collared longspur, and the introduction of grazing at any intensity will likely increase their abundance over time. High stocking rates (up to 0.83 AUM/ha) will benefit this species most and provide essential habitat for a variety of songbirds that prefer early seral vegetation communities such as McCowan's longspur, horned lark, and long-billed curlew (Derner et al. 2009). In addition, my results suggest that managers could intermittently rest pastures grazed at high stocking rates for at least 2 years to restore rangeland health without losing the benefits accrued to chestnut-collared longspur during grazing.

Baird's sparrow is listed as a species of special concern by COSEWIC though the species has no designation or status under SARA as of yet (COSEWIC 2015). In general, this sparrow specie has been associated with plant communities that have intermediate

grass height, limited visual obstruction, and moderate litter depths (Green et al. 2002, Owens and Myres 1973), and one study that actually included sites in the mixed-grass prairie found Baird's sparrow was capable of tolerating moderate grazing intensities (Davis et al. 1999). However, studies conducted at BAGMA suggest this species has low tolerance for even moderate stocking rates, with the possible exception of years when environmental conditions such as precipitation reduce the impacts of grazing. Managing some pastures with light stocking rates or resting pastures would benefit Baird's sparrow. Upland areas with early seral plant communities will likely need to be rested for more than 2 years to create habitat for Baird's sparrow, but in lowland areas 2 years of rest could be sufficient. Grazing management practices undertaken for Baird's sparrow are likely to benefit other species with similar habitat requirements such as Sprague's pipit, which has been classified as a species at risk in Canada (Davis et al. 1999, COSEWIC 2015).

To maintain habitat for species at risk over the long term, managers might consider shifting the pastures targeted for different habitat types, for example short and sparse vegetation for chestnut-collared longspur, every few years instead of attempting to maintain pastures in a static state. The tendency of grazing animals to preferentially forage for new growth in previously grazed areas creates a patchy effect at the landscape level (McNaughton 1984). Furthermore, the likelihood of cattle returning to previously grazed areas is probably greater than was historically observed with bison as livestock generally graze in fenced pastures. Without intentional grazing manipulation this tendency may cause severe damage when pastures are grazed at heavy stocking rates for many consecutive years.

Using grazing to improve ecological integrity

Parks Canada is committed to the enhancement and restoration of ecological integrity within the lands of their purview through the Canada National Parks Act (Canada 1982). Under the Canada National Parks Act, ecological integrity is defined as "a condition that is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes" (Canada 1982, p.1). Ecological integrity is the capacity of an ecosystem to persist, to remain in its native state, and therefore to the resilience of an ecosystem. Ecosystem resilience expresses the ability of the system to withstand stresses placed on the system internally and from external sources. Resilience in an ecosystem is strongest when a diversity of genes, species, and communities native to the region are present (Parks Canada 2013). In the mixed-grass prairie, diversity was produced by the historical disturbances of grazing and fire, which created a shifting plant communities at various successional stages, and the adaptation of organisms to the habitats these disturbances created (Fuhlendorf and Engle 2001). Therefore, grazing is a key ecological process in the mixed-grass ecosystem and Parks Canada has a responsibility to restore this process on the landscape.

Historically bison would have freely roamed across the mixed-grass prairie applying variable grazing pressure to different areas (Fuhlendorf and Engle 2001). In contrast, a variety of stocking rates in combination with rest periods are required to produce a similar range of grazing pressures with livestock. A fundamental goal of the pursuit of ecological integrity is to ensure that all types of naturally occurring habitat within the landscape are present (Parks Canada 2013). Using different stocking rates

increases the diversity of habitat on a landscape by altering vegetation structure (Vavra 2005, Severson and Urness 1994). A variety of habitat is essential if managers wish to ensure habitat is available for the variety of organisms that occur in the mixed-grass prairie.

Applying variable stocking rates and intermittently resting rangeland also promotes a greater diversity of plants. Grazing alters plants species composition in vegetation communities and increases production of certain species (Vavra 2005, Severson and Urness 1994, Payne and Bryant 1994). My results suggest that grazing can favour the expansion and production of some species. Having multiple native grass and forb species present can ensure adequate nutritional forage is available across multiple seasons for grazers including black-tailed prairie dogs, bison, and pronghorn antelope, because production and palatability of different plant species peak at different times during the growing season (Marten 1978, Bork and Irving 2015).

Challenges of managing for both species at risk and ecological integrity

Balancing the enhancement of habitat for species at risk with the promotion of ecological integrity can be challenging. To protect specific species at risk within Grasslands National Park managers need to implement species-specific management plans to protect, expand, or restore critical habitat where possible. However, managing habitat for one species may negatively affect other species (Vavra 2005). In addition, managing land for ecological integrity may require time and money be expended on habitat not beneficial to species at risk. It may be helpful to consider habitat management at a landscape level rather than only at a local level.

