

EFFECTS OF LIVESTOCK GRAZING MANAGEMENT ON THE ECOLOGY OF  
GRASSLAND BIRDS AND THEIR PREDATORS IN A NORTHERN MIXED-  
GRASS PRAIRIE ECOSYSTEM

by

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## DEDICATION

The majority of my study area was located on privately-owned rangelands managed by local ranchers and ranch families for cattle grazing. I cannot express enough gratitude to these kind folks for allowing us access to their lands to conduct our research. Not only did they grant land access, they invited us into their homes and showed us friendship, offered their assistance when we ran into issues in the field, and provided their expertise and insight regarding sustainable rangeland management practices, attained through many years of cattle ranching. In this regard, I would like to personally thank Ron Whited and family, Jason Papineau and family, Duane Ullman, Will McCament, Craig Iverson, Scott Pippert and family, Tim Franzen and family, Greg Pennington and family, Connie Buxbaum and family, and Scott Buxbaum.

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## ABSTRACT

Grassland birds have recently undergone substantial population declines throughout much of their historic ranges in North America. The majority of remaining grassland bird habitat is rangeland managed for livestock production, so grazing management has implications for grassland bird conservation efforts. Populations of mesocarnivores have recently seen range expansions and increased abundance as a result of anthropogenic extirpation of apex predators in grassland ecosystems. Mesocarnivores are often major predators of grassland birds and their nests, so considering the effects of management actions on mesocarnivore occupancy is important within grassland bird conservation efforts. I evaluated the relative effects of three livestock grazing systems on grassland bird abundance and mesocarnivore occupancy in a northern mixed-grass prairie ecosystem of eastern Montana, USA. During 2016–17, I conducted replicated point-count surveys at 150 locations on a 3,000-ha ranch managed with rest-rotation cattle grazing, and 155 locations on adjacent reference properties (4,300-ha) employing season-long or 2-pasture summer-rotational grazing systems to identify grazing management influences on grassland bird abundances. During 2016–17, I deployed remote cameras at 45 locations within rest-rotation grazing systems, and at 45 locations on reference properties to identify grazing management influences on mesocarnivore occupancy. Overall, there was no noticeable benefit of rest-rotation grazing on abundance or species diversity of grassland birds relative to season-long and summer-rotation grazing systems. Species-specific responses to livestock grazing system were found for each of three obligate grassland birds. Support for interactions between grazing system and local rangeland production potential were found, limiting the ability to recommend general livestock management practices for the benefit of grassland bird populations. Additionally, abundance of grasshopper sparrow (*Ammodramus savannarum*;  $\beta = -0.10 \pm 0.03$ ) and western meadowlark (*Sturnella neglecta*;  $\beta = -0.09 \pm 0.03$ ) showed a negative relationship with increasing stocking rate. Occupancy of mesocarnivores was highest in rest-rotation grazing systems, followed by season-long and summer-rotation systems, respectively, and showed a positive relationship with increasing stocking rate ( $\beta = 1.64 \pm 1.10$ ). Regional guidelines for livestock grazing management may be inappropriate in terms of grassland bird conservation efforts in the northern mixed-grass prairie.

## INTRODUCTION AND LITERATURE REVIEW

### Current and Historical Ecology of North America's Grasslands

North America's prairie ecosystems were historically dominated by contiguous native grassland extending from southeastern Alberta and southern Saskatchewan to Texas, and through the Midwestern United States from Wyoming to Illinois. Prior to European settlement, frequent disturbance events on the landscape, characterized by spatial and temporal variability, defined the evolutionary history of these unique systems (Kay 1998). Naturally occurring and Native American induced wildfires, coupled with intensive use of these areas by large grazing ungulates following burn events created a fluctuating landscape that shaped the ecology of North America's prairies (Pyne 1993, Kay 1998).

The unique processes of North America's prairie ecosystems began to decompose following arrival of European settlers to the New World. The disturbances under which prairie ecosystems evolved, namely recurring fire and bison grazing, became significantly limited and replaced with new disturbances, including domestic livestock grazing and widespread cultivation of the prairies for agricultural food production. Thousands of years of graminoid decomposition furnished North America's Great Plains prairies with some of the most fertile soils on Earth, ideal for agricultural production, and the new occupants of these prairies soon realized this agricultural potential, which they were quick to exploit (Smith 1895, Benedict et al. 1996). Following government incentives from the Homestead Act of 1862 and the Enlarged Homestead Act of 1909 in the United States, and the Dominion Lands Act of 1872 in Canada, North America's prairies were

flooded with hundreds of thousands of settlers looking to take advantage of free land (Sabadell et al. 1982, Ostlie et al. 1997, Samson et al. 2004, Holechek et al. 2011).

Cultivation was the major use of lands appropriated by settlers under these Acts, marking the onset of widespread prairie conversion.

Agriculture in North America has progressed significantly since the late 19<sup>th</sup> century, from small- to large-scale production. Currently, over 81 million hectares of native prairie have undergone some form of agricultural development in North America's Midwest and West (Sabadell et al. 1982). As a result, grassland ecosystems have experienced the most significant change from their natural, pre-settlement condition of any ecosystem in North America (Sabadell et al. 1982). Over 50% of temperate grasslands in North America have been converted from their native state, with the largest conversion seen in tallgrass prairie (>95% alteration), followed by the mixed-grass prairie (>70% alteration) and shortgrass prairie (>48% alteration; Howe 1994, Samson et al. 2004, Hoekstra et al. 2005).

Conversion of remnant grasslands to row-crop agriculture is still occurring throughout the mixed- and tallgrass prairies of the United States' Grain Belt region at rates from 1.0 – 5.4% annually, with significant losses in North and South Dakota, Nebraska, Iowa, and Minnesota (Wright and Wimberly 2013). High commodity grain prices, government crop subsidies for ethanol-production, and relatively low profitability for lands enrolled in the Conservation Reserve Program (CRP) provide private landowners with sufficient economic incentive to shift grasslands into agricultural production (Holechek 2007, Fargione et al. 2008, Wright and Wimberly 2013). The

major issue with widespread conversion of native grasslands to cultivation is that homogenous landscapes dominated by row-crop agriculture offer little habitat value to indigenous wildlife (Natural Resources Council 1982, Brennan and Kuvlesky Jr 2005). As a result, grassland wildlife species requiring contiguous, high-quality grassland habitats have experienced dramatic population declines in these areas of extensive agricultural development. Continued alteration of native grasslands in North America reinforces the importance of remnant native habitat throughout the current and historic distributions of grassland wildlife species.

#### Importance of North American Rangelands to Native Grassland Wildlife

Currently, the majority of remaining native grassland in North America is in the form of rangeland managed for livestock grazing (Holechek et al. 2011). Approximately 50% of land cover in the United States is classified as rangeland, i.e., uncultivated land that supports grazing and browsing herbivores (Holechek et al. 2011). The majority of this rangeland is grazed by domestic livestock, giving substantial economic value to grazing as a dominant land use (Holechek et al. 2011). Energy contained in rangeland biomass can be harnessed by the livestock, converting this energy into a product directly consumable by humans (Hormay 1970, Archer and Smeins 1991). In addition to its economic value, grazing of domestic livestock on native grasslands also has the potential to mimic historical ecological processes associated with natural ecosystem structure and functionality (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2012). Livestock grazing on rangelands has been promoted as a wildlife management tool to mimic the grassland disturbance of large and small herbivorous grazers, the American bison (*Bison bison*) and

prairie dog (*Cynomys* spp.), which have both been extirpated from the majority of their historic ranges in North America following Euro-American colonization (Leopold 1933, Samson and Knopf 1994, Benedict et al. 1996). Reflected by their status as large, generalist herbivorous grazers, domestic cattle (*Bos taurus*) have similar foraging habits to bison in regard to how they impact grassland vegetation structure, offering a contemporary substitute for the historic ecological role of bison within prairie landscapes (Stuth 1991, Plumb and Dodd 1993, Knapp et al. 1999, Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004). The ability of livestock to alter vegetation structure and species composition as the existing dominant large herbivore within native grassland habitats often solidifies their status as ecosystem engineers (Bock et al. 1993, Jones et al. 1997, WallisDeVries et al. 1998, Derner et al. 2009).

Livestock grazing on native rangelands is an excellent multipurpose application of land management, as the goal of financial sustainability for ranch managers is potentially aligned with wildlife habitat needs. With habitat loss at the forefront of grassland wildlife population declines, rangelands managed for livestock grazing offer a form of market-based habitat conservation, keeping large areas of native grassland from conversion to agricultural or other anthropogenic development (Brunson and Huntsinger 2008). However, protecting rangelands from development, in itself, is not typically sufficient to sustain proper functionality of these grassland ecosystems.

Grazing domestic livestock on rangelands can either positively or negatively impact rangeland quality, as well as wildlife abundance and species diversity, so proper rangeland management practices are crucial for maintaining the health of these systems

(Risser et al. 1981, Messmer 1990, Krausman et al. 2009). Grazing of grassland vegetation has been shown to facilitate ecological functioning, improve rangeland condition, and increase aboveground vegetation productivity in some grassland ecosystems, and the ecological process of grazing is important for the grassland wildlife species that evolved with and depend upon the vegetation structure created by large herbivorous grazers (Risser 1990, Frank and McNaughton 1993, Fuhlendorf and Engle 2001, Derner et al. 2009, Holechek et al. 2011). However, improper rangeland management, characterized by sustained high-intensity grazing and vegetative defoliation, has resulted in reduced plant biodiversity, along with biomass losses of residual grass, grass roots, and litter, leading to the deterioration of long-term range condition and native grassland habitat (Dyksterhuis 1949, Fleischner 1994, Ostlie et al. 1997, Biondini et al. 1998, Holechek et al. 2011).

Historical intensive overgrazing and disregard for sustainable forage production led to widespread rangeland deterioration in the late 19<sup>th</sup> century, negatively impacting range quality, forage production for livestock, and habitat quality for native wildlife (Smith 1895, Smith 1899, Coughenour 1991, Holechek et al. 2011). In the late 19<sup>th</sup> to mid-20<sup>th</sup> centuries, ranch managers began to realize the economic consequences of continual overgrazing on both livestock production and rangeland quality, resulting in the establishment of sustainable range management principles, followed by the adoption of more tenable grazing practices (Smith 1895, Saab et al. 1995, Holechek et al. 2011, Fuhlendorf et al. 2012). Since this time, research has consistently indicated strong evidence for decreased economic returns following overgrazing by livestock, resulting in

less overgrazing of rangelands for conceivable short-term profit (Torell et al. 1991, Manley et al. 1997, Holechek et al. 1999, Derner et al. 2008). These more conservative rangeland management strategies improved range condition and forage production, while also developing the grazing principle of uniform forage utilization, an ideal still applied in rangeland management by state and federal agencies, and private ranch managers to this day (Bailey 2004, Bailey 2005, Toombs and Roberts 2009, Holechek et al. 2011).

Current grazing management practices often implement “manage to the middle” strategies that employ moderate grazing intensities and attempt even distribution of livestock to achieve consistent utilization of rangeland forage (Williams 1954, Bailey et al. 1996, Fuhlendorf and Engle 2001, Derner et al. 2009, Fuhlendorf et al. 2009, Toombs et al. 2010). Maximizing livestock grazing efficiency on the range through even forage utilization achieves structural consistency in rangeland vegetation to meet the typical desires of range managers (Williams 1954, Anderson 1967). Several management strategies are used to achieve even spatial utilization of forage, including short-duration grazing, twice-over rotational grazing, and other rotational grazing systems, as well as the deliberate locational placement of water and mineral within pastures (Coughenour 1991, Hart et al. 1993, Fuhlendorf and Engle 2001, Toombs and Roberts 2009, Fuhlendorf et al. 2012, Ranellucci et al. 2012).

Although desirable for livestock production, the prevalent management practices used to achieve uniform forage utilization inherently develop homogeneous vegetation structure on rangelands, a consequence that may not be optimal for native grassland wildlife which evolved with the frequent disturbance events that created structural

heterogeneity within prairie ecosystems (Fuhlendorf and Engle 2001, Toombs et al. 2010). The importance of restoring structural heterogeneity to rangelands has recently received much research attention within areas of ecosystem functioning and wildlife habitat management (Wiens 1997, Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, Hovick et al. 2015, Lwiwski et al. 2015). Heterogeneity, as defined in range management, is the variation in stature, composition, density, and biomass of rangeland vegetation (Fuhlendorf and Engle 2001). Promoting heterogeneity on the landscape enhances rangeland biodiversity by mimicking the patchy disturbances under which these prairie ecosystems evolved (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006). Historic disturbance on North American prairies resulted from spatio-temporal variation in drought, natural fire, and native grazers (Knapp et al. 1999, Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006). When bison dominated the grasslands of North America pre-European settlement, they created a mosaic of spatially variable vegetation structure on the landscape through patchy grazing patterns and selective foraging that followed wildfire (Knapp et al. 1999, Askins et al. 2007). Disturbance from fires coupled with intensive, patchy grazing, along with the addition of periodic drought, characterized Great Plains grasslands as truly dynamic ecosystems (Anderson 1982, Ostlie et al. 1997).

### Spatial Variability among Prairie Ecosystems Drives Management

Practices and principles within rangeland management are fundamentally dependent upon geographic location (Holechek et al. 2011). The broad spatial extent of North America's prairie ecosystems accentuates the importance of recognizing innate structural variability when managing rangelands. Merely considering prairies of the Great

Plains, rangeland management actions implemented within the tallgrass prairies of Kansas, Nebraska, and Iowa will not produce similar results when applied to the northern mixed-grass prairies of North Dakota, South Dakota, and eastern Montana. Variable rangeland productivity among prairie ecosystems, driven largely by regional climate, influences the vegetative characteristics within a specific grassland landscape (Holechek et al. 2011). Even within a single prairie ecosystem, the northern mixed-grass prairie for example, annual variability in precipitation from one growing season to the next has been shown to significantly affect range vegetation structure and composition (Lwiwski et al. 2015). Without accounting for these differences between geographic regions in the rangelands' ability to produce vegetation, even on an annual temporal scale, management actions may not improve range condition in terms of climax community regeneration or wildlife habitat quality.

The majority of recent research focused on restoring structural heterogeneity to rangelands comes from tallgrass prairie ecosystems (Voleti et al. 2014), in areas characterized by higher amounts of annual precipitation and often considerably higher values of average rangeland production than mixed- or short-grass prairies (Holechek et al. 2011). In these areas, intensive management practices developed to restore heterogeneity to the prairie landscape, such as 'patch-burn grazing,' have proven quite effective in terms of improving wildlife habitat quality (Fuhlendorf et al. 2006, Churchwell et al. 2008, Coppedge et al. 2008, McNew et al. 2015, Ricketts and Sandercock 2016, Winder et al. 2017). Some of the original research supporting heterogeneity-based rangeland management in the tallgrass and mixed-grass prairies

recommended the application of intensively grazed focal points within pastures, which would shift throughout the pasture over multiple grazing seasons, and allow previously grazed focal points recovery from intensive grazing (Fuhlendorf and Engle 2001). Patch-burn grazing techniques establish heterogeneity within grasslands by subjecting different areas within a pasture to prescribed fire annually, effectively dividing the pasture into regions of variable vegetation structure (Hobbs et al. 1991, Fuhlendorf and Engle 2001). Regions within the pasture not subjected to fire receive less intensive grazing pressure than recently burned areas due to the tendencies of large ungulates to graze selectively on higher quality forage following burn events (Bailey et al. 1996, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2009, Allred et al. 2011). This interaction between fire and grazing, termed ‘pyric-herbivory,’ effectively mimics historical grassland disturbance and creates a mosaic of large-scale, patch-size structural heterogeneity in grassland vegetation on the prairie landscape (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2009).

An alternative conservation-based approach to patch-burn grazing is currently being applied to rangelands in the state of Montana, and may improve wildlife habitat quality and rangeland condition through restoring structural heterogeneity of rangeland vegetation on the landscape without the use of fire (Montana Department of Fish, Wildlife, and Parks 2010). The Montana Department of Fish, Wildlife, and Parks (hereafter “Montana FWP”) collaborates with private ranches and public agencies throughout Montana to influence management of approximately 180,000 ha for improvements in wildlife habitat quality while maintaining sustainable livestock grazing on the rangeland. Incentive programs available to landowners through Montana FWP

include conservation easements and Upland Game Bird Enhancement Program (UGBEP) projects. Within these programs, minimum grazing standards require implementation of a rest-rotation grazing system (Hormay 1970).

The rest-rotation grazing system described by Hormay (1970) was initially designed to maintain healthy rangelands and sustainable annual forage production, and was implemented on the bunchgrass rangelands of northeastern California at the edge of the Great Basin biome and the intermountain transitional zone (Hormay and Talbot 1961). In this region, historical grazing intensity by large ungulates was relatively low, compared to areas of the shortgrass, tallgrass, and mixed-grass prairies of western and mid-western North America, which evolved with relatively intensive grazing pressure. The rest-rotation grazing system incorporates a full year of rest from grazing in a designated pasture within the system, as well as deferment from grazing during the growing season in another pasture (Hormay 1970). Due to the selectivity of grazing livestock, the most palatable grass species are subject to overgrazing (Stuth 1991, Bailey et al. 1998). Continued defoliation of these highly selected species results in lowered capacity for shoot and root growth the following growing season, and loss of stored reserves will eventually lead to death of the plant (Hormay 1970). Allowing multiple pastures deferment from grazing during the growing season is intended to benefit the regrowth of rangeland vegetation and restore vigor to plants that did not evolve in a system historically grazed by large ungulates, and which are not well adapted to heavy grazing (Hormay and Talbot 1961, Hormay 1970).

Although the rest-rotation grazing system was neither designed for improving wildlife habitat nor developed in a grassland ecosystem with evolutionary adaptations to grazing by large herbivores, there is scientific merit for implementing this system in the northern mixed-grass prairie for the benefit of native wildlife. The rest-rotation grazing system hypothetically creates large patches of herbaceous vegetation structure from low to high height and density among pastures within the system. More intensively managed grazing systems, such as rest-rotation grazing, will inherently result in less fine-scale heterogeneity in vegetation structure within a pasture by reducing the potential for livestock forage selectivity (Coughenour 1991, Holechek et al. 2011). Dividing a large pasture into smaller pastures will result in more even forage utilization within the grazed pastures, effectively creating large-scale, patch-heterogeneity on the landscape (Hart et al. 1993, Briske et al. 2008).

In regard to patch-size heterogeneity, the rest-rotation grazing system is conceptually similar to patch-burn grazing, an effective strategy for improving wildlife habitat quality in the tallgrass prairie. Rest-rotation grazing, however, may be a more viable management option for creating patch-heterogeneity in the more arid regions of the northern mixed-grass prairie due to socio-cultural aversions to prescribed fire within rangeland management practices (Sliwinski 2017). Rather than using prescribed fire to concentrate grazing on burned patches or defer grazing from unburned patches on the landscape, the rest-rotation grazing system uses fences to divide a large pasture into smaller pastures that are either heavily grazed or deferred from grazing during one or more parts of the year.

## Conclusion

North America's grasslands have seen some of the greatest alterations of any ecosystem over the past 300 years. The majority of remaining contiguous, native grasslands are in the form of rangelands managed for livestock grazing. As a result, responsible (conservation-based) rangeland management practices are necessary for sustaining or improving range condition and wildlife habitat quality to achieve proper ecosystem functioning. Prairie ecosystems evolved under frequent yet sporadic disturbance events in the form of fire and grazing, creating a dynamic, heterogeneous landscape in terms of rangeland vegetation structure and composition. Economically viable rangeland management practices that restore structural heterogeneity to prairie landscapes and mimic historical disturbance processes have been recently upheld as conservation-based approaches that will achieve proper ecosystem functionality.

One such application of heterogeneity-based management being used by the state of Montana Department of Fish, Wildlife, and Parks is the rest-rotation grazing system. Hypothetically, this system creates patch-heterogeneity in vegetation structure on the landscape through the strategic rotation of both intensive cattle grazing and deferment of grazing among pastures within the system. However, the rest-rotation grazing system has not been tested for effects on wildlife habitat quality in the northern mixed-grass prairie. Results of research comparing rotational grazing systems and season-long grazing have been inconsistent (Holechek et al. 1999), and evaluations of grazing systems in numerous grassland ecosystems have not shown rotational grazing to significantly improve forage production, standing crop biomass, or animal production over that of continuous, season-

long grazing systems (Rogler 1951, Launchbaugh et al. 1978, Manley et al. 1997, Briske et al. 2008, Vermeire et al. 2008).