Management aimed at establishing habitats not represented in the area surrounding the park could ensure that all habitat types within the mixed-grass prairie are present at the landscape level. An underrepresentation of undisturbed and heavily disturbed plant communities exists in the mixed-grass prairie due to the moderate grazing intensities promoted by current grazing management practices (Saab et al. 1995; Fuhlendorf and Engle 2001). For instance, Mankota Community Pasture, which borders the East Block of Grasslands National Park, usually applies moderate stocking rates from 0.34-0.56 AUM/ha. To complement this grazing program stocking rates less than 0.34 AUM/ha and above 0.56 AUM/ha could be applied to pastures in the park, thereby providing a greater range of habitat for species living in the region. Park managers might consider prioritizing heavy grazing in their management plans, as many ranchers in the area choose to avoid high stocking rates to protect rangeland health and thereby ensure production of adequate forage for cattle in future years (personal observation, Molloy 2014). The park has a unique opportunity to create habitat not produced in commercial ranching operations, because unlike ranchers, the park needs to ensure an ecologically viable operation rather than an economically viable one.

Climate and grazing management

Climate can influence plants and consequently change the effects of grazing. To achieve habitat targets managers might consider increasing stocking rates in years with above average precipitation, by increasing livestock numbers or length of grazing period, because increased rainfall has been shown to reduce the effects of grazing (Chase et al. 2000). However, in dry years managers might choose to decrease stocking rate to reduce pressure on plants already limited by low moisture content in soil.

High levels of precipitation may also accelerate recovery and progression to late seral plant communities in pastures being rested. Therefore, in years of high precipitation managers might consider reducing rest period length. Extended periods of drought, in contrast, may limit production potential of plants. Therefore, managers could consider increasing length of rest periods during dry climatic cycles. In addition, to facilitate the park's capacity to adaptively manage grazing, the park may consider setting aside some areas as grass banks to provide emergency grazing, for ranchers involved in grazing agreements with the park, during drought years or other climatic events that reduce plant production and vigor.

In lowland areas, the influence of precipitation on the effects of grazing and recovery from grazing may be reduced because lowland areas already have higher moisture available to plants than upland areas. Managers should consider the effects of increasing stocking rate or changing rest periods separately for lowland and upland areas. In drought years especially, increased manipulation of cattle may be necessary to decrease pressure of grazing in lowland, via mineral blocks, fencing around sensitive riparian areas, or creation of artificial water sources in upland areas, because cattle retreat to lowland areas above certain temperatures (Allred et al. 2013).

Completing an inventory of the different plant communities currently present in Grasslands National Park, and implementing monitoring will be vital if or when the park chooses to begin introducing livestock grazing to an area. For the purposes of habitat creation, taking vegetation structure measurements such as vegetation height density, litter depth, or cover estimates will be important parts of the monitoring program. Monitoring the habitat present will allow managers to make well-informed choices about

habitat enhancement and management, and will also suggest when managers might consider shifting stocking rates or rest periods to account for influences of precipitation.

Summary

In the mixed-grass prairie, grazing is an invaluable tool for producing habitat for species at risk, and as a key ecological process it is vital to the ecological integrity of the system. Both a variety of stocking rates and periods of rest are necessary to meet the needs of the species that depend on the mixed-grass prairie for habitat. Precipitation can also play an important role in determining the effects of grazing on habitat, rangeland health, and rest period required to shift plant communities back to later seral successional stages; therefore, to produce targeted habitat types managers will likely need to adjust stocking rate, rest frequency, and rest length in response to precipitation.

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APPENDIX A

Effects of stocking rate and year on habitat structure, plant species cover, grassland songbird abundance in upland and lowland habitat during pre-grazing year (2006), after four years of grazing (2011), and following grazing exclusion (2012-2014) at Grasslands National Park, Saskatchewan, Canada. Year was classified as a categorical value. All models compared to pre-grazing values. The terms AUM*AUM and AUM*AUM*year were removed from final model if they were not significant, and therefore are not included in the tables below. Bold font indicates a significant *p*-value.

Upland models

Habitat Structure

Dependent Variable	Model Components	Random Variables Included	Year	Variable	Pre-grazing year (2006) baseline			4 Years Grazed (2011) baseline		
					Parameter Estimate	Standard Error	<i>P</i>	Parameter Estimate	Standard Error	<i>p</i>
Vegetation Height-density (Robel 100% Cover)	Year+AUM+Year*AUM+AUM*AUM+Year*AUM*AUM	Pasture and Plot	2006	Intercept	12.2057	0.851	<0.001	NA	NA	NA
				Year	NA	NA	NA	0.4703	0.559	0.4012
				AUM	-9.8222	5.9971	0.103	NA	NA	NA
			Year*AUM	NA	NA	NA	-7.0854	3.9419	0.074	
			AUM*AUM	10.5765	7.4618	0.1579	NA	NA	NA	
			Year*AUM*AUM	NA	NA	NA	15.0466	4.9134	0.003	
			2011	Intercept	NA	NA	NA	11.6969	0.8517	<0.001
				Year	-3.7868	0.5591	0.4154	NA	NA	NA
				AUM	NA	NA	NA	-2.6659	6.0037	0.656
			Year*AUM	7.023	3.9425	0.0763	NA	NA	NA	
			AUM*AUM	NA	NA	NA	-4.4414	7.4758	0.553	
			Year*AUM*AUM	-15.0012	4.9142	0.0026	NA	NA	NA	
			2012	Year	1.056	0.5591	0.0604	1.5301	0.559	0.007
				Year*AUM	1.1553	3.9404	0.7697	-5.9481	3.9419	0.1329
				Year*AUM*AUM	-6.5953	4.9029	0.1801	8.4657	4.9134	0.086
2013	Year	-0.9898	0.5591	0.0782	-0.5157	0.559	0.357			
	Year*AUM	2.8653	3.9404	0.4664	-4.2283	3.9419	0.285			
	Year*AUM*AUM	-2.6649	4.9029	0.5873	12.396	4.9134	0.012			

			2014	Year	-0.6991	0.5591	0.2126	-0.225	0.559	0.688
				Year*AUM	3.8653	3.9404	0.3278	-3.2382	3.9419	0.412
				Year*AUM*AUM	-2.621	4.9029	0.5935	12.44	4.9134	0.012
Litter Depth	Year+AUM+Year*AUM	Pasture and Plot	2007	Intercept	6.8542	0.5405	<0.001	NA	NA	NA
				Year	NA	NA	NA	0.4764	0.491	0.334
				AUM	0.07491	1.0748	0.9445	NA	NA	NA
				Year*AUM	NA	NA	NA	4.4432	0.9844	<0.001
			2011	Intercept	NA	NA	NA	6.3782	0.5407	<0.001
				Year	-0.4764	0.491	0.3334	NA	NA	NA
				AUM	NA	NA	NA	-4.369	1.0825	<0.001
				Year*AUM	-4.443	0.9844	<.001	NA	NA	NA
			2012	Year	2.667	0.4908	<.001	3.1435	0.491	<0.001
				Year*AUM	-4.1886	0.9759	<.001	0.2543	0.9844	0.797
			2013	Year	2.8934	0.4908	<.001	3.3699	0.491	<0.001
				Year*AUM	-2.1726	0.9759	0.0274	2.2703	0.9844	0.022
Litter Cover	Year+AUM+Year*AUM	Pasture and Plot	2006	Intercept	50.6898	2.9775	<0.001	NA	NA	NA
				Year	NA	NA	NA	8.3939	2.8412	0.004
				AUM	3.7729	5.9204	0.5247	NA	NA	NA
				Year*AUM	NA	NA	NA	25.3597	5.6938	<0.001
			2011	Intercept	NA	NA	NA	42.3141	2.9778	<0.001
				Year	-8.3727	2.8145	0.0036	NA	NA	NA
				AUM	NA	NA	NA	-21.6365	5.9633	<0.001
				Year*AUM	-25.4105	5.6967	<.001	NA	NA	NA
			2012	Year	-12.8458	2.8415	<.001	-4.5023	2.8412	0.115
				Year*AUM	-35.7719	5.65	<.001	-10.3624	5.6938	0.070
			2013	Year	2.4424	2.8415	0.391	10.8158	2.8412	<0.001
				Year*AUM	-24.0331	5.65	<.001	1.3763	5.6938	0.809
			2014	Year	6.2684	2.8415	0.0285	14.642	2.8412	<0.001
				Year*AUM	-24.4294	5.65	<.001	0.9801	5.6938	0.864
Bare Ground Occurrence	Year+AUM+Year*AUM	Plot and Frame	2006	Intercept	6.1901	0.4718	<0.001	NA	NA	NA
				Year	NA	NA	NA	3.7868	0.461	<0.001
				AUM	-0.9254	0.9381	0.325	NA	NA	NA
				Year*AUM	NA	NA	NA	-8.4075	0.9238	<0.001
			2011	Intercept	NA	NA	NA	2.4035	0.472	0.001