In general, the effects of grazing systems on grassland wildlife have not been well-established (Schieltz and Rubenstein 2016). My research evaluates the rest-rotation grazing system in terms of its effects on the ecology of obligate grassland birds and their predators in the northern mixed-grass prairie. In Chapter 2, I evaluate the effects of livestock grazing management on the diversity of grassland birds and the abundance of three specific obligate grassland bird species in a northern mixed-grass prairie ecosystem. In Chapter 3, I evaluate the effects of livestock grazing management on the occupancy of mesocarnivores in a northern mixed-grass prairie ecosystem. In Chapter 4, I provide conclusions from my research and offer management recommendations to agencies and private landowners for improving grassland bird habitat quality, and for reducing the potential impacts of mesocarnivore depredation of grassland birds and their nests in northern mixed-grass prairie ecosystems.

CHAPTER TWO

EFFECTS OF LIVESTOCK GRAZING MANAGEMENT ON THE ECOLOGY OF  
GRASSLAND BIRDS IN A NORTHERN MIXED-GRASS  
PRAIRIE ECOSYSTEM

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## CHAPTER TWO

EFFECTS OF LIVESTOCK GRAZING MANAGEMENT ON THE ECOLOGY OF  
GRASSLAND BIRDS IN A NORTHERN MIXED-GRASS PRAIRIE ECOSYSTEM**INTRODUCTION**

Population declines for many species of grassland birds have been well documented using long-term datasets from the North American Breeding Bird Survey, and grassland birds have been cited as the most rapidly declining guild of terrestrial birds in North America during the last 50 years (Knopf 1994;1996, Peterjohn and Sauer 1999, Sauer et al. 2013). Diversity and abundance of grassland birds within grassland ecosystems are considered indicators of habitat quality due to their species-specific habitat requirements, and can be used to assess the effects of local land management practices or the impacts of anthropogenic disturbance within these ecosystems (Browder et al. 2002, VerCauteren and Gillihan 2004, Coppedge et al. 2006, Askins et al. 2007, Rosenberg et al. 2016). Therefore, current grassland bird population trends should not only be disconcerting because of the ecological services these birds fill within grasslands, such as regulation of insect populations (Whelan et al. 2008), but current trends should also raise concern for the overall health of our grassland ecosystems.

Many factors have been associated with the decline of grassland bird populations, including habitat fragmentation, woody vegetation encroachment, and improper or inadequate grassland management (Knopf 1994, Peterjohn and Sauer 1999, Johnson and Igl 2001, Brennan and Kuvlesky Jr 2005). The most significant, however, is the alteration of native breeding and wintering habitat within North America's grassland ecosystems

resulting from widespread agricultural cultivation and other anthropogenic development (Knopf 1994, Johnson and Igl 2001, Brennan and Kuvlesky Jr 2005, Askins et al. 2007). Conserving and properly managing remaining tracts of native grassland habitats are now some of the most important responses to confront current grassland bird population declines (Knopf 1996, Vickery et al. 1999, Askins et al. 2007, With et al. 2008). Intensive agricultural development throughout North America's grassland ecosystems has resulted in rangelands managed for livestock grazing composing the majority of remaining contiguous grassland habitat, emphasizing the importance of maintaining and managing these rangelands as remnant habitat for conserving grassland bird populations (Knopf 1996, Davis et al. 2014). Implementing rangeland management practices that improve grassland habitats to the quality required by grassland birds may act to moderate population declines.

Physical habitat structure is important for birds, as it influences foraging efficiency and nesting success (Cody 1985, Orians and Wittenberger 1991, Bock et al. 1993, Winter et al. 2005). Grassland birds tend to select habitat and establish territories based on cues for suitable vegetation structure upon their arrival to breeding areas (Ahlering and Faaborg 2006). Several factors may contribute to spatial and temporal variability in the structure of vegetation within grassland ecosystems. Annual precipitation significantly influences vegetation structure and composition, and the interaction between moisture and rangeland productivity – i.e., the vegetation produced by a specific ecological site annually – results in wide structural variability within grassland habitats (Ahlering and Faaborg 2006, Vermeire et al. 2008, Lwiwski et al.

2015). Relationships have been found between regional grassland bird densities during the breeding season and previous years' precipitation, likely due to the effect of soil moisture on herbaceous vegetation growth (Igl and Johnson 1999, Niemuth et al. 2008, Lipsey and Naugle 2017). The action of grazing by large herbivores is the other main factor to significantly influence vegetation structure within grassland ecosystems, and grassland birds have shown strong responses to grazed grasslands in terms of habitat selection and demography (Knopf 1996, Fondell and Ball 2004, VerCauteren and Gillihan 2004, Derner et al. 2009, Lwiwski et al. 2015). Species diversity and abundance of grassland birds are often lower in ungrazed pastures compared to grazed pastures, providing evidence that large grazers create components of vegetation structure within prairie habitats that grassland birds historically required (Skinner 1975, Renken and Dinsmore 1987, Messmer 1990, Báldi et al. 2005).

Rangeland management practices that restore structural heterogeneity to prairie landscapes through the use of fire and grazing have recently been promoted within grassland bird conservation (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, Derner et al. 2009). Grassland bird communities are evolutionarily adapted to the variation in vegetation structure created by disturbance events on the landscape (Fuhlendorf and Engle 2001, Pool and Austin 2006). Structural heterogeneity within grassland habitats has been shown to increase diversity and abundance of native grassland birds, and the variations in specific vegetation structure and composition present within grasslands are important habitat requirements selected by grassland birds (Winter et al. 2005, Askins et

al. 2007, Fisher and Davis 2010, Henderson and Davis 2014, Hovick et al. 2015, Lipsey 2015).

Livestock grazing management designed to restore structural heterogeneity to rangelands, such patch-burn grazing, have been successfully applied to areas of the tallgrass prairie, and, in many cases, grassland birds have shown a positive response to these management practices (Fuhlendorf et al. 2006, Churchwell et al. 2008, Coppedge et al. 2008, Hovick et al. 2015, McNew et al. 2015, Davis et al. 2016). Traditionally, prescribed burning was not necessarily promoted as a rangeland management tool in more arid regions of the mixed-grass prairies, especially those at the northern- and western-most extents. The historical fire return interval in these more arid ecosystems was typically longer than that of tallgrass prairie ecosystems, so burning may not consistently result in increased vegetative productivity and is often dependent upon precipitation (Anderson 1982, Umbanhowar Jr 1996). Prescribed burning is not widely accepted by local land managers in semi-arid regions of the mixed-grass prairie, despite recent research suggesting resilience of these areas to fire and supporting use of fire-grazing interactions for mimicking historical disturbance regimes (Gates et al. 2017, Sliwinski 2017, Powell et al. 2018). Therefore, conservation agencies looking to restore grassland heterogeneity for the benefit of native wildlife are restricted in management options, even though the interaction of fire and grazing has been promoted for the conservation of grassland birds in the northern mixed-grass prairie (Richardson et al. 2014).

An alternative heterogeneity-based rangeland management technique is currently being employed in the state of Montana, USA, through the use of a rest-rotation grazing system and intensive manipulation of livestock. This system hypothetically establishes patch-size structural heterogeneity on the landscape similar to patch-burn grazing, creating large areas of variable disturbance, and patches of low to high vegetation height and density annually (Hagen et al. 2004, Derner et al. 2009, Toombs et al. 2010). Recent research has suggested that solely manipulating stocking rates is not adequate to provide the vegetation heterogeneity grassland birds require in the northern mixed-prairie due to spatial and temporal variability in precipitation, justifying the use of a more intensive livestock grazing management system for filling this role in the absence of fire (Lipseý and Naugle 2017, Powell et al. 2018). However, the response of grassland birds to rest-rotation grazing has not been evaluated in the northern mixed-grass prairie. Grassland bird densities and community composition are excellent indicators of the condition and habitat quality of native grasslands due to their species-specific habitat requirements, making them useful for assessing potential effects of rangeland management strategies (Browder et al. 2002, VerCauteren and Gillihan 2004, Coppedge et al. 2006).

Finally, the success of specific livestock grazing systems for improving rangeland or wildlife habitat quality varies widely in the literature (Holechek et al. 1999, Briske et al. 2008, Krausman et al. 2009, Schieltz and Rubenstein 2016). The regional evolution of grassland ecosystems to a continuum of grazing pressures, as well as large-scale differences in average annual rangeland productivity may largely contribute to these inconsistencies, i.e., a livestock grazing system that improves grassland bird habitat

quality in a highly productive tallgrass prairie ecosystem (Fuhlendorf et al. 2006, Coppedge et al. 2008) may not have a similar effect in the semi-arid shortgrass prairie (Augustine and Derner 2015). However, even within a single grassland ecosystem such as the northern mixed-grass prairie, researchers have found variable responses to livestock grazing management in terms of obligate grassland bird habitat selection, ranging from no response to grazing system (Davis et al. 2014), to a positive response to rotational grazing systems (Messmer 1990, Buskness et al. 2001) or a positive response to season-long grazing systems (Ranellucci et al. 2012). Additionally, grassland birds have shown species- or guild-specific responses to livestock grazing intensity within the context of variable rangeland productivity at the landscape-scale (Lipsev and Naugle 2017). I hypothesize that even fine-scale variability in rangeland production potential within the northern mixed-grass prairie should be accounted for within livestock grazing management, and may explain the inconsistencies related to the implementation of livestock grazing systems on grassland bird habitat quality.

I conducted point-count surveys of grassland birds in northeastern Montana, USA, at points randomly located across eight pastures enrolled in one of three livestock grazing systems. I was interested in the effects of livestock grazing management on grassland bird abundance and community composition in the northern mixed-grass prairie. My objectives were to 1) evaluate how species-specific abundances and community composition of grassland birds were affected by livestock grazing management in the context of site-specific rangeland production potential, 2) estimate the importance of vegetation characteristics for grassland birds mediated by livestock grazing treatment, 3)

evaluate the effectiveness of rest-rotation grazing to create patch-heterogeneity in rangeland vegetation structure, as conceptualized by previous researchers, and 4) provide management recommendations to agencies and private landowners for improving habitat quality for grassland birds in northern mixed-grass prairie ecosystems.

I predicted that pastures managed with the conservation-based rest-rotation grazing system would support overall higher abundances and a wider species diversity of grassland birds than pastures managed with more commonly used season-long or summer-rotation grazing systems, as rangeland management efforts focused on restoring patch-heterogeneity to prairie landscapes have been recently promoted to benefit grassland bird conservation. Alternatively, there may be no effect of grazing system on abundance or species diversity of grassland birds, but rather species-specific grassland bird habitat selection is closely tied with particular vegetation conditions at the local-scale (Davis et al. 2014). Finally, I predicted grazing system type would influence fine-scale vegetation conditions and, if the alternative is true, I expected to find relationships between species-specific grassland bird abundance and the local vegetation characteristics mediated by livestock grazing systems.

## **STUDY AREA**

My study area is located within the northern mixed-grass prairie of the Great Plains Missouri Plateau, and situated just northwest of the rugged Little Missouri Badlands. The study site is centered on a ~3,000-ha Upland Gamebird Enhancement Program (UGBEP) project established by the Montana Department of Fish, Wildlife, and Parks (hereafter “Montana FWP”) in 1993, located in eastern Richland County, Montana,

20 km southeast of Sidney, Montana (48° 30' N, 104° 04' W; Figure 1). Five pastures of ~4,300-ha bordering the UGBEP were used as reference treatments, with three pastures located on private lands adjacent to the UGBEP in Montana, and two pastures located on U.S. Forest Service National Grasslands adjacent to the UGBEP in McKenzie County, North Dakota.

Montana FWP collaborates with private ranches throughout the state of Montana to influence management of native rangeland for improvements in wildlife habitat quality, while maintaining economically sustainable livestock production. Incentive programs available to landowners through Montana FWP include conservation easements and the Upland Game Bird Enhancement Program, which is designed to “effectively and responsibly conserve and enhance upland game bird habitats and populations – providing quality public hunting opportunities for present and future generations” (Montana Department of Fish, Wildlife, and Parks 2015). Montana FWP also manages grazing leases on Wildlife Management Areas, Department of Natural Resources and Conservation (DNRC) lands leased by Montana FWP, and an assortment of Bureau of Land Management, U.S. Forest Service, and private lands that are managed under the terms of lease agreements (Kelvin Johnson, Montana FWP, pers. comm.). For all programs and leases, Montana FWP currently manages grazing on ~182,000 ha, of which ~81,000 ha are managed under rest-rotation grazing systems (Rick Northrup, Montana FWP, pers. comm.).

The study area in eastern Montana is dominated by contiguous rangelands managed for cattle grazing, and is characterized by rolling, gently sloping plains

(generally < 5 degrees; Bluemle 1991). Elevation ranges from 660 to 730 meters above sea level. Annual precipitation is variable, but long-term average (1911 – 2017) was ~360 ± 86 mm (SD), based on the nearest weather station (Savage 1.0 S, MT US, 20 km west) to the study site (NOAA 2017). Precipitation 12 months prior to 2016 field work (April 2015 – March 2016) was 288 mm, and prior to 2017 field work (April 2016 – March 2017) was 392 mm (NOAA 2017). Mean annual temperature is ~6°C. Winter temperatures range from -40°C to 5°C and summer temperatures range from 8°C to 43°C (NOAA 2017). Vegetation on the study site is composed of mainly graminoids, including western wheatgrass (*Pascopyrum smithii*), little bluestem (*Schizachyrium scoparium*), needle-and-thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), Kentucky bluegrass (*Poa pratensis*), and blue grama (*Bouteloua gracilis*), along with low- to mid-height shrubs, including western snowberry (*Symphoricarpos occidentalis*), silver sagebrush (*Artemisia cana*), skunkbrush sumac (*Rhus trilobata*), silver buffaloberry (*Shepherdia argentea*), chokecherry (*Prunus virginiana*), wild roses (*Rosa* spp.), and creeping juniper (*Juniperus horizontalis*), as well as two prevalent sub-shrub species, winterfat (*Krascheninnikovia lanata*), and fringed sagewort (*Artemisia frigida*).

## **METHODS**

### **Sampling**

I collected data during two grassland bird breeding seasons (May – June, 2016–17). Prior to the 2016 field season, I randomly generated 305 survey points across gradients of habitat conditions within a Montana FWP Upland Gamebird Enhancement Program project managed under rest-rotation grazing, and on adjacent private and federal

lands managed under season-long or 2-pasture summer-rotation grazing systems (Table 1, Figure 1). I used the same survey points during the 2017 field season, as grassland birds show low site fidelity among breeding seasons (Jones et al. 2007). Additionally, I was not interested in effects between seasons, such as colonization or extinction, allowing us to pool data between field seasons, resulting in a robust sample size of 610 independent grassland bird survey points.

In each year, I surveyed 150 points within rest-rotation grazing systems, with 50 points in each of the three pasture treatments. Within enrolled conservation easements and Upland Gamebird Enhancement Program projects, Montana FWP minimum grazing standards require implementation of a 3-pasture rest-rotation grazing system (Hormay 1970). Minimum grazing standards are designed to improve rangeland condition and increase the structural heterogeneity of grassland vegetation on the landscape for the benefit of native grassland wildlife (Montana FWP 2010).

Table 1. Pastures of study, size, and number of bird survey points in eastern Montana during 2016–17.

Pasture <sup>1</sup>	Grazing System	Size (ha)	Bird Survey Points
Rest.Ro1	Rest-rotation	1,169	61
Rest.Ro2	Rest-rotation	1,107	54
Rest.Ro3	Rest-rotation	730	35
Summ.Ro1	2-Pasture Summer-rotation	550	22
Summ.Ro2	2-Pasture Summer-rotation	1,908	59
Summ.Ro3	2-Pasture Summer-rotation	277	15
Se.Long1	Season-long	856	40
Se.Long2	Season-long	413	20

<sup>1</sup> Pasture locations within the study area are displayed in Appendix A, Figure A1.

*Grazing systems descriptions* – Within the 3-pasture rest-rotation grazing systems in my study area, cattle were turned out to the first pasture in late May, moved to the

second pasture mid-August, and turned in for the season after 8 – 10 weeks; the third pasture in the system was rested from grazing. For comparison to the conservation-based rest-rotation grazing system implemented on Montana FWP's UGBEP project in eastern Montana, my study included two more commonly employed grazing systems. I surveyed 155 points on reference pastures adjacent to the UGBEP project, with 60 points located within season-long grazing systems, and 95 points within 2-pasture summer-rotation grazing systems. Season-long grazing systems in the study area allowed cattle to graze continuously from May or early June through October or mid-November. Within 2-pasture summer-rotation grazing systems in the study area, cattle were turned out to the first pasture in early June, moved to the second pasture after 6 – 8 weeks, and turned in for the season early November. The summer-rotation grazing systems in my study area stocked cattle in the same pastures each year, during approximately the same period of the summer grazing season. This is unlike typical 2-pasture deferred-rotations grazing systems, where pastures are not grazed during the same period of the summer grazing season in consecutive years.

Avian point count surveys began after all grassland bird species had arrived for the breeding season, and were completed within a 4-week period to assume breeding population closure. To avoid double counting of individuals and assure statistical independence, survey points were spaced  $\geq 300$  m apart. Points were located  $\geq 200$  m from pasture boundaries to avoid counting birds using multiple treatments,  $\geq 400$  m from oil pads, and  $\geq 250$  m from gravel roads to control for bird avoidance of these areas (Thompson et al. 2015). At each randomly generated location, grassland birds were

surveyed with three consecutive, yet independent 5-minute point count surveys. This survey method maximized observer efficiency, while simultaneously achieving population closure between survey visits, an assumption commonly required for statistical modeling of these types of data (Royle 2004, Kéry et al. 2005). A single trained observer identified and tallied all birds detected visually or aurally within 100 m of the survey point, noting the time of first detection and the distance from observer to the bird when it was first detected (0-25 m, 26-50 m, 51-75 m, 76-100 m; Ralph et al. 1993). Other data recorded included sex (dimorphic species only), vocalization, and behavior of each identified bird. At each survey location, the observer recorded the date and time, percent overcast, precipitation, temperature, and wind speed. Point count surveys were conducted from one-half hour before sunrise through no later than 0900h MST. Sunrise ranged from 0515h MST at the beginning of the survey season in mid-May to 0459h MST at the end of the survey season in mid-June. Surveys were not conducted if average wind speed exceeded 16 km/hr, or during rainfall.

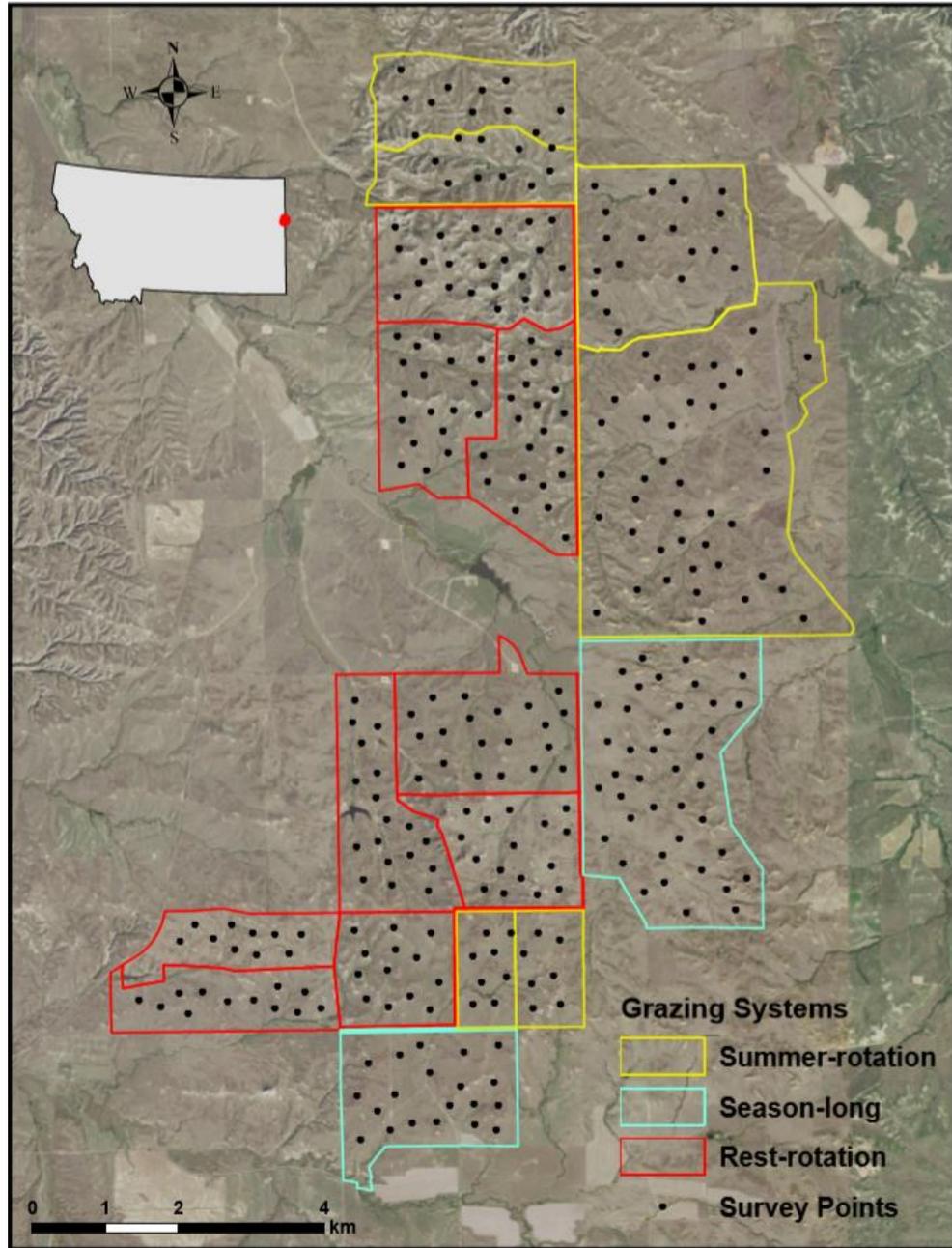


Figure 1. Study area in Richland County, Montana, and McKenzie County, North Dakota, USA during 2016–17. Avian point count survey locations within pastures on the Montana FWP Upland Gamebird Enhancement Program project managed in a rest-rotation grazing system, and on adjacent pastures managed in season-long or 2-pasture summer-rotation grazing systems.

Local vegetation conditions were measured within bird survey areas the same day point count surveys were conducted. I established three 20-m transects within 100 m of each survey point, with one transect located at the survey point and oriented in a random direction, and two transects located and oriented randomly within 100 m of the survey point. Subplots were spaced 5 m apart along each transect. At each subplot, I measured visual obstruction from the north at a distance of 2 m and a height of 0.5 m (VOR; Robel et al. 1970). At each subplot, I measured vegetation coverages using methods of Daubenmire (1959), where overlapping coverages of residual grass, litter, forb, and bare ground were recorded in one of six percentage classes (0–5, 5–25, 25–50, 50–75, 75–95, and 95–100 %). Midpoints of percentage classes were recorded for each vegetation coverage measurement. I measured heights (cm) of the nearest plant to the center of the frame for each residual grass, litter, and forb. I conducted line-intercept surveys along each of three 20-m transects to estimate shrub foliar cover (hereafter “shrubs cover”) within point count survey areas. The species of each shrub intersecting the transect was recorded, as well as the height and length of the shrub as it crossed the transect (Canfield 1941). I estimated slope at each bird survey location by averaging three measurements of slope (degrees) recorded at each of the three habitat transects within the survey area.

I used ArcMap 10.4 to digitize the wooded coulees and pasture fences within the study area using five band 1-m resolution aerial imagery from the National Agricultural Imagery Program (NAIP) developed by the U.S. Farm Service Agency (ESRI 2011, v10.4). Data was obtained from Montana State Library GIS Clearinghouse and North Dakota GIS Hub Data Portal. I intersected bird survey locations with these digitized

wooded coulee and fence layers (ESRI 2011, v10.1). I used the ArcMap ‘Calculate Geometry’ tool to estimate the area of wooded coulee within 100-m, 500-m, and 1,000-m radial areas of bird survey plots, and to estimate the total length of fences within 500-m and 1,000-m radial areas of bird survey plots to calculate fence densities (ESRI 2011, v10.1).

Rangeland managers implement grazing systems based on the expected annual vegetative production of rangelands in an average year. I quantified rangeland production potential associated with each bird survey area using Soil Survey Geographic Database (SSURGO) ecological site data from the Natural Resources Conservation Service (NRCS) Web Soil Survey (NRCS 2017). NRCS defines rangeland production as “the amount of vegetation that can be expected to grow annually in a well-managed area that is supporting the potential natural plant community” (NRCS 2017). Previous researchers have found NRCS estimates of rangeland production potential based on SSURGO ecological site data were reasonable estimates of true average rangeland productivity (Relyea et al. 2000). I calculated the weighted average rangeland production potential within 100 m of each bird survey location using the representative values (RV) of rangeland production for each ecological site type in the study area (Appendix B, Table B1), effectively accounting for point count areas which encompassed multiple ecological sites. I used the representative values of rangeland production potential, as precipitation during the years prior to field work was approximately average, and the RV’s are based on an average year’s precipitation.

I interviewed landowners to gather cattle turn-out/turn-in dates and number of head stocked to calculate stocking rates for the pastures within the study area. These dates and numbers were validated by observation of when and approximately how many cattle were present in pastures during both summer grazing seasons. I calculated stocking rates within pastures based on an animal unit month (AUM), the amount of forage, measured on a dry weight basis, to feed a 1,000-lb cow-calf pair for a 30-day period (Holechek et al. 2011). The average cow-calf pair grazing on the pastures within the study area was approximately 1,400 lbs (635 kg) based on landowner interviews, so I accounted for this in my calculation of stocking rate. Typically, stocking rates consider all pastures within a multi-pasture grazing system, resulting in a single stocking rate for the system. I calculated the stocking rates of each individual pasture within the 3-pasture rest-rotation and 2-pasture summer-rotation grazing systems because I was interested in the indirect effects of livestock grazing on grassland bird abundance and diversity through the alteration of vegetation structure by grazing livestock. Grassland bird selection of breeding territory is likely based on residual vegetation from previous growing seasons, as the majority of new growth initiates after grassland bird breeding territories have been established in the northern mixed-grass prairie. Stocking rates from the previous year's grazing season were used as a predictor of grassland bird abundance, as breeding territories have already been established within pastures prior to cattle turn-out dates in the study area (Ahlering and Merkord 2016).

## Statistical Analyses

I evaluated the effects of vegetation conditions on grassland bird abundance at the local-scale (100-m radius from the survey point) and landscape-scale (500-m and 1,000-m radius from the survey point), and rangeland production potential, stocking rate, and grazing system on grassland bird abundance at the management-level. The local- and landscape-scale habitat variables were considered for their direct effect on abundance of grassland birds through species-specific habitat use, whereas the three management-level variables were considered for their indirect effect on grassland bird abundance through the ability of livestock grazing practices to alter vegetation structure. Rangeland production potential is included in the management-level model set because range managers consider the average production potential of rangelands when implementing grazing systems or manipulating livestock stocking rates. I conducted all analyses in program R (R Core Team 2016) with use of packages ‘unmarked’ (Fiske and Chandler 2011) and ‘AICcmodavg’ (Mazerolle 2013) to identify specific effects on abundance of each focal species, where N-mixture modeling allowed for simultaneous estimation of detection probability and abundance.

The binomial N-mixture model simultaneously estimates detection probability and abundance of unmarked individuals identified during spatially replicated count data. The model assumes absence of false positive detections, and population closure, where births/deaths and emigration/immigration are equal to zero for the duration of the surveying period (Royle 2004). By conducting replicated surveys within a period of population closure, detection probability can be can be quantified, resulting in unbiased

estimates of abundance. To meet the closure assumption, I conducted repeated avian point count surveys within the same morning at each point. Additionally, meeting the assumptions of adequate spatial replication is necessary for the validation of N-mixture models (Kéry and Royle 2015). During two field seasons, I conducted 3 replicated point count surveys at 610 spatially independent sites. I measured local vegetation conditions at each of 610 bird survey location immediately following the survey during both seasons, and evaluated the effect of vegetation conditions on avian detection probabilities and local relative abundance during the same seasons point counts were conducted. This eliminated a potential year-effect among local-scale vegetation conditions within the survey area and associated local abundances of focal species.

For each covariate included in detection and abundance models, I evaluated whether a linear, quadratic, or pseudo-threshold (pseudo-asymptotic) effect (Franklin et al. 2000) was best supported for its influence on avian detection probability or abundance. I tested all covariates for multicollinearity, removing those which were highly correlated (Pearson's correlation estimate  $|r| > 0.6$ ) from analyses. Litter cover and litter depth were highly correlated. I removed litter cover and included the variable litter depth in analyses, as previous researchers have suggested that measurements of litter cover may underestimate the true amount of litter available, and litter depth is a better metric (Ricketts and Sandercock 2016). Wooded coulee edge and wooded coulee area were highly correlated at all spatial scales; I removed wooded coulee edge and included the variable wooded coulee area in analyses as some obligate grassland birds avoid wooded habitat, and some facultative grassland birds require a certain amount of wooded habitat.

Wooded coulee area at the two landscape scales (500-m and 1,000-m radius from the survey point) were correlated, as well as fence density at these two landscape scales. I evaluated which spatial scale (500-m or 1,000-m) for wooded coulee area and fence density was best supported for its influence on species-specific abundance, and included the more influential of the two spatial scales in the final landscape-scale model for each focal species.

I used stepwise model selection techniques (backward selection) to identify the factors influencing detection probability and abundance for each focal grassland bird species, where I started with a highly parameterized model and eliminated uninformative parameters based on their lack of influence on species-specific detection probabilities or abundance of focal grassland bird species (Montgomery et al. 2012, Ahlering and Merkord 2016). Most of the vegetation conditions I measured in the field have previously been shown to influence grassland bird detection probability or local abundance (Fisher and Davis 2010, Ahlering and Merkord 2016), so stepwise model selection was most appropriate in the absence of any *a priori* hypotheses. Models related to species-specific detection probabilities of grassland birds were fit prior to fitting models for local abundance.

Variables considered to influence detection probability of grassland birds were observer, year, Julian day (139 – 175), time of day, wind speed, average slope, shrub cover, and shrub height. Visual obstruction, grass coverage and height, litter depth, bare ground, and woody vegetation prevalence have previously been cited as important correlates of grassland bird abundance (Grant et al. 2004, Fisher and Davis 2010,

Thompson et al. 2014). Variables considered to influence local abundance were visual obstruction reading (VOR), standard deviation of visual obstruction readings (sdVOR), residual grass coverage, residual grass height, litter depth, bare ground coverage, shrub cover, shrub height, and wooded coulee area. I eliminated potential effects of the variables typically associated with grassland bird avoidance at the landscape-scale, such as roads, oil wells, open water, and agriculture by buffering these areas prior to establishing avian point count survey locations. As a result, only two variables were considered to influence abundance of grassland birds the landscape-scale (500-m and 1000-m), wooded coulee area and fence density.

I used Akaike's Information Criterion adjusted for finite samples ( $AIC_c$ ) to compare models and identify important variables to include in the final detection or abundance model for each grassland bird species. Supported models with large model weights ( $w_i$ ) and  $AIC_c$  values  $\leq 2$  from the best-fit model were considered parsimonious (Burnham et al. 2011). When a supported model differed from the best-fit model by a single parameter, I considered the additional parameter to be uninformative and excluded this parameter from inclusion in the final model (Arnold 2010). I built a candidate model set for the management-level effects on avian abundance based on *a priori* hypotheses, which included additive effects, along with 2- and 3-way interactions (Table 2). Factors hypothesized to affect avian abundance at the management-level were grazing system, stocking rate, and rangeland production potential.

I assessed model fit for the top model within local-, landscape-, and management-level analyses for each focal species from 1,000 simulated datasets using the

Nmix.gof.test function within R package AICcmodavg (Mazerolle 2013). Goodness-of-fit tests indicated  $\hat{c}$  estimates between 0.75 and 1.0, and p-values  $> 0.95$  for the most parsimonious models within each model set, providing evidence the models adequately fit the data. The best-fit model within local-, landscape-, and management-level analyses was then used to generate predictions of focal species abundance over the range of values for each variable, while holding other variables included in the best-fit model at their means. When multiple models shared support ( $\Delta AIC_c$  values  $\leq 2$ ), model averaged estimates were used to generate predictions of grassland bird detection probabilities and local abundance. Supported models were organized for model-averaged prediction within an unmarkedFitList using the fitList function in R package ‘unmarked’ (Fiske and Chandler 2011).

Table 2. Candidate model set for the management-level effects on avian abundance in eastern Montana during 2016–17.

<b>Model</b>	<b>Description</b>
Null	Null Model
Mod1	Grazing System
Mod2	Stocking Rate
Mod3	Rangeland Production Potential
Mod4	Grazing System + Stocking Rate
Mod5	Grazing System + Rangeland Production Potential
Mod6	Stocking Rate + Rangeland Production Potential
Mod7	Grazing System + Stocking Rate + Rangeland Production Potential
Mod8	Grazing System $\times$ Stocking Rate
Mod9	Grazing System $\times$ Rangeland Production Potential
Mod10	Rangeland Production Potential $\times$ Stocking Rate
Mod11	Grazing System $\times$ Stocking Rate + Rangeland Production Potential
Mod12	Grazing System $\times$ Rangeland Production Potential + Stocking Rate
Mod13	Grazing System $\times$ Stocking Rate $\times$ Rangeland Production Potential

## **Grassland Bird Community Composition**

I conducted a principle component analysis (PCA) of the 31 grassland-associated species detected during bird surveys (Appendix C, Table C1) to assess the effects of livestock grazing management on grassland bird community composition. Multivariate analyses allowed for the detection of patterns among many species within a community in relation to variables of interest, such as habitat metrics or treatment effects (Conner and Adkisson 1977). However, this approach does not consider heterogeneity in detection probabilities of the grassland bird species within my study area. Previous researchers have suggested that failure to account for variable detection probabilities of species among habitats may lead to biased ecological inferences (McNew and Handel 2015). I considered this potential source of bias, but assumed constant detection probability of species among treatments within my study area. Conducting multiple visits to sites increases the probability of species detection, and results in less biased estimates of species occurrence when compared to single-visit surveys. Additionally, the relatively high detection probability of grassland bird species during the breeding season and the relatively low species diversity within grassland ecosystems when compared to other ecosystems (Wiens 1973, Cody 1985, Rahmig et al. 2009) helped justify my assumption of constant detection probability of grassland bird species among treatments.

I created a matrix of presence/absence designation for all grassland-associated species at each of 610 survey sites within three livestock grazing systems. I used the principle component object created from the species matrix to plot the grassland bird community associated with each survey site relative to the three grazing systems. I

assessed grassland bird community separation among grazing systems from ellipses of 95% probability based on a normal distribution using ‘ggbiplot,’ an extension within R package ‘ggplot2’ (Vu 2011, Wickham 2016).

### **Effects of Grazing System on Local Vegetation Conditions**

To evaluate whether vegetation conditions varied among grazing treatments, I tested for significant differences ( $p < 0.05$ ) among vegetation measurements using a Kruskal-Wallis non-parametric test, as the assumptions for evaluation using a one-way ANOVA were not met for every variable.

## **RESULTS**

I conducted 1,830 point count surveys within eight pastures managed for cattle grazing: two pastures managed in season-long grazing systems, three pastures in 2-pasture summer-rotation grazing systems, and three pastures in rest-rotation grazing systems. I identified a total of 68 species during point count surveys, 31 of which were grassland-associated species (Appendix C1). I defined grassland-associated species as a “species that has become adapted to and reliant on some variety of grassland habitat for part or all of its life cycle” (Vickery et al. 1999). I selected three focal species as representative of three broader guilds of grassland birds, where ‘guild’ was defined as an assemblage of grassland bird species with overlapping niche requirements within their habitats (Root 1967). Within my study area in the northern mixed-grass prairie, the grasshopper sparrow (*Ammodramus savannarum*) was representative of the dense grass guild of grassland birds (Dechant et al. 2002b, Fritcher et al. 2004, Lipsey and Naugle 2017), the vesper sparrow (*Pooecetes gramineus*) was representative of the sparse grass

guild (Browder et al. 2002, Dechant et al. 2002a), and the western meadowlark (*Sturnella neglecta*) was representative of the generalist guild (Davis and Lanyon 2008). These three ground-nesting obligate grassland species have specific habitat requirements of native grasslands for breeding, recruitment, and survival throughout the summer grazing season (Poole 2005). These three species also had the three largest sample sizes within my study. Given these three focal species were not sexually dimorphic and the majority of detections were of vocalizing males defending breeding territory, my estimates were not of true abundance, but rather were estimates of local relative abundance. I assumed that the bias in sex-specific detection probability was consistent among treatments for the three focal species, making relative abundance an appropriate metric to assess local grassland bird populations.

### **Grasshopper Sparrow**

Grasshopper sparrows were detected at 498 (82%) of survey sites. The average ( $\pm$  SE) probability of detecting a grasshopper sparrow at my study area was  $0.819 \pm 0.008$ . The top model describing grasshopper sparrow detection probability, with full support included variables Julian day, time of day, slope, and shrub height (Appendix D, Table D1). The probability of detecting a grasshopper sparrow decreased with slope and time of day, and showed a quadratic relationship with Julian day and shrub height, where detection was maximized during the middle of the survey season (~160 Julian day) and a shrub height of ~30 cm (Appendix E, Figure E1).

After accounting for detection probability, three models shared support ( $\Delta AIC_c \leq 2.0$ ) for local-scale habitat effects on abundance of grasshopper sparrows (Appendix D,

Table D2). Models including the main effects of residual grass height, litter depth, bare ground, shrub cover, and wooded coulee area had the majority of support ( $w_i = 0.90$ ). Grasshopper sparrow abundance showed a quadratic relationship with bare ground coverage, where abundance was maximized at ~10% bare ground coverage (Figure 2). Grasshopper sparrow abundance also showed a quadratic relationship with residual grass height and litter depth, where abundance was maximized at ~15 cm and ~3 cm, respectively (Figure 2). Grasshopper sparrow abundance declined with increasing shrub cover ( $\beta = -0.10 \pm 0.04$ ), and also showed a negative pseudo-threshold (seemingly binary) relationship with proportion wooded coulee, where from 0 – 1 % wooded coulee within the point count area, abundance decreased dramatically ( $\beta = -0.34 \pm 0.04$ ; Figure 2).

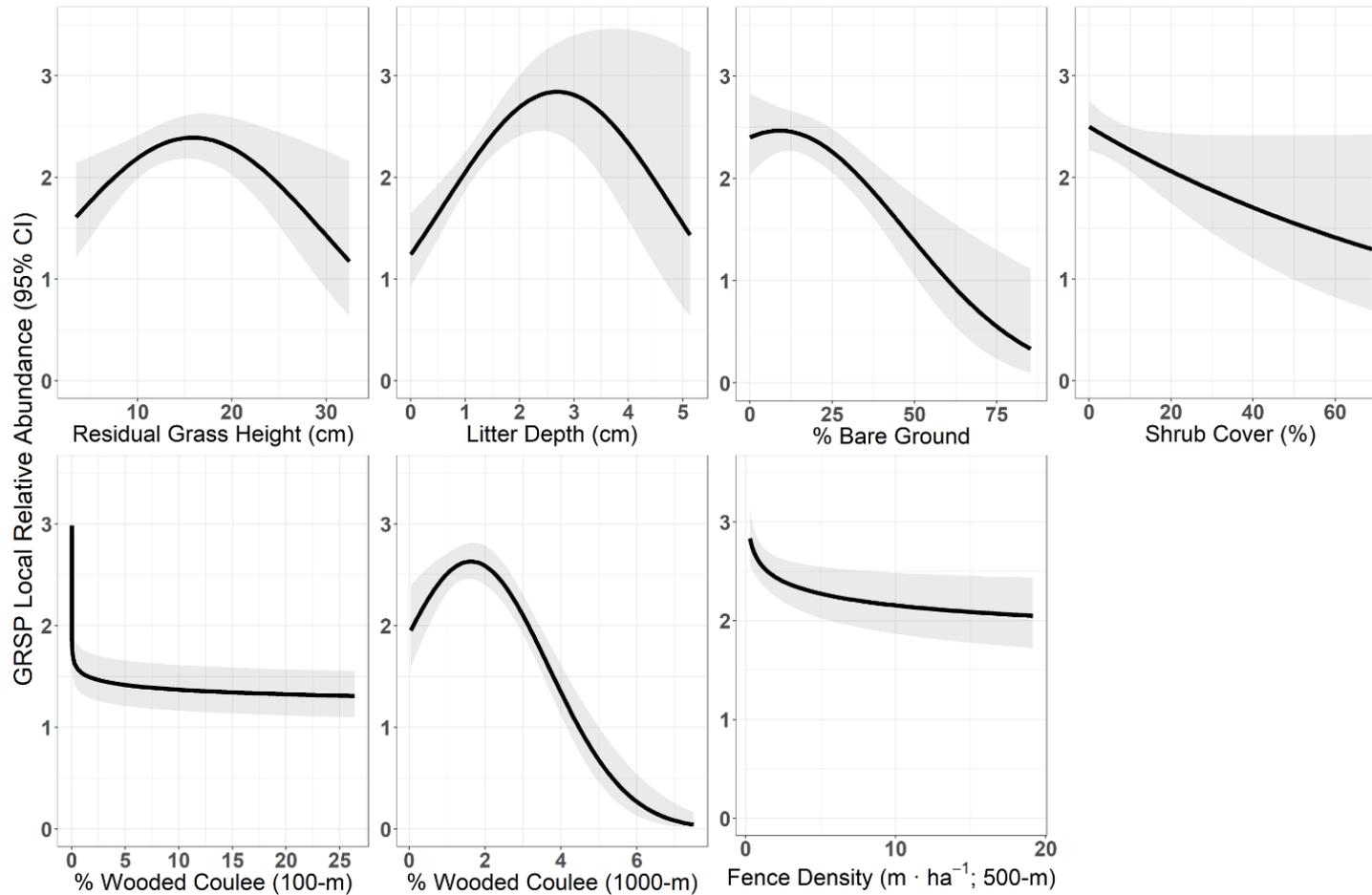


Figure 2. The top local-scale habitat model describing local abundance of grasshopper sparrows in eastern Montana during 2016–17 included support for residual grass height, litter depth, bare ground coverage, shrub cover, and wooded coulee coverage. The top landscape-scale habitat model included support for fence density within a 500-m radial area and the proportion wooded coulee within a 1,000-m radial area from the survey point.