	Year	-3.7868	0.461	<0.001	NA	NA	NA
	AUM	NA	NA	NA	7.4809	0.9455	<0.001
	Year*AUM	8.407	0.9238	<0.001	NA	NA	NA
2012	Year	-3.7209	0.4673	<0.001	0.06616	0.4675	0.888
	Year*AUM	7.9375	0.9238	<0.001	-0.4701	0.9314	0.614
2013	Year	-4.1751	0.4608	<0.001	-0.3882	0.461	0.401
	Year*AUM	4.0083	0.9162	<0.001	-4.3992	0.9238	<0.001
2014	Year	-3.1195	0.4608	<0.001	0.6674	0.461	0.149
	Year*AUM	3.72	0.9162	<0.001	-4.6875	0.9238	<0.001

Plant Species Cover

Dependent Variable	Model Components	Random Variables Included	Year	Variable	Pre-grazing year (2006) baseline			4 Years Grazed (2011) baseline		
					Parameter Estimate	Standard Error	<i>p</i>	Parameter Estimate	Standard Error	<i>P</i>
<i>Hesperostipa comata</i>	Year + AUM Year*AUM + AUM*AUM+Year*AUM*AUM	Pasture and Plot	2006	Intercept	1.900	0.228	<0.001	NA	NA	NA
				Year	NA	NA	NA	0.654	0.182	<0.001
				AUM	1.367	1.600	0.394	NA	NA	NA
				Year*AUM	NA	NA	NA	-2.704	1.202	0.026
				AUM*AUM	-2.905	2.011	0.150	NA	NA	NA
			Year*AUM*AUM	NA	NA	NA	3.271	1.529	0.034	
			2011	Intercept	NA	NA	NA	0.827	0.253	0.017
				Year	-0.658	0.182	<0.001	NA	NA	NA
				AUM	NA	NA	NA	4.066	1.650	0.015
				Year*AUM	2.752	1.202	0.023	NA	NA	NA
				AUM*AUM	NA	NA	NA	-6.169	2.085	0.004
			Year*AUM*AUM	-3.334	1.529	0.030	NA	NA	NA	
			2012	Year	-0.605	0.182	0.001	0.051	0.196	0.796
				Year*AUM	0.261	1.249	0.835	-2.455	1.303	0.061
				Year*AUM*AUM	-0.251	1.581	0.874	3.033	1.660	0.069
2013	Year	-0.721	0.184	<0.001	-0.065	0.199	0.742			
	Year*AUM	1.412	1.216	0.247	-1.313	1.272	0.303			
	Year*AUM*AUM	-1.102	1.527	0.471	2.198	1.608	0.173			
2014	Year	-3.774	1.112	<0.001	-0.418	0.211	0.049			
	Year*AUM	2.359	1.288	0.069	-0.389	1.339	0.772			
	Year*AUM*AUM	-1.761	1.595	0.271	1.564	1.672	0.351			
<i>Pascopyron smithii</i>	Year + AUM + Year*AUM + AUM*AUM +Year*AUMAUM	Pasture and Plot	2006	Intercept	0.383	0.362	0.331	NA	NA	NA
				Year	NA	NA	NA	-1.569	0.213	<0.001
				AUM	-5.660	2.309	0.015	NA	NA	NA
				Year*AUM	NA	NA	NA	-0.739	0.437	0.092
				AUM*AUM	6.688	2.840	0.020	NA	NA	NA
			2011	Intercept	NA	NA	NA	1.953	0.333	0.001
				Year	1.569	0.213	<.0001	NA	NA	NA
				AUM	NA	NA	NA	-4.922	2.289	0.033