The top landscape-scale habitat model describing grasshopper sparrow abundance included variables fence density within a 500-m radius and the proportion wooded coulee within a 1,000-m radius of survey points (Appendix D, Table D3). Grasshopper sparrow abundance showed a negative pseudo-asymptotic relationship with increasing fence density (500-m), where abundance decreased sharply from 0 to 5  $\text{m} \cdot \text{ha}^{-1}$  ( $\beta = -0.08 \pm 0.03$ ; Figure 2). Grasshopper sparrow abundance showed a quadratic relationship with increasing proportion coulee (1,000-m), where abundance was maximized at  $\sim 1.75\%$  wooded coulee, and decreased sharply beyond 2% wooded coulee at the 1,000-m scale (Figure 2).

The top management-level model for grasshopper sparrow, which had the majority of model support ( $\text{AIC}_c w_i = 0.86$ ), included an interaction between grazing system and rangeland production potential, and main effect of stocking rate (Appendix D, Table D4). Grasshopper sparrow abundance showed a positive relationship with increasing rangeland production potential in season-long grazing systems ( $\beta = 0.25 \pm 0.11$ ;  $-0.02 \pm 0.07$ ), while a quadratic relationship was supported in summer-rotation ( $\beta = 0.60 \pm 0.08$ ;  $-0.30 \pm 0.08$ ) and rest-rotation grazing systems ( $\beta = 0.38 \pm 0.05$ ;  $-0.18 \pm 0.04$ ), where abundance was maximized at intermediate production potential (Figure 3). Grasshopper sparrow abundance showed a negative relationship with increasing stocking rate ( $\beta = -0.10 \pm 0.03$ ), and the effect was similar among grazing systems (Figure 4).

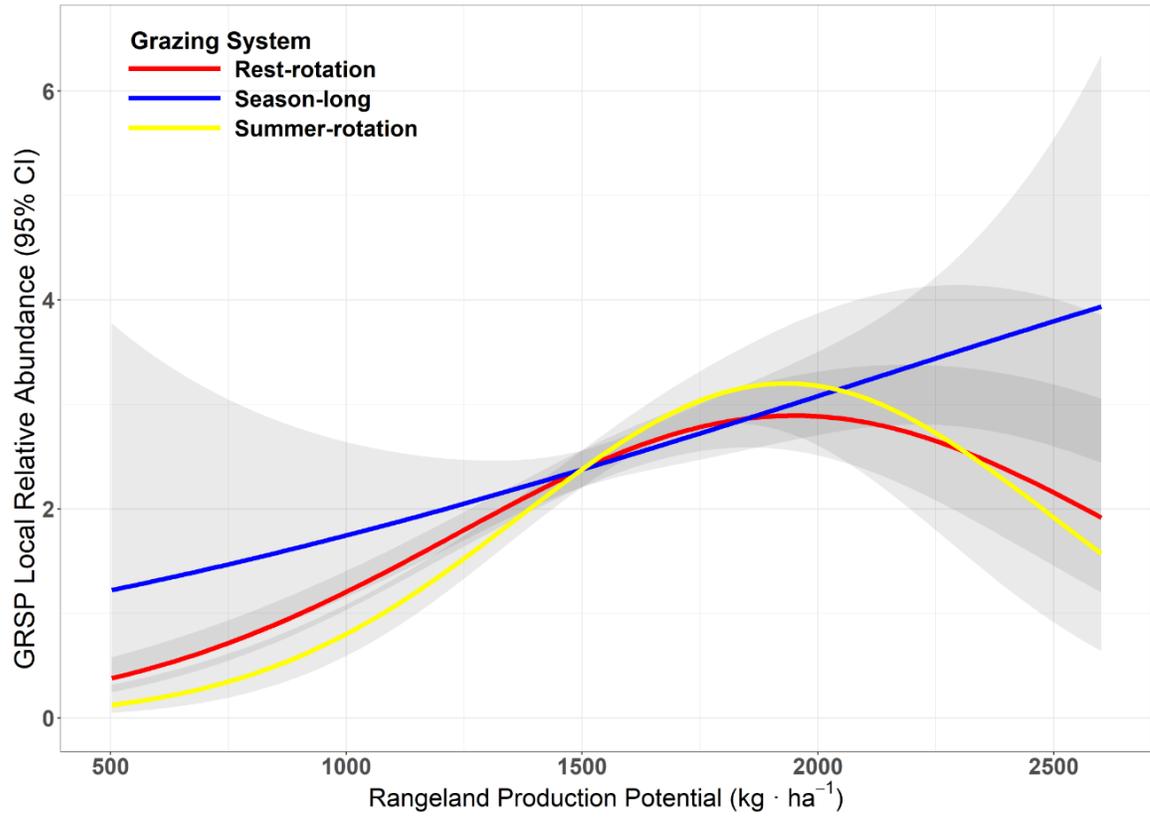


Figure 3. The top management-level model describing grasshopper sparrow abundance in eastern Montana during 2016–17 included an interaction between grazing system and rangeland production potential.

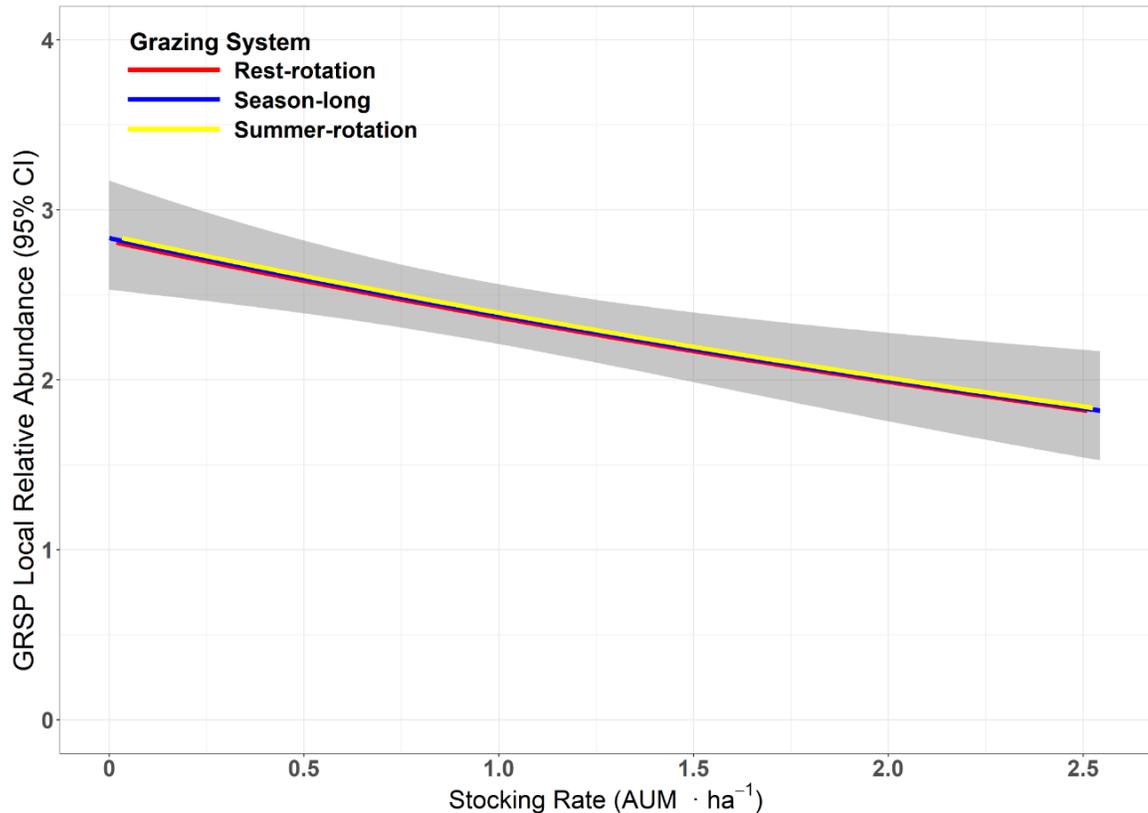


Figure 4. The top management-level model describing grasshopper sparrow abundance in eastern Montana during 2016–17 included the main effect of stocking rate.

### Vesper Sparrow

Vesper sparrows were detected at 376 (62%) of survey sites. The average ( $\pm$  SE) probability of detecting a vesper sparrow at my study area was  $0.523 \pm 0.020$ . Two models shared support ( $\Delta\text{AIC}_c \leq 2.0$ ) for effects on detection probability of vesper sparrow. The top model describing vesper sparrow detection probability included effects of year, Julian day, and wind speed (Appendix D, Table D1). An additional variable, shrub height, was supported in the next top model ( $\Delta\text{AIC}_c \leq 2.0$ ), but the 95% CI for effect size overlapped 0 and the effect was considered non-informative. Detection probabilities were higher in 2017 than 2016, decreased with wind speed, and showed a

quadratic relationship with Julian day, where vesper sparrow detection probability was highest at the beginning and end of the survey season (Appendix E, Figure E2).

After accounting for detection probability, five models shared support ( $\Delta\text{AIC}_c \leq 2.0$ ) for local-scale habitat effects on abundance of vesper sparrows (Appendix D, Table D2). Models including the main effects of visual obstruction, forb coverage, litter depth, bare ground coverage, and shrub cover had the majority of support ( $w_i = 0.68$ ). Vesper sparrow abundance showed a positive relationship with increasing bare ground coverage ( $\beta = 0.18 \pm 0.05$ ), litter depth ( $\beta = 0.11 \pm 0.05$ ), and forb coverage ( $\beta = 0.08 \pm 0.05$ ), and a negative relationship with visual obstruction ( $\beta = -0.11 \pm 0.05$ ; Figure 5, Appendix F, Table F1). Vesper sparrow abundance showed a positive pseudo-asymptotic relationship with shrub cover ( $\beta = 0.17 \pm 0.05$ ), where from 0 – 1 % shrub cover, abundance increased sharply, and beyond 1 % shrub cover the effect on abundance was similar (Figure 5, Appendix F, Table F1). Residual grass height and coverage were not included in the top model, but a model including these variables did have support ( $\Delta\text{AIC}_c < 1$ ). Vesper sparrow abundance showed a positive relationship with residual grass height ( $\beta = 0.07 \pm 0.05$ ), and a negative relationship with residual grass coverage ( $\beta = -0.07 \pm 0.06$ ).

Two models shared support ( $\Delta\text{AIC}_c \leq 2.0$ ) for landscape-scale effects on abundance of vesper sparrows. Supported variables included fence density and the amount of wooded coulee within a 1,000-m radius from survey points (Appendix D, Table D3). Vesper sparrow abundance showed a negative relationship with increasing fence density ( $\beta = -0.07 \pm 0.04$ ) and a positive pseudo-asymptotic relationship with increasing wooded coulee at the 1,000-m scale ( $\beta = 0.16 \pm 0.05$ ; Figure 5).

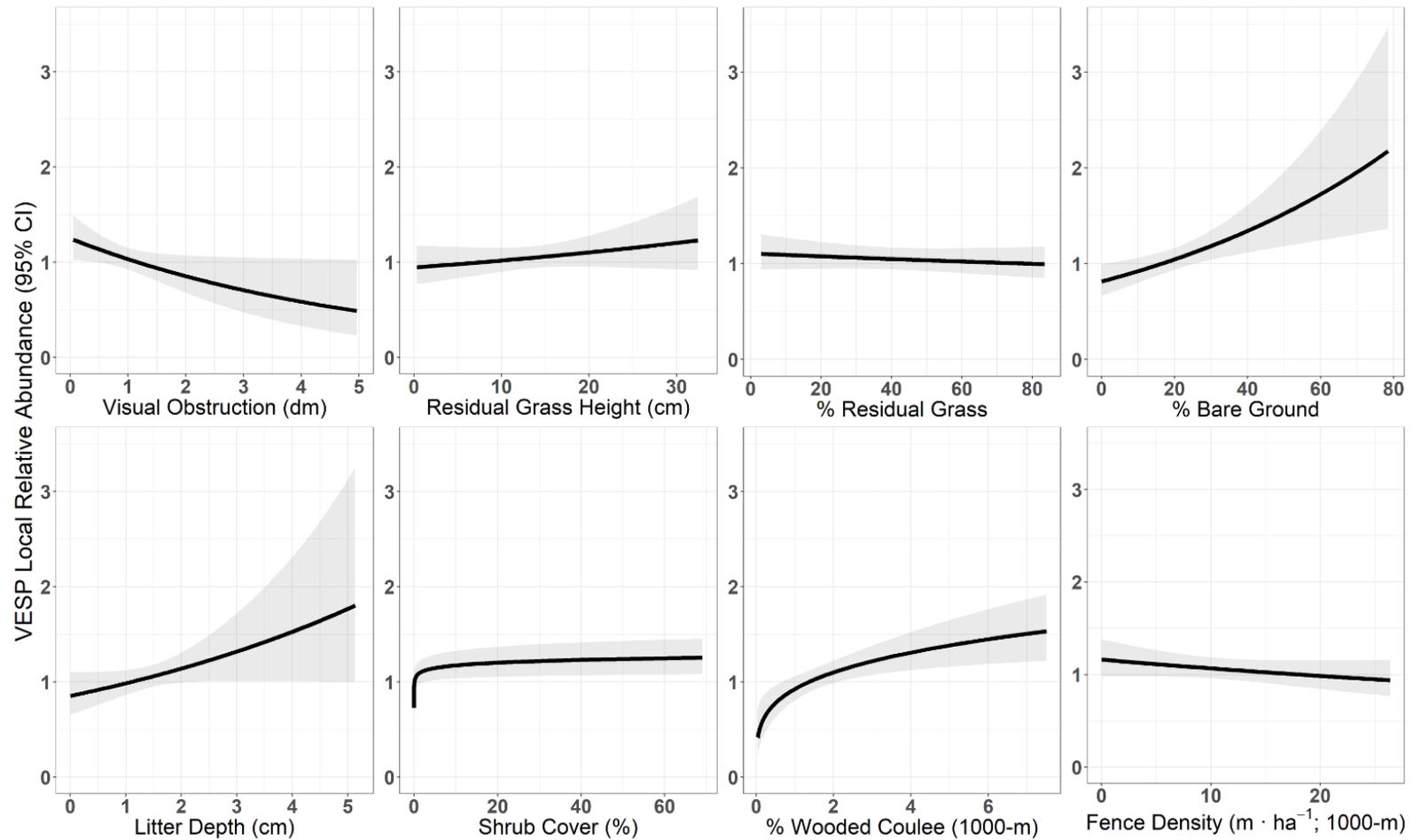


Figure 5. The top local-level habitat model describing abundance of vesper sparrow in eastern Montana during 2016–17 included support for visual obstruction, litter depth, bare ground, and shrub cover. The top landscape-scale model abundance included support for fence density and the amount of wooded coulee within a 1000-m radial area from the survey point.

Two models shared support ( $\Delta AIC_c < 2.0$ ) for management-level effects on vesper sparrow abundance (Appendix D, Table D4). The top model ( $w_i = 0.61$ ), included main effects of grazing system and rangeland production potential, and the next top model ( $w_i = 0.33$ ) included main effects of grazing system, rangeland production potential, and stocking rate. Vesper sparrow abundance was highest in summer-rotation grazing systems, followed by rest-rotation and season-long grazing systems, respectively (Figure 6, 7). Vesper sparrow abundance tended to decrease with rangeland production potential ( $\beta = -0.15 \pm 0.05$ ), and the effect was similar among grazing systems (Figure 6). The effect of stocking rate on vesper sparrow abundance is negligible ( $\beta = -0.04 \pm 0.05$ ); stocking rate appears to be an uninformative parameter.

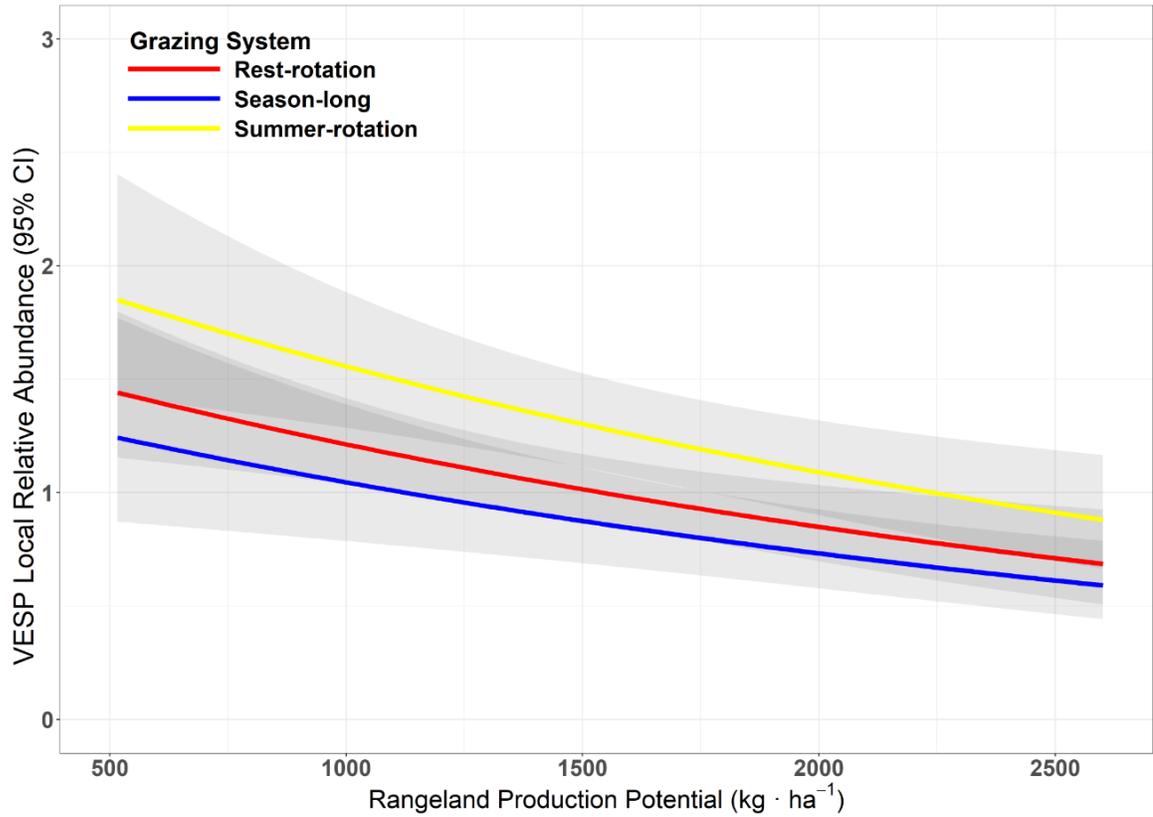


Figure 6. The top management-level model describing vesper sparrow abundance in eastern Montana during 2016–17 included main effects of grazing system and rangeland production potential.