				Year*AUM	0.739	0.437	0.092	NA	NA	NA
				AUM*AUM	NA	NA	NA	6.688	2.840	0.020
			2012	Year	1.489	0.213	<.0001	-0.081	1.583	0.611
				Year*AUM	0.655	0.434	0.133	-0.083	0.305	0.785
			2013	Year	0.660	0.229	0.004	-0.910	0.180	<0.001
				Year*AUM	0.778	0.464	0.095	0.039	0.347	0.911
			2014	Year	0.724	0.229	0.002	-0.845	0.180	<0.001
				Year*AUM	0.180	0.472	0.703	-0.559	0.358	0.120
<i>Taraxacum</i>	Year+AUM+Year*AUM	Pasture	2006	Intercept	-0.781	0.389	0.085	NA	NA	NA
<i>Officinale</i>		and Plot		Year	NA	NA	NA	-0.856	0.352	0.016
				AUM	-2.457	1.095	0.026	NA	NA	NA
				Year*AUM	NA	NA	NA	-3.012	1.034	0.004
			2011	Intercept	NA	NA	NA	0.075	0.305	0.813
				Year	0.856	0.352	0.016	NA	NA	NA
				AUM	NA	NA	NA	0.588	0.588	0.347
				Year*AUM	3.012	1.034	0.004	NA	NA	NA
			2012	Year	0.755	0.359	0.037	-0.101	0.266	0.704
				Year*AUM	1.301	0.337	0.000	-0.686	0.504	0.175
			2013	Year	1.905	1.030	0.066	0.445	0.235	0.060
				Year*AUM	2.118	1.032	0.042	-1.106	0.457	0.016
			2014	Year	3.012	1.034	0.004	0.348	0.240	0.148
				Year*AUM	2.326	1.053	0.028	-0.894	0.459	0.053
<i>Selaginella</i>	Year+AUM+Year*AUM	Pasture	2006	Intercept	7.446	2.322	<0.001	NA	NA	NA
<i>densa</i>		and Plot		Year	NA	NA	NA	-22.178	2.190	<0.001
				AUM	0.310	4.618	0.525	NA	NA	NA
				Year*AUM	NA	NA	NA	-10.765	4.388	0.015
			2011	Intercept	NA	NA	NA	29.654	2.323	<0.001
				Year	22.213	2.190	<0.001	NA	NA	NA
				AUM	NA	NA	NA	11.002	4.650	0.019
				Year*AUM	10.680	4.389	0.016	NA	NA	NA
			2012	Year	6.531	2.189	0.003	-15.683	2.190	<0.001
				Year*AUM	8.607	4.353	0.049	-2.073	4.388	0.637
			2013	Year	2.204	2.189	0.315	-20.009	2.190	<0.001
				Year*AUM	8.247	4.353	0.060	-2.433	4.388	0.580

2014	Year	3.854	2.189	0.080	-18.359	2.190	<0.001
	Year*AUM	2.866	4.353	0.511	-7.813	4.388	0.076

Songbird Abundance

Dependent Variable	Model Components	Random Variables Included	Pre-grazing year (2006) baseline					4 Years Grazed (2011) baseline		
			Year	Variable	Parameter Estimate	Standard Error	<i>p</i>	Parameter Estimate	Standard Error	<i>p</i>
Baird's Sparrow	Year+AUM+Year*AUM+AUM*AUM+Year*AUM*AUM	Pasture And plot	2006	Intercept	6.502	0.450	<0.001	NA	NA	NA
				Year	NA	NA	NA	-1.030	0.479	0.033
				AUM	3.264	3.172	0.305	NA	NA	NA
				Year*AUM	NA	NA	NA	10.267	3.377	0.003
				AUM*AUM	-4.617	3.946	0.244	NA	NA	NA
				Year*AUM*AUM	NA	NA	NA	-12.676	4.202	0.003
			2012	Intercept	NA	NA	NA	7.532	0.450	<0.001
				Year	1.030	0.479	0.033	NA	NA	NA
				AUM	NA	NA	NA	-7.003	3.172	0.029
				Year*AUM	-10.267	3.377	0.003	NA	NA	NA
				AUM*AUM	NA	NA	NA	8.059	3.946	0.043
				Year*AUM*AUM	12.676	4.202	0.003	NA	NA	NA
			2013	Year	-2.851	0.479	<0.001	-3.881	0.479	<0.001
				Year*AUM	-3.460	3.377	0.307	6.805	3.377	0.046
				Year*AUM*AUM	4.833	4.202	0.252	-7.843	4.202	0.064
2014	Year	1.251	0.479	0.010	0.221	0.479	0.645			
	Year*AUM	-9.201	3.377	0.007	1.066	3.377	0.753			
	Year*AUM*AUM	11.275	4.202	0.008	-1.401	4.202	0.739			
Chestnut-collared Longspur	Year+AUM+Year*AUM	Pasture	2006	Intercept	4.636	0.556	<0.001	NA	NA	NA
				Year	NA	NA	NA	3.232	0.542	<0.001
				AUM	-1.233	1.021	0.229	NA	NA	NA
				Year*AUM	NA	NA	NA	-6.942	1.078	<0.001
			2012	Intercept	NA	NA	NA	1.404	0.556	0.036
				Year	-3.232	0.542	<0.001	NA	NA	NA
				AUM	NA	NA	NA	5.709	1.021	<0.001
				Year*AUM	6.942	1.078	<0.001	NA	NA	NA
			2013	Year	-3.943	0.542	<0.001	-0.711	0.542	0.191