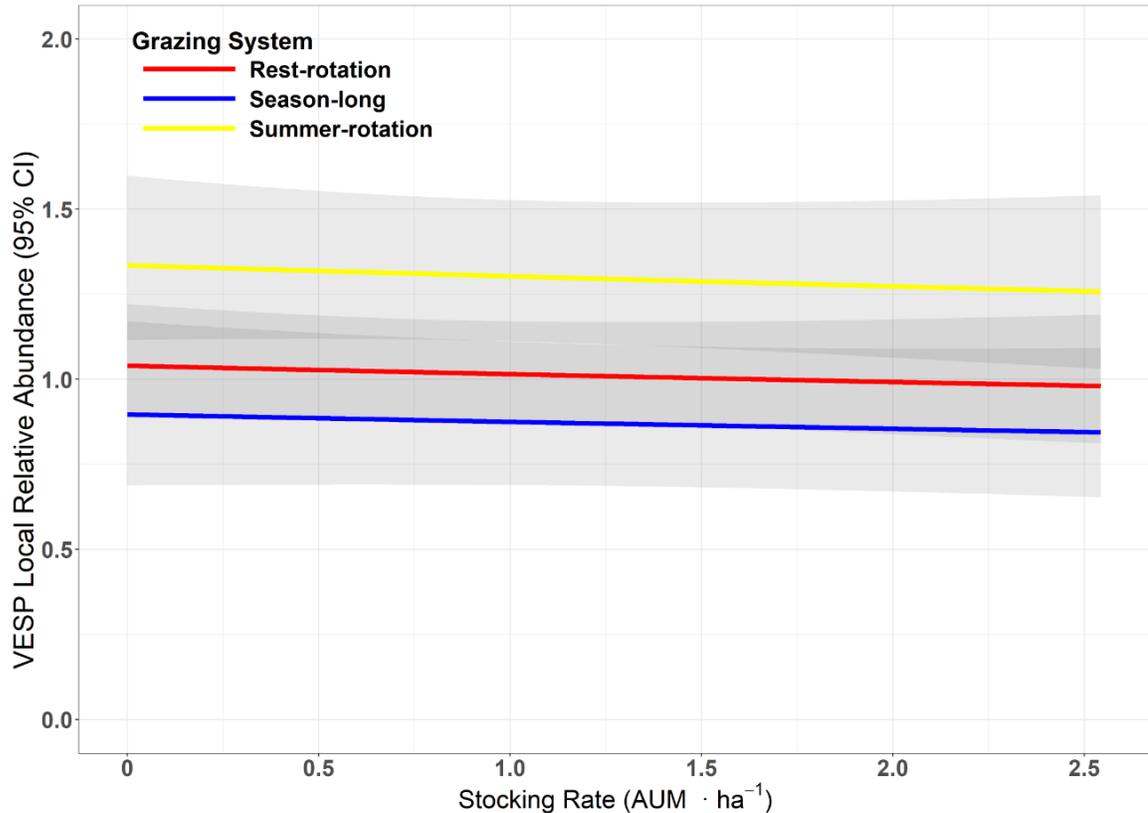


Figure 7. The next-top management-level model ( $\Delta AIC_c < 2$ ) describing vesper sparrow abundance in eastern Montana during 2016–17 included support for stocking rate, but the 95% CI for effect size overlapped 0 and the effect appears to be non-informative.

### Western Meadowlark

Western meadowlarks were detected at 554 (91%) of survey sites. The average ( $\pm$  SE) probability of detecting a western meadowlark at my study area was  $0.622 \pm 0.015$ .

Two models shared support ( $\Delta AIC_c \leq 2.0$ ) for effects on detection probability of western meadowlark. The top model describing western meadowlark detection probability included support for year, Julian day, average slope, and wind speed (Appendix D, Table D1). Wind speed was not supported in the next top model, and the 95% CI for effect size overlapped 0, indicating this variable was an uninformative parameter. Western

meadowlark detection probabilities were higher in 2017 than 2016, and decreased with increasing Julian day and slope (Appendix E, Figure E3).

After accounting for detection probability, four models shared support ( $\Delta AIC_c \leq 2.0$ ) for local-scale habitat effects on abundance of western meadowlarks (Appendix D, Table D2). Models including the main effects of visual obstruction, residual grass coverage, forb coverage, litter depth, and bare ground coverage had the majority of support ( $w_i = 0.68$ ). Western meadowlark abundance showed a negative relationship with visual obstruction ( $\beta = -0.16 \pm 0.04$ ), residual grass coverage ( $\beta = -0.11 \pm 0.04$ ), and bare ground coverage ( $\beta = -0.09 \pm 0.04$ ; Table 3, Figure 8). Western meadowlark abundance showed a positive pseudo-asymptotic relationship with increasing litter depth ( $\beta = 0.22 \pm 0.05$ ) and forb coverage ( $\beta = 0.09 \pm 0.03$ ; Table 3, Figure 8).

The top landscape-scale habitat model describing western meadowlark abundance included the main effect of wooded coulee (1000-m), where abundance responded negatively to increasing amounts of wooded coulee within 1,000-m radius of survey points ( $\beta = -0.05 \pm 0.03$ ). However, model selection results included support ( $\Delta AIC_c \leq 2.0$ ) for the null model, indicating little support for landscape-scale effects on abundance of western meadowlarks.

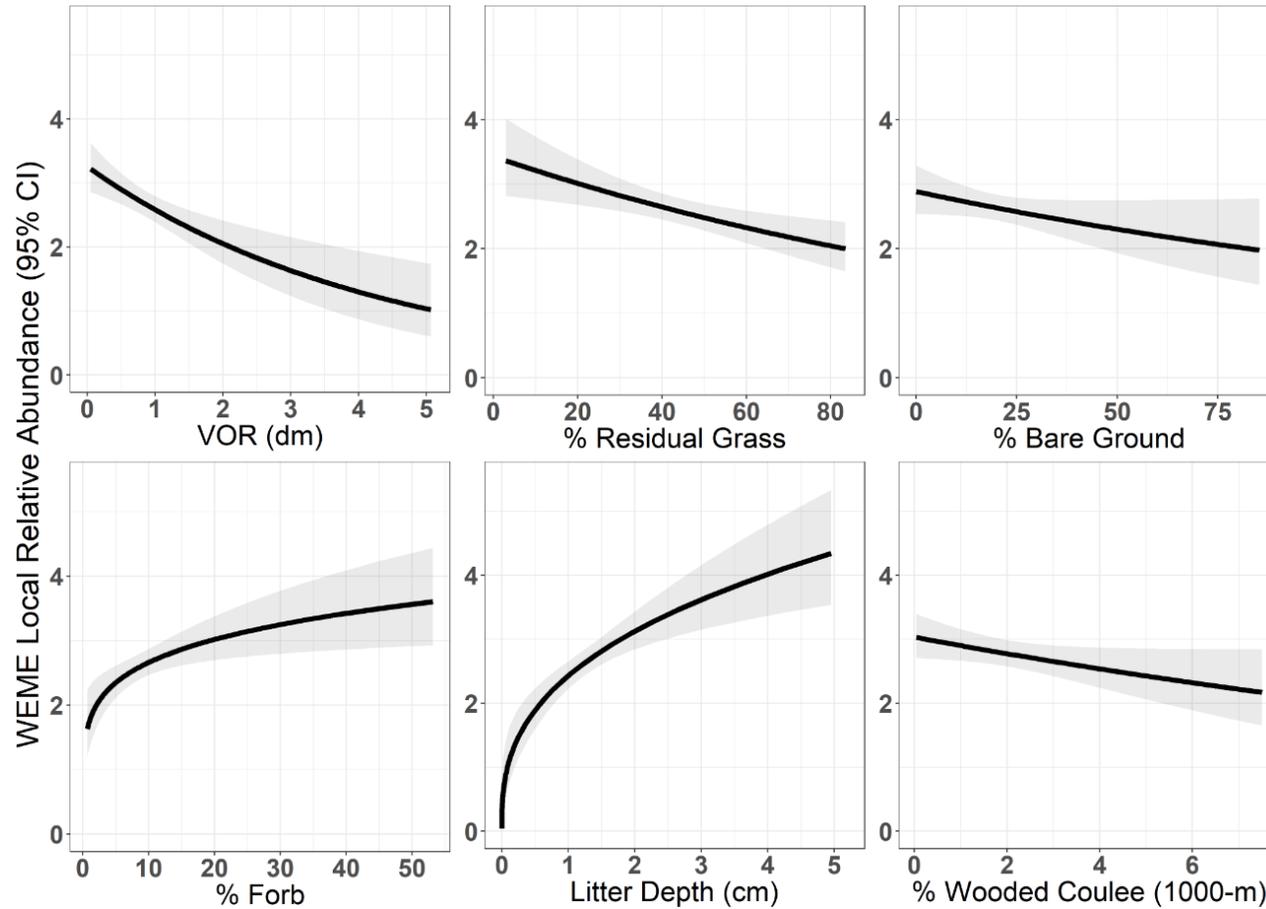


Figure 8. The top local-level habitat model describing western meadowlark abundance in eastern Montana during 2016–17 included support for visual obstruction, residual grass coverage, bare ground coverage, and forb coverage. The top landscape-scale model describing western meadowlark abundance included support for percent wooded coulee (1,000-m). Model selection results included support ( $\Delta AIC_c \leq 2.0$ ) for the null model, indicating little support for landscape-scale effects.

Two models shared support ( $\Delta AIC_c < 2.0$ ) for management-level effects on western meadowlark abundance (Appendix D, Table D4). The top model ( $w_i = 0.57$ ) included main effects of rangeland production potential and stocking rate, and the next top model ( $w_i = 0.24$ ) included an interaction between grazing system and rangeland production potential, and main effect of stocking rate. Western meadowlark abundance showed a positive pseudo-asymptotic relationship with rangeland production potential, where abundance increased with increasing production potential ( $\beta = 0.11 \pm 0.03$ ; Figure 9). Abundance of western meadowlark was highest in summer-rotation grazing systems in areas of low production potential ( $<1,000 \text{ kg} \cdot \text{ha}^{-1}$ ) and lowest in summer-rotation systems in areas of high production potential ( $>1,500 \text{ kg} \cdot \text{ha}^{-1}$ ), while the effect was similar between rest-rotation and season-long grazing systems (Figure 9). Western meadowlark abundance showed a negative pseudo-asymptotic (seemingly binary) relationship with stocking rate ( $\beta = -0.09 \pm 0.03$ ), where from 0 to  $0.1 \text{ AUM} \cdot \text{ha}^{-1}$  abundance decreased sharply, and increases in stocking rate beyond  $0.1 \text{ AUM} \cdot \text{ha}^{-1}$  did not affect western meadowlark abundance (Figure 10).

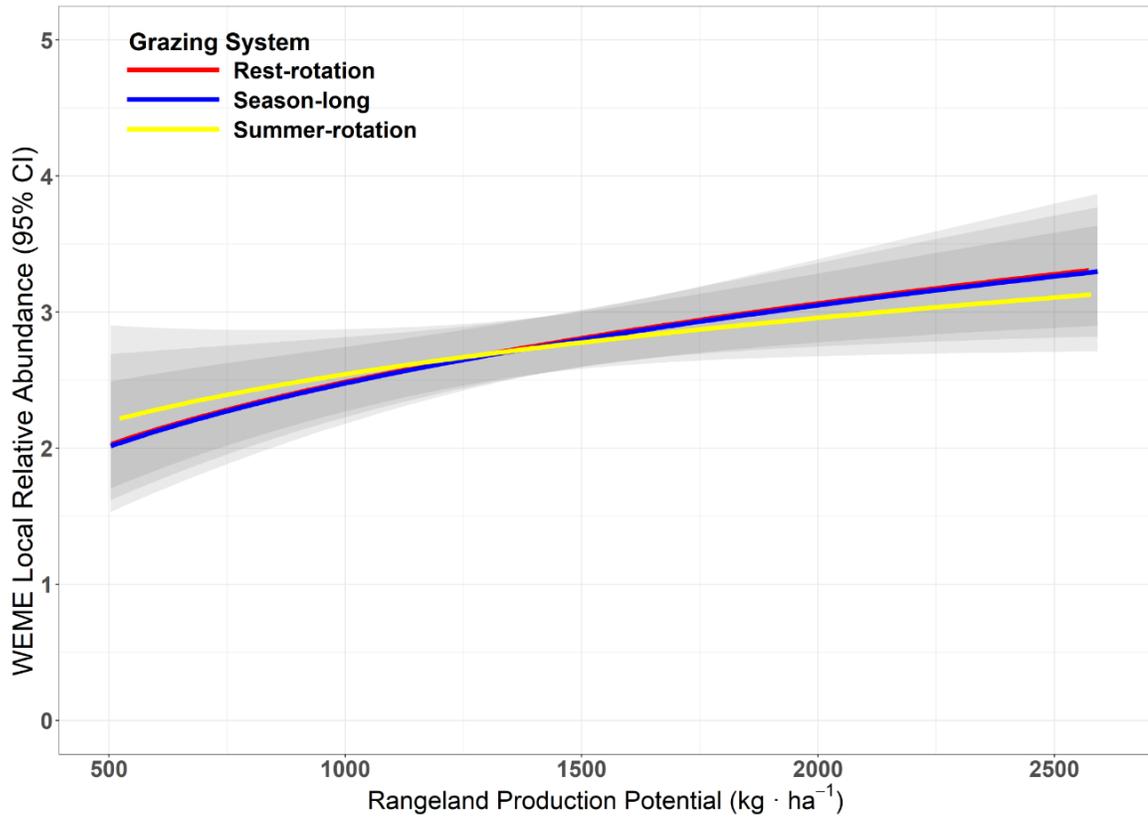


Figure 9. The top management-level model describing western meadowlark abundance in eastern Montana during 2016–17 included a main effect of rangeland production potential. The next top model ( $\Delta AIC_c < 2$ ), included support for an interaction between grazing system and rangeland production potential.

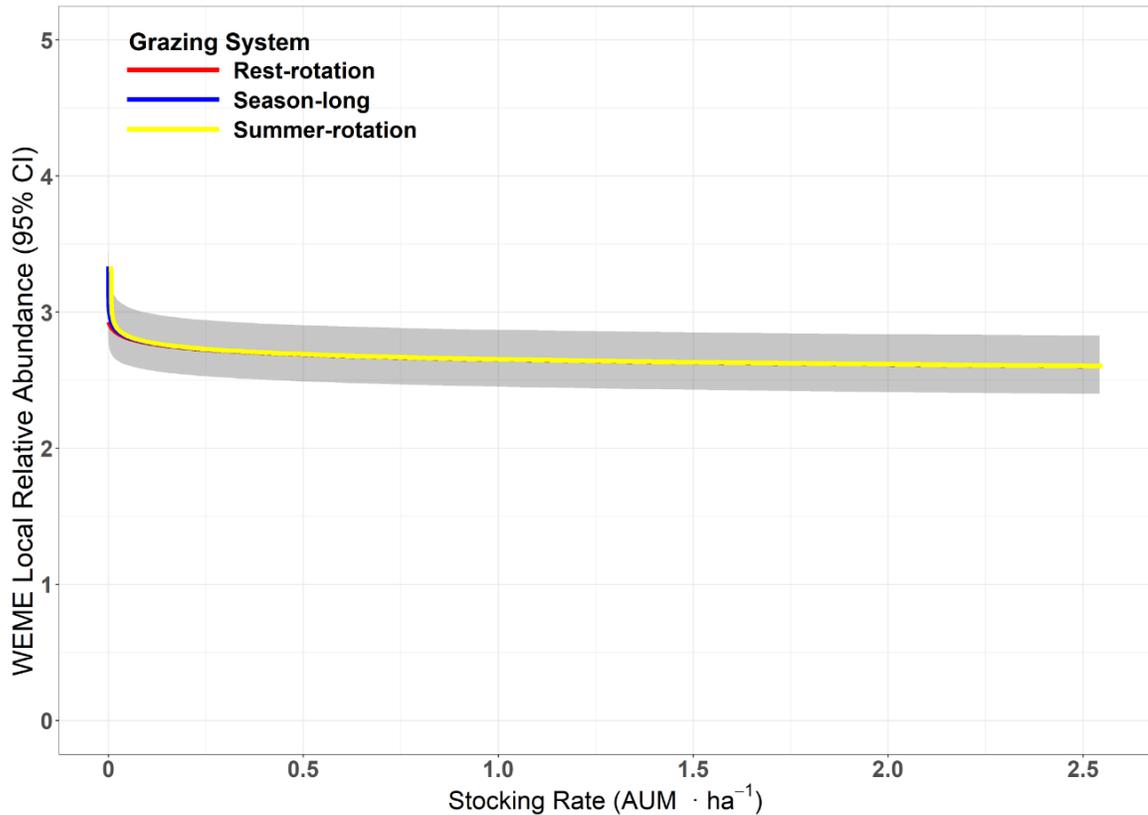


Figure 10. The top management-level model describing western meadowlark abundance in eastern Montana during 2016–17 included main effect of stocking rate.

### Grassland-Associated Species

I detected 31 grassland-associated species during point count surveys (Appendix C, Table C1), and at least one grassland bird was detected at each of 610 bird survey locations. This analysis combined all 31 grassland-associated species into one group, i.e. ‘grassland birds,’ for each visit to bird survey locations. This specific analysis is not an index of grassland bird biodiversity, but rather an evaluation of the relationships between vegetation conditions or rangeland management and the overall abundance of all grassland birds. The average ( $\pm$  SE) probability of detecting a grassland bird at my study area was  $0.622 \pm 0.015$ . Two models shared support ( $\Delta AIC_c \leq 2.0$ ) for effects on detection probability of grassland birds (Appendix D, Table D1). Models including the

main effects of year, observer, Julian day, time, wind speed, and average slope had the majority of AIC<sub>c</sub> weight ( $w_i = 0.72$ ). Detection probability of total grassland birds was higher in 2017 than 2016, and observer 1 had the highest detection probability, followed by observers 2 and 3, respectively (Appendix E, Figure E4). Grassland bird detection probabilities decreased with increasing Julian day, time of day, and slope.

After accounting for detection probability, four models shared support ( $\Delta\text{AIC}_c \leq 2.0$ ) for local-scale habitat effects on abundance of grassland birds (Appendix D, Table D2). Models including the main effects of visual obstruction, residual grass coverage, forb coverage, litter depth, and wooded coulee area had the majority of AIC<sub>c</sub> weight ( $w_i = 0.76$ ). Grassland bird abundance showed a positive relationship with forb coverage ( $\beta = 0.05 \pm 0.02$ ) and a negative relationship with visual obstruction ( $\beta = -0.05 \pm 0.02$ ) and residual grass coverage ( $\beta = -0.04 \pm 0.02$ ; Figure 11, Appendix F, Table F1). Grassland bird abundance showed a quadratic relationship with litter depth, where abundance was maximized at ~3 cm litter depth (Figure 11). Grassland bird abundance showed a positive pseudo-asymptotic relationship with wooded coulee ( $\beta = 0.04 \pm 0.02$ ), where from 0 – 1 % coulee, abundance increased sharply, and increases beyond 1 % coulee did not affect grassland bird abundance (Figure 11).

The top landscape-scale habitat model describing local abundance of all grassland birds included variables wooded coulee and fence density within a 500-m and 1,000-m radius of survey points, respectively (Appendix D, Table D3). Grassland bird abundance decreased with increasing fence density ( $\beta = -0.03 \pm 0.02$ ), and showed a positive pseudo-asymptotic relationship with wooded coulee at the 500-m scale ( $\beta = 0.03 \pm 0.02$ ).

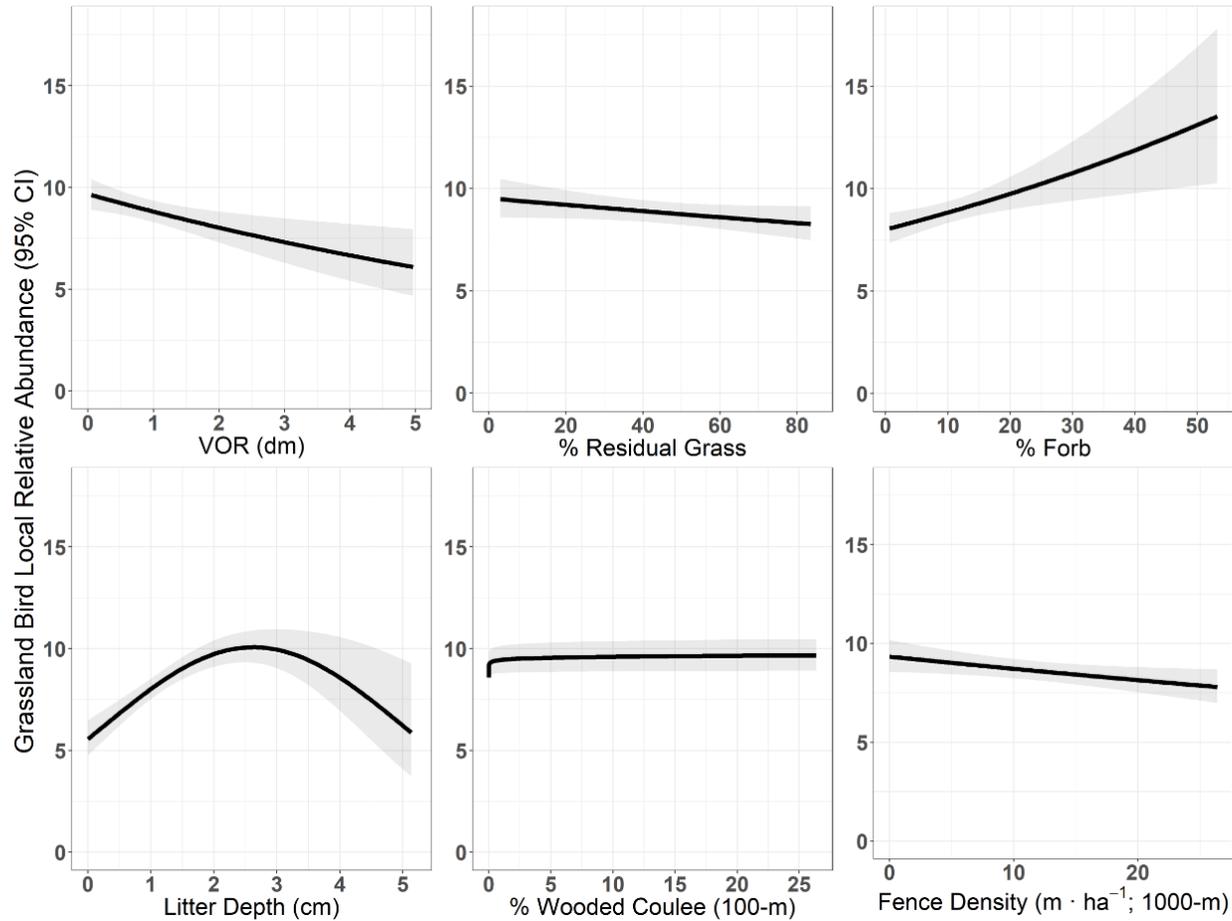


Figure 11. The top local-level habitat model describing grassland bird abundance in eastern Montana during 2016–17 included support for visual obstruction, residual grass coverage, forb coverage, litter depth, and wooded coulee (100-m). The top landscape-scale habitat model describing grassland bird abundance included support for fence density (1000-m) and percent wooded coulee (500-m), where the relationship was similar at the 100-m scale.

Three models shared support ( $\Delta AIC_c < 2.0$ ) for management-level effects on grassland-associated species abundance. The top model ( $w_i = 0.35$ ) included main effects of grazing system, stocking rate, and rangeland production potential. The next two top models included main effects of grazing system and stocking rate ( $w_i = 0.29$ ), and the main effects of stocking rate and rangeland production potential ( $w_i = 0.17$ ; Appendix D, Table D4). Grassland bird abundance was highest in summer-rotation grazing systems, followed by season-long and rest-rotation grazing systems, respectively (Figures 12, 13). Grassland bird abundance increased with increasing rangeland production potential ( $\beta = 0.03 \pm 0.02$ ), decreased with increasing stocking rates ( $\beta = -0.06 \pm 0.02$ ), and the effect was similar among grazing systems (Figures 12, 13).

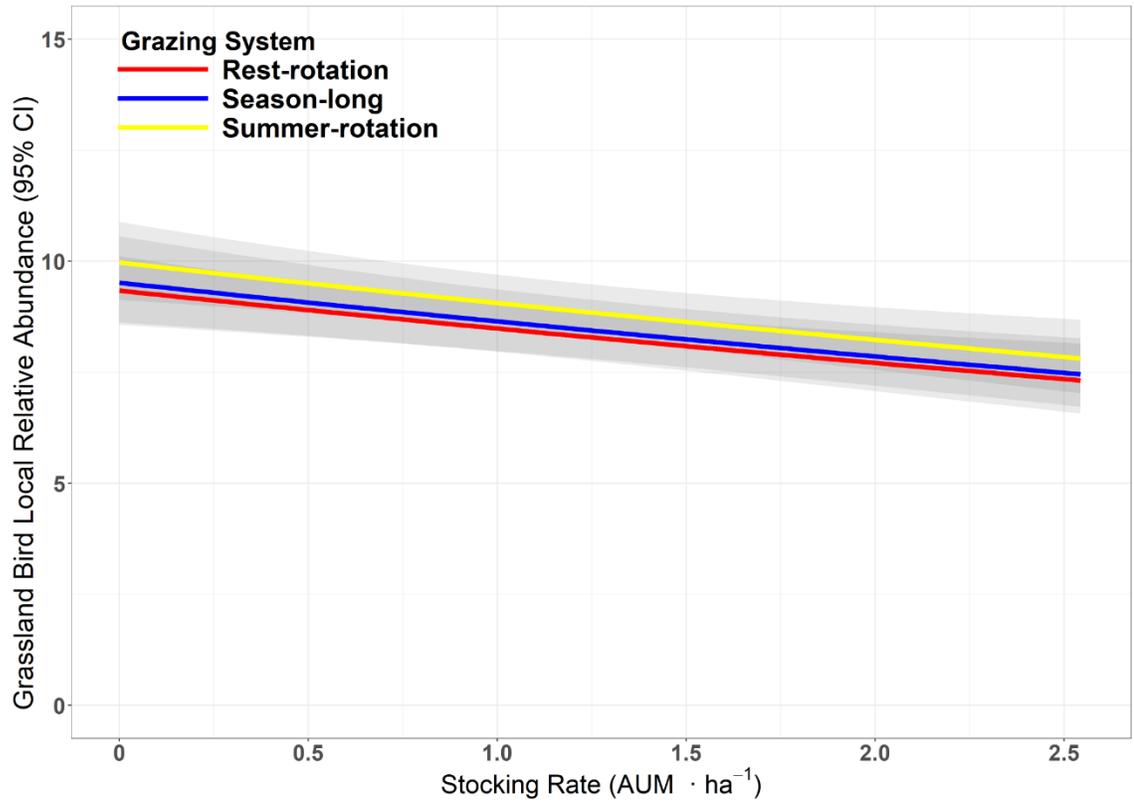


Figure 12. The top management-level model describing grassland bird abundance in eastern Montana during 2016–17 included main effects of grazing system, stocking rate, and rangeland production potential.

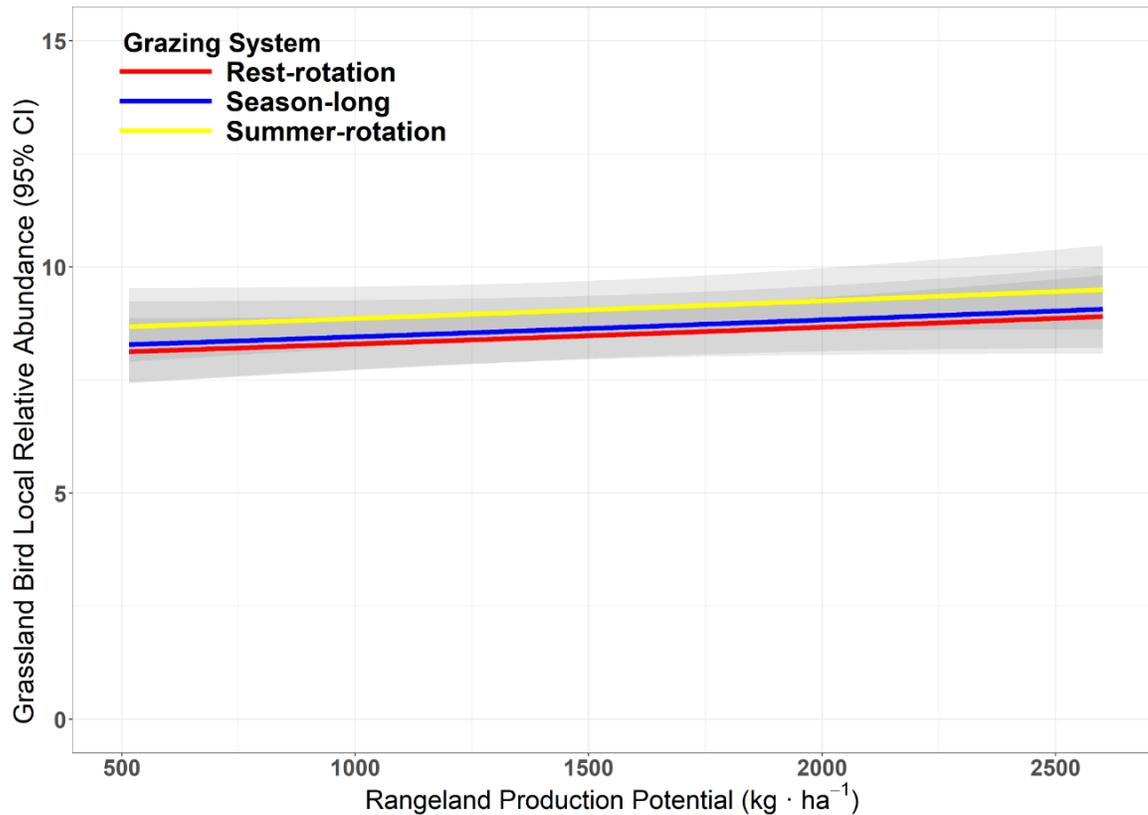


Figure 13. The top management-level model describing grassland bird abundance in eastern Montana during 2016–17 included main effects of grazing system, stocking rate, and rangeland production potential.

### Grassland Bird Community Composition

I detected 31 grassland-associated species during point count surveys within 8 pastures of 3 grazing systems (Appendix C, Table C1). I recorded 29 species in pastures employing rest-rotation grazing systems, 28 species in pastures employing summer-rotation grazing systems, and 22 species in pastures employing season-long grazing systems. I evaluated the effects of livestock grazing management on grassland bird community composition, using PCA to identify community separation among grazing systems. Grassland bird community separation among grazing systems was minimal, indicated by overlapping 95% confidence ellipses around grassland bird communities

recorded within each grazing system (Figure 14). The rest-rotation and summer-rotation grazing systems had nearly identical community composition, and I found some evidence that these two grazing systems supported a more diverse grassland bird community than season-long grazing systems (Figure 14). The PCA biplot also showed patterns of species occurrence, where occurrence of grasshopper sparrow, horned lark (*Eremophila alpestris*), upland sandpiper (*Bartramia longicauda*), bobolink (*Dolichonyx oryzivorus*), Sprague's pipit (*Anthus spragueii*), and Baird's sparrow (*Ammodramus bairdii*) was similar, but tended to be opposite of lark sparrow (*Chondestes grammacus*), field sparrow (*Spizella pusilla*), eastern kingbird (*Tyrannus tyrannus*), western kingbird (*Tyrannus verticalis*), mourning dove (*Zenaida macroura*), and chipping sparrow (*Spizella passerina*). The latter group tended to have closer association to rest-rotation and summer-rotation grazing systems, and the first group tended to have closer association to season-long grazing systems.

I also evaluated grassland bird community composition among the three treatments within the rest-rotation grazing system: grazing during the growing season (treatment A), post-growing season grazing (B), and year-long rest from grazing (C). I detected 29 grassland-associated species within pastures employing the rest-rotation grazing system; 24 species were detected in treatment A, 22 species in treatment B, and 26 species in treatment C. I found similar grassland bird community composition among the three treatments, indicated by overlapping ellipses of 95% probability around the grassland bird communities associated with each treatment (Figure 15). Similar tendencies emerged compared to those of the community analysis among grazing

systems, in terms of grassland bird species occurrence patterns. I found grasshopper sparrow, Sprague’s pipit, bobolink, horned lark, and northern harrier tended to occur at similar sites, and opposite of those sites where lark sparrow, field sparrow, western kingbird, eastern kingbird, mourning dove, and chipping sparrow occurred (Figure 15).

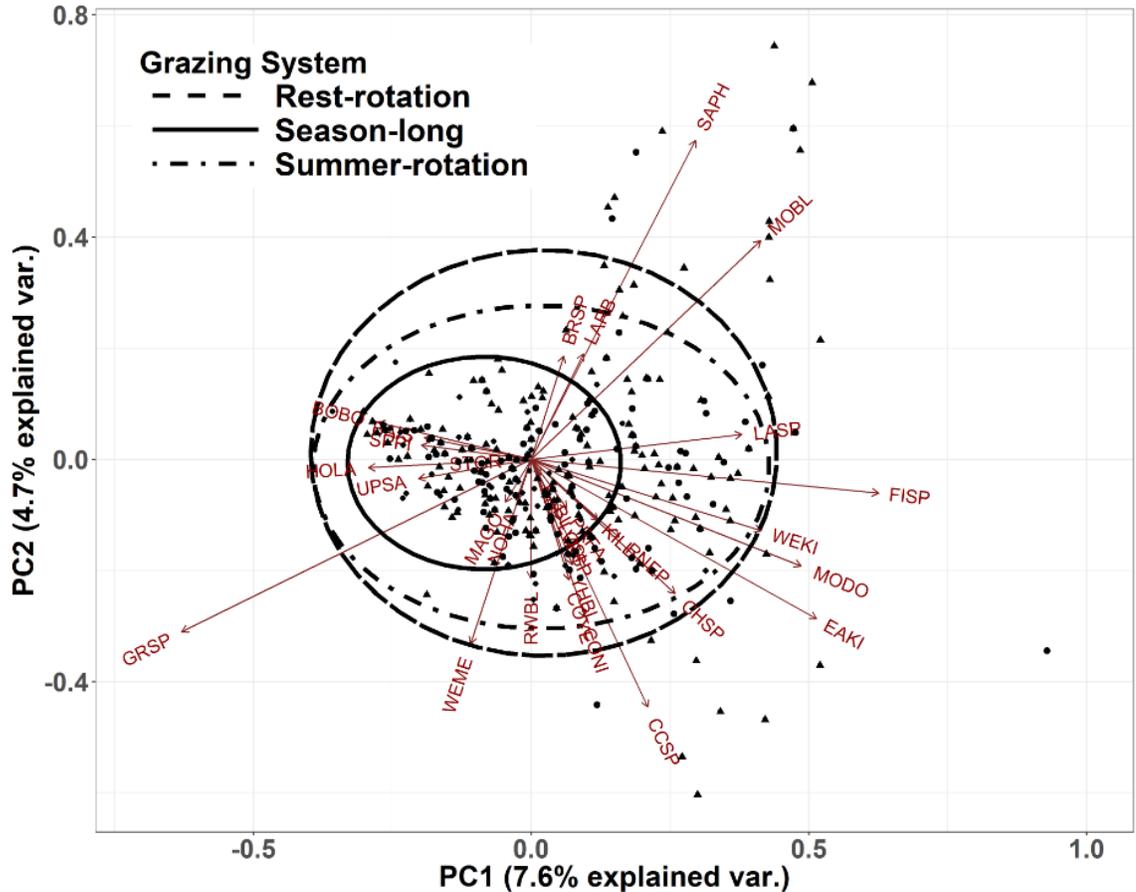


Figure 14. Grassland bird community composition among grazing systems in eastern Montana during 2016–17. Ellipses represent 95% CI around the grassland bird communities associated with each of three grazing systems. Diamonds represent sites in season-long grazing systems, circles represent sites in summer-rotation grazing systems, and triangles represents sites in rest-rotation grazing systems.

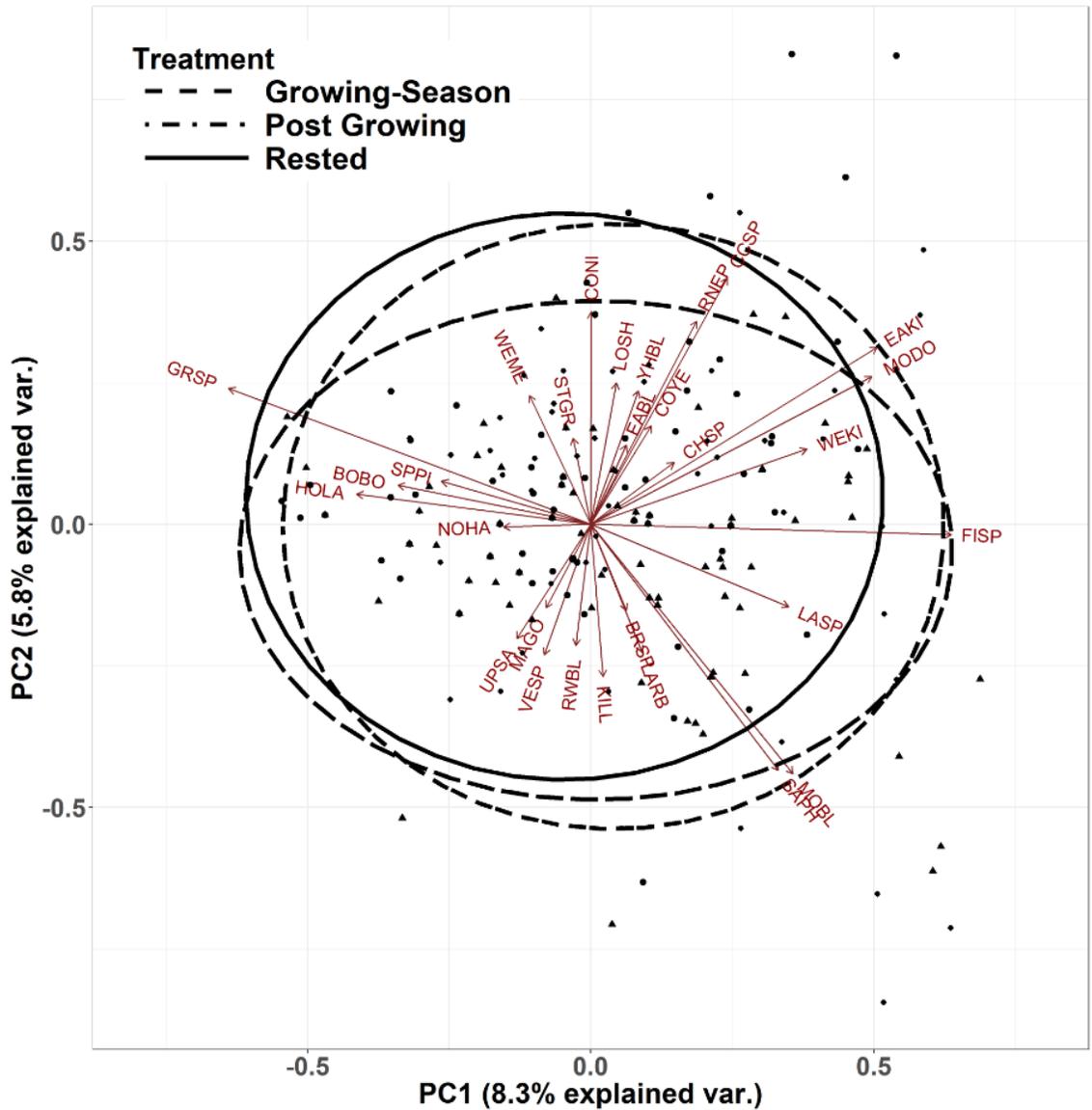


Figure 15. Grassland bird community composition among the three treatments within rest-rotation grazing systems in eastern Montana during 2016–17. Ellipses represent 95% CI around the grassland bird communities associated with each of three treatments within the rest-rotation grazing system. Triangles represent sites in the growing-season treatment, diamonds represent sites in the post growing-season treatment, and circles represent sites in rested treatments.