				Year*AUM	5.423	1.078	<0.001	-1.519	1.078	0.160
			2014	Year	-4.544	0.542	<0.001	-1.312	0.542	0.016
				Year*AUM	2.468	1.078	0.023	-4.474	1.078	<0.001
Savannah Sparrow	Year AUM	Year*AUM	Pasture	2006	Intercept	1.540	0.304	<0.001	NA	NA
					Year	NA	NA	NA	-3.318	0.430
					AUM	1.000	0.604	0.099	NA	NA
					Year*AUM	NA	NA	NA	2.890	0.854
				2012	Intercept	NA	NA	NA	4.858	0.304
					Year	3.318	0.430	<0.001	NA	NA
					AUM	NA	NA	NA	-1.890	0.604
					Year*AUM	-2.890	0.854	<0.001	NA	NA
				2013	Year	2.357	0.430	<0.001	-0.961	0.430
					Year*AUM	-0.925	0.854	0.280	1.965	0.854
				2014	Year	1.362	0.430	0.002	-1.956	0.430
					Year*AUM	-1.084	0.854	0.206	2.890	0.854

Lowland models

Habitat Structure

Dependent Variable	Model Components	Random Variables Included	Year	Variable	Pre-grazing year (2006) baseline			4 Years Grazed (2011) baseline		
					Parameter Estimate	Standard Error	<i>p</i>	Parameter Estimate	Standard Error	<i>p</i>
Litter Depth	Year+AUM+Year*AUM+AUM*AUM+Year*AUM*AUM	Pasture	2007	Intercept	6.187	0.576	<0.001	NA	NA	NA
				Year	NA	NA	NA	1.374	0.796	0.086
				AUM	7.367	4.060	0.072	NA	NA	NA
				Year*AUM	NA	NA	NA	12.759	5.608	0.024
				AUM*AUM	-9.933	5.052	0.051	NA	NA	NA
				Year*AUM*AUM	NA	NA	NA	-14.082	6.978	0.045
			2011	Intercept	NA	NA	NA	4.813	0.576	<0.001
				Year	-1.374	0.796	0.086	NA	NA	NA
				AUM	NA	NA	NA	-5.392	4.060	0.186
				Year*AUM	-12.759	5.608	0.024	NA	NA	NA
				AUM*AUM	NA	NA	NA	4.149	5.052	0.413
				Year*AUM*AUM	14.082	6.978	0.045	NA	NA	NA
			2012	Year	0.553	0.796	0.488	1.928	0.796	0.017
				Year*AUM	-9.796	5.608	0.083	2.964	5.608	0.598
				Year*AUM*AUM	10.711	6.978	0.127	-3.371	6.978	0.630
			2013	Year	1.148	0.796	0.151	2.522	0.796	0.002
				Year*AUM	-7.363	5.608	0.191	5.396	5.608	0.337
				Year*AUM*AUM	7.594	6.978	0.278	-6.488	6.978	0.354
2014	Year	-2.325	0.796	0.004	-0.951	0.796	0.234			
	Year*AUM	-6.724	5.608	0.232	6.035	5.608	0.284			
	Year*AUM*AUM	10.044	6.978	0.152	-4.038	6.978	0.564			
Vegetation	Year+AUM+Year*AUM	Pasture and Plot	2006	Intercept	13.654	1.812	<0.001	NA	NA	NA
Height-density (Robel 100% Cover)	AUM*AUM+Year*AUM*AUM			Year	NA	NA	NA	0.108	0.977	0.912
				AUM	29.812	12.770	0.021	NA	NA	NA
				Year*AUM	NA	NA	NA	39.763	6.888	<0.001
				AUM*AUM	-45.615	15.889	0.005	NA	NA	NA
				Year*AUM*AUM	NA	NA	NA	-48.809	8.570	<.0001