### Effects of Grazing System on Local Vegetation Conditions

I compared local grassland vegetation conditions within 610 avian point count survey areas among the three grazing systems. Using season-long grazing as the reference, I found a number of vegetation conditions whose means were significantly lower or higher in rest-rotation or summer-rotation grazing systems based on the Kruskal-Wallis test by ranks ( $p < 0.05$ ), and supported by non-overlapping 95% confidence intervals (Appendix G, Table G1). Overall residual grass coverage (mean  $\pm$  SE) was lower in rest-rotation systems ( $37.7 \pm 0.9\%$ ) than season-long systems ( $47.6 \pm 1.5\%$ ,  $p < 0.005$ ) and summer-rotation systems ( $42.1 \pm 1.2\%$ ,  $p < 0.005$ ). Mean litter depth was lower in rest-rotation grazing systems ( $1.3 \pm 0.04$  cm) than season-long systems ( $1.6 \pm 0.07$  cm,  $p < 0.005$ ). Mean bare ground coverage was higher in rest-rotation ( $22.4 \pm 0.8\%$ ,  $p < 0.005$ ) and summer-rotation ( $19.8 \pm 1.0\%$ ,  $p < 0.005$ ) grazing systems than season-long systems ( $15.5 \pm 1.1$ ). Mean forb coverage was higher in rest-rotation systems ( $11.0 \pm 0.3\%$ ,  $p < 0.05$ ) than summer-rotation systems ( $9.8 \pm 0.3\%$ ). Mean shrub cover and shrub height were higher in rest-rotation and summer-rotation grazing systems than season-long systems (Appendix G, Table G1). Mean percent wooded coulee on the landscape at the 100-m, 500-m, and 1000-m scales were higher in rest-rotation and summer-rotation grazing systems than season-long systems (Appendix G, Table G1).

Mean fence density ( $\text{m} \cdot \text{ha}^{-1}$ ) within 500-m and 1000-m of bird survey points was significantly higher in rest-rotation grazing systems than season-long or summer-rotation systems. Average stocking rates were lower in rest-rotation ( $0.92 \pm 0.05 \text{ AUM} \cdot \text{ha}^{-1}$ ,  $p < 0.005$ ) and summer-rotation ( $0.97 \pm 0.02 \text{ AUM} \cdot \text{ha}^{-1}$ ,  $p < 0.005$ ) systems than season-

long grazing systems ( $1.3 \pm 0.02$  AUM  $\cdot$  ha<sup>-1</sup>). Average rangeland production potential was lower in rest-rotation ( $1,372 \pm 27$  kg  $\cdot$  ha<sup>-1</sup>,  $p < 0.005$ ) and summer-rotation ( $1,518 \pm 26$  kg  $\cdot$  ha<sup>-1</sup>,  $p < 0.005$ ) grazing systems than season-long systems ( $1,789 \pm 29$  kg  $\cdot$  ha<sup>-1</sup>).

I evaluated local vegetation conditions among the three grazing treatments within the rest-rotation grazing system (growing season, post seed-ripe, and rested), based on cattle stocking from the previous year's grazing season. The grazing periods for each of these treatments are approximately June 1 – August 15 for grazing during the growing season, August 15 – November 15 for grazing after the growing season (post seed-ripe), and rest from grazing for one grazing season. Using the growing-season treatment as the reference, I found a number of vegetation conditions whose means were significantly lower or higher in post seed-ripe or rested treatments, based on the Kruskal-Wallis test by ranks ( $p < 0.05$ ), and supported by non-overlapping 95% confidence intervals (Appendix G, Table G2). Rested pastures had higher visual obstruction readings (VOR), residual grass heights, and litter depth than pastures grazed during the growing season or post seed-ripe (Appendix G, Table G2). Rested pastures had lower bare ground coverage ( $18.3 \pm 1.2\%$ ) than pastures grazed during the growing season ( $24.7 \pm 1.5\%$ ,  $p < 0.005$ ) or post seed-ripe ( $24.2 \pm 1.4\%$ ,  $p < 0.005$ ). Pastures grazed post seed-ripe had lower residual grass coverage ( $32.5 \pm 1.3\%$ ) than pastures grazed during the growing season ( $40.3 \pm 1.9\%$ ,  $p < 0.005$ ) or pastures rested from grazing ( $39.9 \pm 1.5\%$ ,  $p < 0.005$ ). Rested pastures had higher average rangeland production potential than grazed pastures ( $p < 0.005$ ), which may have accounted for some of the effects I found in local vegetation conditions in these pastures compared to grazed pastures.

## DISCUSSION

Grassland birds have displayed guild-specific (dense-grass vs. sparse-grass) habitat selection along gradients of low to high rangeland productivity at the landscape scale (Lipseley and Naugle 2017). Researchers have suggested that in wet years, sparse-grass species will tend to select areas of lower rangeland productivity, and that higher livestock grazing intensity in these years may help create desirable habitat for the sparse-grass guild. Contrarily, in dry years, dense-grass species will tend to select areas of higher rangeland productivity, and lower grazing intensity in these years may help create desirable habitat for the dense-grass guild (Lipseley and Naugle 2017). I evaluated the response of grassland birds to rangeland production potential in the context of both livestock grazing systems and stocking rates in eastern Montana, during two years of nearly average precipitation. The wide range of annual rangeland production potential among pastures within my study area made this an ideal site to evaluate the effects of rangeland production potential on abundance of grassland birds.

Results from my analyses indicated relationships between the relative local abundances of three grassland obligate bird species and three management-scale variables: grazing system, stocking rate, and rangeland production potential. The effect of rangeland production potential on the local abundance of grasshopper sparrow and western meadowlark depended upon the specific livestock grazing system. The ability of an ecological site to produce the vegetation structure required by a specific species or guild of grassland birds varies annually depending upon soil moisture (Lipseley and Naugle 2017). Even during average years, my results indicate that the response of grassland birds

to grazing system may not be similar across areas of variable rangeland production potential within grassland ecosystems, and the effects of grazing system on grassland bird ecology may be mediated by rangeland production. These findings suggest that inconsistencies within published literature reporting effects of livestock grazing systems on the ecology of grassland birds, even within a single prairie ecosystem (i.e., northern mixed-grass prairie; Messmer 1990, Buskness et al. 2001, Ranellucci et al. 2012, Davis et al. 2014) may be due to the influence of variable rangeland productivity or other mediating factors among study sites.

The typical range management goals of rotational grazing systems are even distribution and consistent forage utilization among pastures, and the implementation of this type of rotational system has been suggested to work at cross-purposes with wildlife conservation goals of increasing structural heterogeneity within rangelands (Toombs and Roberts 2009). The effect of grazing system was supported for each of three obligate grassland birds. Abundance of grasshopper sparrow, representing the dense-grass guild, was generally highest in season-long grazing systems. Abundance of vesper sparrow, representing the sparse-grass guild, was highest in summer-rotation grazing systems. The main effect of grazing system was also supported in the most parsimonious model for all grassland-associated species combined, and predicted abundance was highest in summer-rotation grazing systems. These results are inconsistent with my hypothesis that grassland birds will generally benefit from rest-rotation grazing, a system that conceptually creates patch-heterogeneity on the landscape when compared to the two more commonly employed grazing systems in my study area. Additionally, my analysis of grassland bird

community composition among the three grazing systems showed that summer-rotation and rest-rotation grazing systems had nearly identical apparent species diversity and community composition. The diversity of grassland birds was also similar among the three treatments (grazing during the growing-season, grazing post seed-ripe, and rested from grazing) within the rest-rotation grazing system, with no guild-specific distinction among treatments. Overall, I did not find support for a noticeable benefit of rest-rotation grazing on abundance or diversity of grassland birds relative to two more commonly employed grazing systems, season-long and summer-rotation grazing, in mixed-grass prairie rangelands of northeastern Montana.

There are a number of potential explanations for my results at the management-level, the most probable being 1) the rest-rotation grazing system did not create patch-heterogeneity in vegetation structure on the rangeland, 2) the rest-rotation grazing system created patch-heterogeneity, but not at the scale required by grassland birds at my study area, 3) the response of grassland birds to patch-heterogeneity at my study area is conditional upon precipitation, and was not apparent during 2 years of average conditions, 4) grassland birds at my study area do not select for patch-heterogeneity, but rather require small-scale, within-pasture heterogeneity, or 5) grassland birds at my study area do not require structural heterogeneity within their habitats. My evaluation of local vegetation conditions among pasture types within the rest-rotation grazing system found that the system did create patch-size heterogeneity in rangeland vegetation structure among treatments, as conceptualized by previous researchers (Hagen et al. 2004, With et al. 2008, Toombs et al. 2010). Pastures rested from livestock grazing the previous year

had significantly ( $p < 0.05$ ) higher visual obstruction, residual grass height, and litter depth, and significantly lower bare ground than the two grazed treatments, and the post-seed ripe grazing treatment had significantly lower residual grass coverage than the other two treatments.

Because the rest-rotation grazing system created patch-heterogeneity in vegetation structure, the level of heterogeneity or the scale at which it occurred may not have been that required by the suite of grassland birds occupying my study area. Despite patch-heterogeneity, overall residual grass coverage and height, and litter depth were lower, and bare ground coverage was higher in rest-rotation grazing systems than season-long or summer-rotation grazing systems. Additionally, my analysis of the vegetation conditions associated with only the rested treatment within the rest-rotation system showed that this system fell short of a major objective; it failed to create patches of dense-grass habitat compared to vegetation conditions created by adjacent season-long or summer-rotation grazing systems. While the rested treatment within the rest-rotation grazing system did have taller residual grass height on average, residual grass coverage was higher and bare ground coverage was lower in season-long and summer-rotation grazing systems than the rested treatment within rest-rotation grazing systems, and average litter depth between the rested treatment of rest-rotation systems and season-long grazing systems was similar. As a result, the only patches of structurally distinct vegetation that the rest-rotation grazing system may have created compared to the other grazing systems within my study area were patches of sparse-grass vegetation structure, characterized by low residual grass height and density, low litter depth, and high bare ground coverage. The mean stocking

rate within growing-season treatments was  $1.36 \text{ AUM} \cdot \text{ha}^{-1}$ , and within post growing-season treatments was  $1.46 \text{ AUM} \cdot \text{ha}^{-1}$ . A year of rest from grazing may not be adequate to overcome the impact of higher stocking rates the previous two years within grazed treatments, in terms of producing dense-grass vegetation structure for grassland birds at the patch-scale.

Assuming breeding season abundances of grassland birds within contiguous native grasslands of the northern mixed-grass prairie are reliable indicators of habitat quality (Bock and Jones 2004), my evaluation of local vegetation conditions among the three grazing systems showed that season-long systems created relatively higher habitat quality for dense-grass species, and rest-rotation grazing systems created relatively higher quality habitat for sparse-grass species. The relationship between grazing system and predicted abundance of the dense-grass representative, the grasshopper sparrow, was not similar among grazing systems, but rather depended upon rangeland production potential. Local relative abundance of grasshopper sparrow was highest in summer-rotational grazing systems in areas of moderate rangeland production potential ( $1,500 - 2,000 \text{ kg} \cdot \text{ha}^{-1}$ ), but in areas of lower ( $<1,250 \text{ kg} \cdot \text{ha}^{-1}$ ) and higher ( $>2,200 \text{ kg} \cdot \text{ha}^{-1}$ ) production potential, season-long grazing systems tended to support greater abundances of grasshopper sparrow. Local abundance of the sparse-grass representative, the vesper sparrow, was highest in summer-rotation grazing systems, followed by rest-rotation and season-long grazing systems, respectively. This result is unexpected based on my evaluation of vegetation conditions among grazing systems, as rest-rotation grazing appeared to create the shortest, sparsest vegetation among the three grazing systems.

However, abundance of vesper sparrows decreased with rangeland production potential, possibly indicating that within the sparse-grass guild, habitat selection may be more closely tied to specific conditions within regions of lower rangeland productivity than to the vegetation structure created by grazing systems. Additionally, two true sparse-grass representatives, chestnut-collared longspur (*Calcarius ornatus*) and McCown's longspur (*Rhynchophanes mccownii*), were not present within my study area during two seasons of intensive surveying. Based on my habitat evaluation among grazing systems, the rest-rotation grazing system may have created the most ideal longspur vegetation structure of the grazing systems in my study, and recent research in a grassland-sagebrush ecosystem of central Montana observed positive associations between McCown's longspur abundance and rest-rotation grazing systems (Golding and Dreitz 2017). If rangeland productivity is the main driver of habitat selection within the sparse-grass guild of grassland birds, rest-rotation grazing within an area of highly variable rangeland production potential, such as that found within my study area, may not provide suitable habitat at the appropriate scale for this guild of grassland birds.

The scale at which grassland birds require heterogeneity within their breeding habitats is generally inconsistent in the literature (Wiens 1997, Derner et al. 2009, Hovick et al. 2015). Small scale, within-pasture heterogeneity is often a product of selective foraging by grazing livestock, especially when stocking rates are low to moderate and livestock are allowed to graze season-long, resulting in pastures that have areas of light and heavily grazed vegetation (Coughenour 1991, Bailey et al. 1998, Fuhlendorf and Engle 2001, Joseph et al. 2003, Bailey 2005). Within most pastures, areas near water

sources and areas with highly palatable or higher quality forage will experience heavy grazing, and areas far from water sources or with less palatable forage will experience less intensive grazing (Hormay 1970, Coughenour 1991, Stuth 1991, Hart et al. 1993). In larger pastures, livestock will not always occupy the entire area, but rather move around on the landscape and create small-scale heterogeneity within the pasture (Coughenour 1991). My results are consistent with previous work that suggest within-pasture heterogeneity created by selectively foraging livestock may create vegetation structure at the appropriate scale required by ground-nesting grassland birds in the northern mixed-grass prairie (Lusk and Koper 2013).

Fuhlendorf and Engle (2001) suggest that the small-scale heterogeneity created by moderate intensity, continuous grazing may not produce adequate spatial heterogeneity to fulfill the diverse requirements of grassland bird species that occupy rangelands. Rather, more intensive grazing systems that develop larger areas of structurally similar vegetation should be employed to create large-scale, patch-heterogeneity. Although the rest-rotation grazing system seemed to create patch-size heterogeneity among treatments, I did not find evidence supporting its benefit to grassland birds over season-long grazing or summer-rotation grazing systems, in terms of obligate grassland bird abundance or grassland bird community composition within my study area during years of average precipitation conditions. My results may differ from previous work because much of the research supporting intensive management for the restoration of patch-heterogeneity in herbaceous vegetation structure has come from tallgrass prairie ecosystems (Fuhlendorf et al. 2006, Hovick et al. 2015). Additionally, the tallgrass prairie inherently has the

lowest heterogeneity in herbaceous vegetation structure in the absence of disturbance due to higher precipitation and rangeland productivity, while the mixed-grass prairies inherently have greater heterogeneity in the absence of disturbance due to greater environmental variability (Wiens 1974). Although many ecological effects among grassland systems at the regional scale are not directly comparable, my results suggest that researchers in all prairie ecosystems should consider local variation in rangeland productivity, along with other potential factors that may mediate the effects of grazing management on grassland bird ecology.

Unlike recent research from more productive tallgrass prairie ecosystems (Ahlering and Merkord 2016), I did not find a positive relationship between local abundance and stocking rate for three focal obligate grassland birds or for all grassland-associated species combined. The effect of increasing stocking rates on local abundance of grasshopper sparrow, western meadowlark, and overall grassland bird abundance was negative, while vesper sparrow abundance was unrelated to variation in stocking rates at the specific stocking rates used within my study. Additionally, the effect of stocking rate on abundance of grassland birds was consistent across grazing systems. The consistently negative response of grasshopper sparrow to increasing stocking rates, coupled with the quadratic response of this species to residual grass height and litter depth and negative relationship with bare ground coverage, supports previous research and suggests that suitable habitat is available for the dense-grass guild under light intensities of livestock grazing in the northern mixed-grass prairie (Bock et al. 1993, Sutter et al. 1995, Lusk and Koper 2013). These results contradict those from studies in more productive grassland

ecosystems, where grazing or other disturbance is required to create suitable habitat for all guilds of obligate bird species, from sparse-grass to dense-grass (Temple et al. 1999, Rahmig et al. 2009, Ahlering and Merkord 2016).

Typically classified as a generalist, the western meadowlark actually displayed strong selection for a number of specific habitat metrics within my study area, where vegetation conditions at the ground level appear to be more important than vertical cover. Local abundance of western meadowlark showed a positive pseudo-asymptotic relationship with forb coverage and litter depth, where abundance was highest at maximum forb coverage and litter depth, and abundance showed a negative linear relationship with increasing bare ground, visual obstruction, and residual grass coverage. Grassland-associated birds in my study area generally selected areas with higher forb coverage, moderate litter depth, and lower visual obstruction and residual grass coverage. Several species of grassland birds have exhibited negative responses to edge effects within prairie ecosystems, of which include avoidance of edges and/or lower nesting success near edges, often a result of either higher rates of predation along edges or higher rates of brood parasitism by brown-headed cowbirds in these areas (Johnson and Temple 1990, Winter et al. 2000, Patten et al. 2006). My study site was located in a landscape of contiguous native prairie, and my study design allowed for control of potential edges through the exclusion of water features, gravel or paved roads, and oil wells, to each of which grassland birds have shown avoidance (Sliwinski and Koper 2012, Thompson et al. 2015). Only two landscape-scale variables, wooded coulee and fence density, were associated with abundance of grassland birds within my study area. Wooded coulees

make up a small component of my study area, but still cause abrupt changes from grassland habitat to woodland features, and being the only edge-type habitat present, may have similar ecological effects of edges in more fragmented prairie habitats where these effects have been well-studied (Johnson and Temple 1990, Winter et al. 2000). This implication was supported for grasshopper sparrow and western meadowlark, which generally showed a negative relationship to increasing amounts of wooded coulee at the landscape scale.

Grasshopper sparrow, vesper sparrow, and all grassland-associated species showed a consistent negative relationship with increasing fence density on the landscape, while western meadowlark showed no response. Fences may be perceived as edge habitat within these contiguous rangelands, as fencelines are often associated with stark changes in vegetation structure among pastures. Fence density (500-m spatial scale) was highest in rest-rotation grazing systems ( $10.5 \pm 0.4 \text{ m} \cdot \text{ha}^{-1}$ ), followed by summer-rotation ( $8.3 \pm 0.5 \text{ m} \cdot \text{ha}^{-1}$ ), and season-long ( $6.3 \pm 0.6 \text{ m} \cdot \text{ha}^{-1}$ ), respectively. Intensive grazing systems such as rest-rotation or short-duration systems, which divide large pastures into multiple smaller pastures and establish greater amounts of fence on rangeland landscapes may negatively impact grassland bird use based on these subtle edge effects. Additionally, if areas near fencelines function to increase predator use (Pedlar et al. 1997), grassland birds may be reducing perceived predation risk by avoiding areas in close proximity to fences.

My research is the first in the northern mixed-grass prairie to evaluate the effects of both livestock grazing systems and stocking rates on the ecology of grassland birds in

the context of variable rangeland production potential. I found species-specific responses to livestock grazing differ even at small spatial extents, and may be mediated by rangeland productivity. Thus, regional or distribution-wide guidelines for livestock grazing management are inappropriate. In productive tallgrass prairies of southeastern North Dakota, Ahlering and Merkord (2016) found a positive relationship between grasshopper sparrow abundance and grazing intensity, where abundance was maximized at some of the highest grazing intensities within study pastures. In contrast, my results from less productive mixed-grass prairies of North Dakota and Montana indicate that grasshopper sparrows respond negatively to increasing stocking rates. These regional variations in grassland bird response to grazing provides evidence for conservation agencies to implement grazing management at the local scale.

Future research should consider the effects of livestock grazing systems on grassland bird demographic rates in the northern mixed-grass prairie. I found a significant effect of grazing system type on the abundance of obligate grassland birds. Previous research, however, has suggested that wildlife densities may be a poor indicator of reproductive success, and management recommendations based on abundance estimates do not consider the potential for source-sink dynamics (Van Horne 1983, Vickery et al. 1992b, Patten and Kelly 2010). Direct effects of livestock grazing on grassland bird demography, such as destruction or trampling by livestock, are typically considered insignificant (Bleho et al. 2014). However, these effects may be significant for some species, and incidence of nest trampling tends to increase with stocking rate (Fondell and Ball 2004, Nack and Ribic 2005, Sutter and Ritchison 2005, Bleho et al. 2014). Although

Bleho et al. (2014) found no effect of livestock grazing system on grassland bird nest success in Canadian grasslands, grazing systems which act to defer livestock grazing during grassland bird nesting seasons have potential to benefit grassland bird nesting success due to the exclusion of cattle (Fondell and Ball 2004). Grassland bird nest success in grazed compared to ungrazed grasslands is species-dependent, but researchers have found higher nest success in ungrazed plots for some species (Fondell and Ball 2004, Sutter and Ritchison 2005). Additionally, indirect effects associated with livestock grazing may negatively impact grassland bird reproductive success. Management practices that result in uniform utilization of rangeland vegetation could contribute to higher rates of nest predation, as predator search efficiency and predation of ground-nesting bird nests decrease with increasing structural heterogeneity in vegetation (Bowman and Harris 1980).