	2011	Intercept	NA	NA	NA	13.546	1.812	0.000
		Year	-0.108	0.977	0.912	NA	NA	NA
		AUM	NA	NA	NA	-9.951	12.770	0.437
		Year*AUM	-39.763	6.888	<0.001	NA	NA	NA
		AUM*AUM	NA	NA	NA	3.194	15.889	0.841
		Year*AUM*AUM	48.809	8.570	<0.001	NA	NA	NA
	2012	Year	1.199	0.977	0.222	1.308	0.977	0.183
		Year*AUM	-20.200	6.888	0.004	19.563	6.888	0.005
		Year*AUM*AUM	24.687	8.570	0.005	-24.122	8.570	0.006
	2013	Year	-0.382	0.977	0.697	-0.274	0.977	0.780
		Year*AUM	-20.592	6.888	0.003	19.172	6.888	0.006
		Year*AUM*AUM	28.486	8.570	0.001	-20.323	8.570	0.019
	2014	Year	-1.847	0.977	0.061	-1.739	0.977	0.078
		Year*AUM	-23.125	6.888	0.001	16.638	6.888	0.017
		Year*AUM*AUM	33.371	8.570	<.001	-15.438	8.570	0.074
Bare Ground	2006	Intercept	1.821	0.370	0.003	NA	NA	NA
		Year	NA	NA	NA	0.024	0.201	0.905
		AUM	-1.726	2.636	0.514	NA	NA	NA
		Year*AUM	NA	NA	NA	-4.430	1.472	0.003
		AUM*AUM	1.436	3.288	0.663	NA	NA	NA
		Year*AUM*AUM	NA	NA	NA	4.658	1.849	0.013
	2011	Intercept	NA	NA	NA	1.801	0.370	0.003
		Year	-0.021	0.201	0.917	NA	NA	NA
		AUM	NA	NA	NA	2.635	2.589	0.311
		Year*AUM	4.368	1.472	0.004	NA	NA	NA
		AUM*AUM	NA	NA	NA	-3.128	3.220	0.333
		Year*AUM*AUM	-4.577	1.849	0.015	NA	NA	NA
	2012	Year	-0.056	0.199	0.781	-0.036	0.199	0.858
		Year*AUM	1.517	1.456	0.299	-2.841	1.388	0.043
		Year*AUM*AUM	-0.335	1.827	0.855	4.230	1.729	0.016
	2013	Year	-0.432	0.210	0.041	-0.411	0.210	0.052
		Year*AUM	1.428	1.521	0.350	-2.940	1.460	0.046
		Year*AUM*AUM	-0.883	1.907	0.644	3.695	1.815	0.044
	2014	Year	-0.326	0.208	0.120	-0.304	0.209	0.148

Year*AUM	2.076	1.491	0.166	-2.309	1.429	0.109
Year*AUM*AUM	-1.232	1.855	0.508	3.366	1.761	0.058

Plant Species Cover

Dependent Variable	Model Components	Random Variables Included	Year	Variable	Pre-grazing year (2006) baseline			4 Years Grazed (2011) baseline		
					Parameter Estimate	Standard Error	<i>p</i>	Parameter Estimate	Standard Error	<i>p</i>
Blue grama (<i>Bouteloua gracilis</i>)	Year + AUM + Year*AUM + AUM*AUM+Year*AUM*AUM	Plot	2006	Intercept	0.887	0.431	0.085	NA	NA	NA
				Year	NA	NA	NA	1.248	0.465	0.008
				AUM	-8.288	3.500	0.019	NA	NA	NA
				Year*AUM	NA	NA	NA	8.208	3.530	0.021
				AUM*AUM	9.269	4.358	0.035	NA	NA	NA
			Year*AUM*AUM	NA	NA	NA	8.895	4.316	0.041	
			2011	Intercept	NA	NA	NA	0.360	0.519	0.514
				Year	-1.245	0.465	0.008	NA	NA	NA
				AUM	NA	NA	NA	0.134	3.501	0.969
				Year*AUM	8.132	3.526	0.022	NA	NA	NA
				AUM*AUM	NA	NA	NA	0.446	4.261	0.917
			2012	Year	-0.374	0.385	0.333	0.871	0.483	0.073
				Year*AUM	0.189	3.716	0.960	7.910	3.711	0.035
				Year*AUM*AUM	0.436	4.633	0.925	9.194	4.534	0.044
			2013	Year	-0.986	0.435	0.025	0.260	0.522	0.619
Year*AUM	-2.166	4.619		0.640	-5.175	3.747	0.169			
Year*AUM*AUM	2.963	3.751		0.431	6.640	4.522	0.144			
2014	Year	-1.255	0.465	0.008	0.008	0.548	0.989			
	Year*AUM	4.839	3.700	0.193	-3.327	3.697	0.370			
	Year*AUM*AUM	-3.927	4.504	0.385	4.913	4.407	0.267			
Lesser spikemoss (<i>Selaginella densa</i>)	Year+AUM+Year*AUM+ AUM*AUM+Year*AUM*AUM	Pasture and Plot	2006	Intercept	1.136	0.459	0.048	NA	NA	NA
				Year	NA	NA	NA	1.026	0.237	<0.001
				AUM	-8.929	3.126	0.005	NA	NA	NA
				Year*AUM	NA	NA	NA	1.635	0.482	0.001
			AUM*AUM	10.020	3.866	0.011	NA	NA	NA	
			2011	Intercept	NA	NA	NA	2.161	0.440	0.003

	Year	1.026	0.237	<0.001	NA	NA	NA
	AUM	NA	NA	NA	7.295	3.112	0.021
	Year*AUM	1.635	0.482	0.001	NA	NA	NA
	AUM*AUM	NA	NA	NA	10.020	3.866	0.011
2012	Year	0.788	0.243	0.002	0.238	0.202	0.241
	Year*AUM	1.716	0.492	0.001	0.081	0.379	0.831
2013	Year	0.071	0.257	0.783	0.955	0.229	<0.001
	Year*AUM	1.827	0.510	0.001	0.192	0.404	0.635
2014	Year	0.341	0.251	0.177	0.685	0.211	0.001
	Year*AUM	1.476	0.506	0.004	0.159	0.399	0.669

Songbird Abundance

Dependent Variable	Model Components	Random Variables Included	Year	Variable	Pre-grazing year (2006) baseline			4 Years Grazed (2011) baseline		
					Parameter Estimate	Standard Error	<i>p</i>	Parameter Estimate	Standard Error	<i>P</i>
Baird's Sparrow	Year+AUM+Year*AUM	Pasture	2006	Intercept	5.083	0.546	<0.001	NA	NA	NA
				Year	NA	NA	NA	0.531	0.730	0.468
				AUM	0.145	1.085	0.894	NA	NA	NA
				Year*AUM	NA	NA	NA	2.729	1.452	0.062
			2012	Intercept	NA	NA	NA	4.552	0.546	<0.001
				Year	-0.531	0.730	0.468	NA	NA	NA
				AUM	NA	NA	NA	-2.584	1.085	0.019
				Year*AUM	-2.729	1.452	0.062	NA	NA	NA
			2013	Year	-3.943	0.730	<0.001	-3.412	0.730	<0.001
				Year*AUM	0.428	1.452	0.769	3.157	1.452	0.032
			2014	Year	-0.525	0.730	0.474	0.007	0.730	0.993
				Year*AUM	0.568	1.452	0.696	3.297	1.452	0.025
Grasshopper Sparrow	Year+AUM+Year*AUM+AUM*AUM+Year*AUM*AUM	Pasture and plot	2006	Intercept	-0.547	0.378	0.198	NA	NA	NA
				Year	NA	NA	NA	0.313	0.491	0.524
				AUM	-4.097	3.853	0.290	NA	NA	NA
				Year*AUM	NA	NA	NA	-8.362	4.529	0.068
				AUM*AUM	3.567	5.050	0.482	NA	NA	NA
				Year*AUM*AUM	NA	NA	NA	11.213	6.037	0.066
			2012	Intercept	NA	NA	NA	-0.219	0.317	0.516
				Year	0.3388	0.429	0.430	NA	NA	NA
				AUM	NA	NA	NA	3.784	2.259	0.032
				Year*AUM	7.749	4.460	0.085	NA	NA	NA
				AUM*AUM	NA	NA	NA	-7.011	3.184	0.030
				Year*AUM*AUM	-10.392	5.096	0.084	NA	NA	NA
			2013	Year	-0.571	0.630	0.367	-0.887	0.593	0.138
				Year*AUM	16.293	26.415	0.539	8.764	24.994	0.727
				Year*AUM*AUM	-60.090	100.940	0.553	-49.954	96.346	0.605
			2014	Year	1.691	0.410	<.001	1.362	0.356	<0.001

				Year*AUM	3.611	4.086	0.379	-4.246	2.645	0.112
				Year*AUM*AUM	-4.920	5.379	0.364	5.644	3.692	0.130
Savannah Sparrow	Year+AUM+Year*AUM+AUM*AUM+Year*AUM*AUM	Pasture and Plot	2006	Intercept	2.296	0.517	0.004	NA	NA	NA
				Year	NA	NA	NA	-3.028	0.531	<0.001
				AUM	3.219	3.646	0.379	NA	NA	NA
				Year*AUM	NA	NA	NA	12.257	3.743	0.002
				AUM*AUM	-3.443	4.536	0.450	NA	NA	NA
				Year*AUM*AUM	NA	NA	NA	-9.128	4.658	0.053
			2012	Intercept	NA	NA	NA	5.325	0.517	<0.001
				Year	3.028	0.531	<0.001	NA	NA	NA
				AUM	NA	NA	NA	-9.039	3.646	0.015
				Year*AUM	-12.257	3.743	0.002	NA	NA	NA
				AUM*AUM	NA	NA	NA	5.685	4.536	0.213
				Year*AUM*AUM	9.128	4.658	0.053	NA	NA	NA
			2013	Year	1.152	0.531	0.032	-1.876	0.531	<0.001
				Year*AUM	-7.413	3.743	0.050	4.845	3.743	0.199
				Year*AUM*AUM	7.073	4.658	0.132	-2.055	4.658	0.660
			2014	Year	0.851	0.531	0.112	-2.178	0.531	<0.001
				Year*AUM	-5.674	3.743	0.133	6.583	3.743	0.082
				Year*AUM*AUM	2.980	4.658	0.524	-6.148	4.658	0.190