## **MANAGEMENT IMPLICATIONS**

My results and those of previous researchers suggest that contiguous grasslands managed in season-long or summer-rotational grazing systems, with light to moderate stocking rates ( $0.3$  to  $1.4 \text{ AUM} \cdot \text{ha}^{-1}$ ), may provide structural habitat heterogeneity at the appropriate scale (within-pasture) required by grassland birds in northern mixed-grass prairies. Two main influences of within-pasture structural heterogeneity in these systems are livestock forage selectivity, coupled with considerable environmental variability within northern mixed-grass prairie landscapes (Bailey et al. 1998, Fuhlendorf and Engle 2001, Lipsey and Naugle 2017). Significant interactions between grazing management and local rangeland productivity may severely limit our ability to recommend general

management practices to benefit grassland bird populations, or even specific species, on rangelands managed for livestock production. Based on my results and other recent grassland bird research, I suggest management occur at the local, individual pasture scale. Effective management of rangelands for grassland bird conservation in the northern mixed-grass prairie requires continuous consideration of, 1) species or guilds (sparse-grass, dense-grass, etc.) of management concern, 2) variable rangeland productivity at the local (pasture) scale, 3) local annual precipitation prior to the summer grazing season and the interaction of rangeland productivity and precipitation at the pasture level, and 4) livestock utilization of rangeland vegetation within a specific pasture in the context of each of these variables. The universal implementation of conservation-based rangeland management practices in the northern mixed-grass prairie may fail to reach conservation goals due to this need for meticulous, local-scale management considerations rather than general ‘wildlife-friendly’ rangeland management (Davis et al. 2014). Nevertheless, I did find a consistent negative relationship with increased livestock stocking rate on abundance of grassland birds. This response indicates that implementation of high stocking rates may negatively impact grassland birds in the northern mixed-grass prairie, and should be avoided in this region.

Employing conservation-based, rest-rotation livestock grazing management did not result in significant increases in grassland bird abundance or shifts in grassland bird community composition within my study area in the northern mixed-grass prairie during years of average precipitation. Realistically, reversing the decline of grassland bird populations in the northern mixed-grass prairie may depend on our ability to preserve

large tracts of grassland habitat (Davis 2004), given the use of prescribed fire to manage rangelands for the restoration of patch-heterogeneity is currently not a socially-acceptable option (Sliwinski 2017). Resources or funds being used to manage rangelands for the conservation of grassland birds in this region would likely be more beneficial if they were allocated to native grassland acquisition or to preventing grassland conversion or development. Another option for conservation organizations that do not have the funds to purchase grassland or to sponsor lands for enrollment in easements, is through working closely with local conservation-minded ranch managers. This may involve identifying specific values of a ranch in regard to wildlife conservation, and then providing ranch managers with information on how to maximize habitat quality for species of interest or for a guild of grassland species, in the context of spatial and temporal variability. Engaging local landowners to support ranch-specific management would be time and resources well-spent in terms of grassland wildlife conservation, and should also be promoted over general conservation-based grazing management guidelines.

Results from my study indicate that establishing conservations easements which keep grassland ecosystems from further human development, rather than allocating funds for the implementation of rest-rotation grazing systems, would be more beneficial for the conservation of grassland birds in the northern mixed-grass prairie. However, my study was conducted during two years of average precipitation conditions, resulting in a potential caveat to these management recommendations. Researchers have suggested that patch-heterogeneity based rangeland management may provide ecological benefits in the face of increasingly variable annual precipitation, especially in drought years (Ricketts

and Sandercock 2016, Fuhlendorf et al. 2017). This hypothesis is supported by research evaluating livestock gains in years of below average precipitation conditions, where results indicated that patch-heterogeneity based rangeland management may buffer the effects of precipitation on cattle gains (Allred et al. 2014). Further research may be needed to evaluate the response of grassland birds to livestock grazing management, specifically conservation-based rangeland management such as rest-rotation grazing, in years of extreme conditions.

CHAPTER THREE

EFFECTS OF LIVESTOCK GRAZING MANAGEMENT ON THE OCCUPANCY OF  
MESOCARNIVORES IN A NORTHERN MIXED-GRASS  
PRAIRIE ECOSYSTEM

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## CHAPTER THREE

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MESOCARNIVORES IN A NORTHERN MIXED-GRASS PRAIRIE ECOSYSTEM**INTRODUCTION**

The extirpation or acute population reductions of apex predators throughout much of their historic ranges in North America has resulted in increased abundances and range expansions of secondary predators, an ecological phenomenon known as “mesopredator release” (Soulé et al. 1988, Crooks and Soulé 1999, Prugh et al. 2009, Brashares et al. 2010). The removal of apex predators from terrestrial ecosystems disrupts the balances among predators in the highest ecological trophic levels, allowing for population expansions of small- and medium-sized predators (hereafter "mesocarnivores" ; Elmhagen and Rushton 2007, Prugh et al. 2009, Ritchie and Johnson 2009). Mesocarnivore populations are supported by diet flexibility and resource sharing, as they have adapted to a wide variety of prey items and do not often exhibit prey-specific selection typical of apex predators (Prugh et al. 2009). Resulting mesocarnivore population growth and range expansions have increased pressure on the mesocarnivore prey base within numerous ecosystems throughout North America, and has been attributed to ecosystem instability, along with population declines of birds, small mammals, and reptiles (Ritchie and Johnson 2009, Brashares et al. 2010).

Grassland birds have undergone steep population declines throughout a majority of their historic range over the past century (Knopf 1994;1996, Peterjohn and Sauer 1999,

Sauer et al. 2013). Mesocarnivores can have a substantial impact on the annual fecundity of ground-nesting birds in grassland ecosystems through their depredation of eggs and young at nest sites while foraging, as well as predation of fledglings and adults while hunting (Vickery et al. 1992a, Rollins and Carroll 2001, Hovick et al. 2011, Ribic et al. 2012). Mesocarnivores are a major cause of nest mortality in ground-nesting birds within numerous grassland ecosystems (Crabtree et al. 1989, Sargeant et al. 1993, Pasitschniak-Arts and Messier 1995, Renfrew and Ribic 2003, Hartman and Oring 2009, Pietz et al. 2012, Lyons et al. 2015). Depredation is the main cause of nest failure for most grassland birds (Ricklefs 1969, Davis 2003, Jones et al. 2010, Kerns et al. 2010), and birds inhabiting grasslands experience higher rates of predation than those inhabiting other ecosystems, such as forests or wetlands (Martin 1993). These concerns emphasize the importance of considering nest predators and their potential impacts on grassland bird reproductive output within grassland bird management and conservation efforts.

In the northern mixed-grass prairie, mesocarnivore predators of grassland birds and their nests include the American badger (*Taxidea taxus*), American mink (*Neovison vison*), coyote (*Canis latrans*), least weasel (*Mustela nivalis*), long-tailed weasel (*Mustela frenata*), Northern raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), short-tailed weasel (*Mustela erminea*), and striped skunk (*Mephitis mephitis*; Sargeant et al. 1993, Seabloom et al. 2011, Foresman 2012, Burr et al. 2017). Mesocarnivores are typically considered adaptive generalists with high habitat plasticity and, unlike grassland birds, often show a positive response to increased habitat edge associated with prairie fragmentation (Gates and Gysel 1978, Johnson and Temple 1990, Andr n 1995, Donovan et al. 1995, Winter et

al. 2000, Brashares et al. 2010). Fragmentation of the landscape creates more edge habitat, facilitating functional responses of mesocarnivores, and results in compounding ecological effects on grassland bird populations (Johnson and Temple 1990, Renfrew and Ribic 2003, Ritchie and Johnson 2009). Roads, exurban development, and energy development are another form of habitat fragmentation that have been shown to displace grassland birds, alter behavioral or functional responses of mesocarnivores, and often increase mesocarnivore densities in these areas (Frey and Conover 2006, Ruiz-Capillas et al. 2013, Hovick et al. 2014, Thompson et al. 2015). Even when grassland birds avoid nesting in close proximity to edge habitat, rates of nest depredation may not be improved if habitat patches are small and fragmented (Renfrew et al. 2005).

Managing prairies for livestock grazing typically results in less fragmented, more contiguous grassland habitat for obligate grassland birds. Rangelands managed for livestock grazing contribute the majority of remaining native grassland bird habitat (Knopf 1996, Davis et al. 2014). However, researchers have suggested that even large areas of native grassland habitat may not be adequate to sustain grassland bird populations in light of recent population trends (With et al. 2008). Although lowering rates of nest predation has been suggested to benefit grassland bird conservation efforts (Johnson et al. 2012), research evaluating the effects of livestock grazing or rangeland management practices on grassland bird nest predators in prairie ecosystems is lacking. Researchers have hypothesized that livestock grazing increases predator activity (Fuller and Gough 1999), and have found occupancy of certain mesocarnivores is higher in grazed than ungrazed grasslands (Gese and Thompson 2014). Few studies have evaluated

the direct effects of livestock grazing management on mesocarnivore activity. In southern Saskatchewan, American badger activity, based on burrow occurrence, in upland grassland habitats was negatively correlated with stocking rate at the pasture scale (Bylo et al. 2014). Within a grassland ecosystem in central Scotland, increased grazing intensity was associated with decreased activity of red fox, likely a result from the negative response of small mammal prey to increased grazing intensity (Villar et al. 2013, Evans et al. 2015). Research evaluating the effects of livestock grazing systems and stocking rates on the occupancy of mesocarnivores in the northern mixed-grass prairie is needed.

Results from my evaluation of livestock grazing management on the abundance of obligate grassland birds showed a strong effect of rangeland production potential for three focal species (Chapter 2). To my knowledge, there is no research evaluating the effects of site-specific rangeland productivity on the occupancy of mesocarnivores. However, previous researchers have suggested that resource productivity within an ecosystem may influence predator ecology (Holt and Polis 1997, Elmhagen and Rushton 2007, Brashares et al. 2010). In the presence of apex predators, mesocarnivore populations may be suppressed in systems of high resource productivity (Elmhagen and Rushton 2007, Prugh et al. 2009). Additionally, resource productivity has a strong influence on intraguild interactions among predators within ecosystems (Holt and Polis 1997, Borer et al. 2003). Therefore, including a metric of rangeland productivity may be important when evaluating the effects of livestock grazing management on the occupancy of mesocarnivores.

In general, mesocarnivores have been understudied in many ecosystems due to their cryptic nature and difficulty to survey and capture (Wilson et al. 1996, Kelly and Holub 2008). Advances in digital remote camera technology have made camera trapping an effective survey method for detecting a variety of mammal assemblages in numerous habitats across ranges of environmental conditions (Silveira et al. 2003, O'Connell Jr et al. 2006, Kelly and Holub 2008, Vine et al. 2009, Barrett et al. 2012, Lesmeister et al. 2015, Wilmers et al. 2015). Occupancy modeling techniques which account for heterogeneity in detection probabilities can be applied to camera trap data, where mesocarnivore presence or absence is used to establish species occupancy patterns, space use, temporal activity, and intraguild interactions (MacKenzie et al. 2006, O'Connell Jr et al. 2006, Lesmeister et al. 2015).

I conducted camera trap surveys of mesocarnivores in northeastern Montana, USA, at sites randomly located across eight pastures enrolled in one of three livestock grazing systems. I was interested in the effects of livestock grazing management on mesocarnivore occupancy in the northern mixed-grass prairie. My objectives were to 1) evaluate how occupancy of mesocarnivores was affected by livestock grazing management in the context of site-specific rangeland production potential, 2) estimate the importance of habitat characteristics for mesocarnivore occupancy, and 3) provide management recommendations to agencies and private landowners for reducing the potential impacts of mesocarnivore depredation of grassland birds and their nests in northern mixed-grass prairie ecosystems.

The conservation-based rest-rotation grazing system hypothetically creates patch-heterogeneity on the landscape, and this structural heterogeneity may reduce predator foraging efficiency (Bowman and Harris 1980). I predicted that pastures managed in rest-rotation grazing systems would have lower mesocarnivore occupancy than pastures managed in more commonly used season-long or summer-rotation grazing systems due to the negative effect of habitat heterogeneity on foraging efficiency. Alternatively, patch-heterogeneity created by rest-rotation grazing may increase the amount of perceived edge density, which may result in numerical or functional responses from mesocarnivores (Gates and Gysel 1978, Andr n 1995). Finally, there may be no effect of grazing system on occupancy of mesocarnivores, but rather mesocarnivore site occupancy depends upon local- or landscape-scale habitat variables.

## **STUDY AREA**

My study area is located within the northern mixed-grass prairie of the Great Plains Missouri Plateau, and situated just northwest of the rugged Little Missouri Badlands. The study site is centered on a ~3,000-ha Upland Gamebird Enhancement Program (UGBEP) project established by the Montana Department of Fish, Wildlife, and Parks (hereafter “Montana FWP”), located in eastern Richland County, Montana, 20 km southeast of Sidney, Montana (48° 30’ N, 104° 04’W; Figure 16). Five pastures of ~4,300-ha bordering the UGBEP project were used as reference treatments, with three pastures located on private lands adjacent to the UGBEP project in Montana, and two pastures located on United States Forest Service National Grasslands adjacent to the UGBEP project in McKenzie County, North Dakota.

Montana FWP collaborates with private ranches throughout the state of Montana to influence management of native rangeland for improvements in wildlife habitat quality, while maintaining economically sustainable livestock production on the ranches. Incentive programs available to landowners through Montana FWP include conservation easements and the Upland Game Bird Enhancement Program. Montana FWP also manages grazing leases on Wildlife Management Areas, Department of Natural Resources and Conservation (DNRC) lands leased by Montana FWP, and a mix of Bureau of Land Management, U.S. Forest Service, and private lands that are managed under the terms of lease agreements (Kelvin Johnson, Montana FWP, pers. comm.). For all programs and leases, Montana FWP currently manages grazing on ~182,000 ha, of which ~81,000 ha are managed under rest-rotation grazing systems (Rick Northrup, Montana FWP, pers. comm.).

The study area is dominated by contiguous rangelands managed for cattle grazing, and is characterized by rolling, gently sloping plains (generally < 5 degrees; Bluemle 1991). Elevation ranges from 660 to 730 meters above sea level. Annual precipitation is variable, but long-term average (1911 – 2017) was  $\sim 360 \pm 86$  mm (SD), based on the nearest weather station (Savage 1.0 S, MT US, 20 km west) to the study site (NOAA 2017). Precipitation 12 months prior to 2016 field work (April 2015 – March 2016) was 288 mm, and prior to 2017 field work (April 2016 – March 2017) was 392 mm (NOAA 2017). Mean annual temperature is  $\sim 6^{\circ}\text{C}$ . Winter temperatures range from  $-40^{\circ}\text{C}$  to  $5^{\circ}\text{C}$  and summer temperatures range from  $8^{\circ}\text{C}$  to  $43^{\circ}\text{C}$  (NOAA 2017). Vegetation on the study site is composed of mainly graminoids, including western wheatgrass (*Pascopyrum*

*smithii*), little bluestem (*Schizachyrium scoparium*), needle-and-thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), Kentucky bluegrass (*Poa pratensis*), and blue grama (*Bouteloua gracilis*), along with low- to mid-height shrubs, including western snowberry (*Symphoricarpos occidentalis*), silver sagebrush (*Artemisia cana*), skunkbrush sumac (*Rhus trilobata*), silver buffaloberry (*Shepherdia argentea*), chokecherry (*Prunus virginiana*), wild roses (*Rosa* spp.), and creeping juniper (*Juniperus horizontalis*), as well as two prevalent sub-shrub species, winterfat (*Krascheninnikovia lanata*), and fringed sagewort (*Artemisia frigida*).

## **METHODS**

### **Field Sampling**

I collected data during two summer field seasons (May – July, 2016–17). Using ArcGIS (ESRI 2011, v10.1), I randomly generated 180 camera trap survey sites (90 each season) across gradients of habitat conditions within a Montana FWP Upland Gamebird Enhancement Program project managed under rest-rotation grazing, and on adjacent private and federal lands managed under season-long or 2-pasture summer-rotation grazing systems (Table 3, Figure 16). Within the 3-pasture rest-rotation grazing systems in my study area, cattle were turned out to the first pasture in late May, moved to the second pasture mid-August, and turned in after grazing the second pasture for 8 – 10 weeks; the third pasture in the system was rested from grazing. Season-long grazing systems in my study area allowed cattle to graze continuously from May or early June through October or mid-November. Within 2-pasture summer-rotation grazing systems in my study area, cattle were turned out to the first pasture in early June, moved to the

second pasture after 6 – 8 weeks, and turned in for the season in early November. The summer-rotation grazing systems in my study stocked cattle in the same pastures each year during approximately the same period of the summer grazing season. This is unlike typical 2-pasture deferred-rotation grazing systems, where pastures are not grazed during the same period of the summer grazing season in consecutive years. I was not interested in changes in occupancy between seasons, such as colonization or extinction, so different sites were sampled during each field season to optimize sampling to evaluate spatial patterns in mesocarnivore occupancy.

Table 3. Pastures of study, size, and number of camera trap sites in eastern Montana during 2016–17.

<b>Pasture<sup>1</sup></b>	<b>Grazing System</b>	<b>Size (ha)</b>	<b>Camera Traps<sup>2</sup></b>
Rest.Ro1	Rest-rotation	1,169	31
Rest.Ro2	Rest-rotation	1,107	29
Rest.Ro3	Rest-rotation	730	20
Summ.Ro1	2-Pasture Summer-rotation	550	12
Summ.Ro2	2-Pasture Summer-rotation	1,908	26
Summ.Ro3	2-Pasture Summer-rotation	277	8
Se.Long1	Season-long	856	26
Se.Long2	Season-long	413	12

<sup>1</sup> Pasture locations within the study area are displayed in Appendix A, Figure A1.

<sup>2</sup> Of 180 camera trap sites surveyed, 16 were censored from analyses.

I deployed one passive infrared remote field camera (Browning BTC 5HD, Browning, Morgan, UT) at each of 90 camera trap sites during three sampling sessions in 2016 and 2017 (Table 3). Thus, 30 remote cameras were used to survey 180 sites during two field seasons. Sampling sessions ranged from 20 – 25 days (Table 4), and one sampling occasion was defined as a 5-day (120 hour) period. Partial sampling days (days of camera installation or removal) were excluded from sampling periods.

Table 4. Sampling periods for mesocarnivore camera trapping in eastern Montana during 2016–17.

<b>Year</b>	<b>Sampling Period</b>	<b>Date Range<sup>1</sup></b>
2016	1	134 – 158
2016	2	160 – 179
2016	3	182 – 201
2017	1	139 – 163
2017	2	165 – 184
2017	3	186 – 205

<sup>1</sup> Julian day (1 – 365).

To maximize mesocarnivore detections, camera traps were set in the most optimal location within 200 m of the site, often areas along habitat edges where predators typically prefer to hunt and forage (Andr n 1995), or along game trails. Camera traps were spaced > 250 m apart to satisfy the assumption of site independence (Lesmeister et al. 2015). However, selection for the most optimal camera trap location within 200 m of the site unknowingly resulted in 20 camera traps set < 250 m from another camera trap. Of these, 8 were spaced 200 – 250 m apart and included in analyses, while 12 were less than 200 m apart and censored from analyses. Additionally, 4 camera trap sites were censored due to camera malfunction (2), cattle destruction (1), or theft (1). Of 180 original camera sites, 164 sites were used in analyses.

Due to the relatively small size of my study area (~7,000 ha), and the large home range of some mesocarnivores (coyote, summer range > 1,500 ha; Gosselink et al. 2003), the assumption of spatial independence of camera sites may be violated. As such, the definition of occupancy in my study is not necessarily true occupancy, but rather habitat use of mesocarnivores, as defined by Krausman (1999). Habitat use is a relevant and informative metric, as my main objective for this aspect of the study is to evaluate the

influence of livestock grazing management on mesocarnivore use. This definition of occupancy will allow comparison among grazing systems in terms of mesocarnivore habitat use.

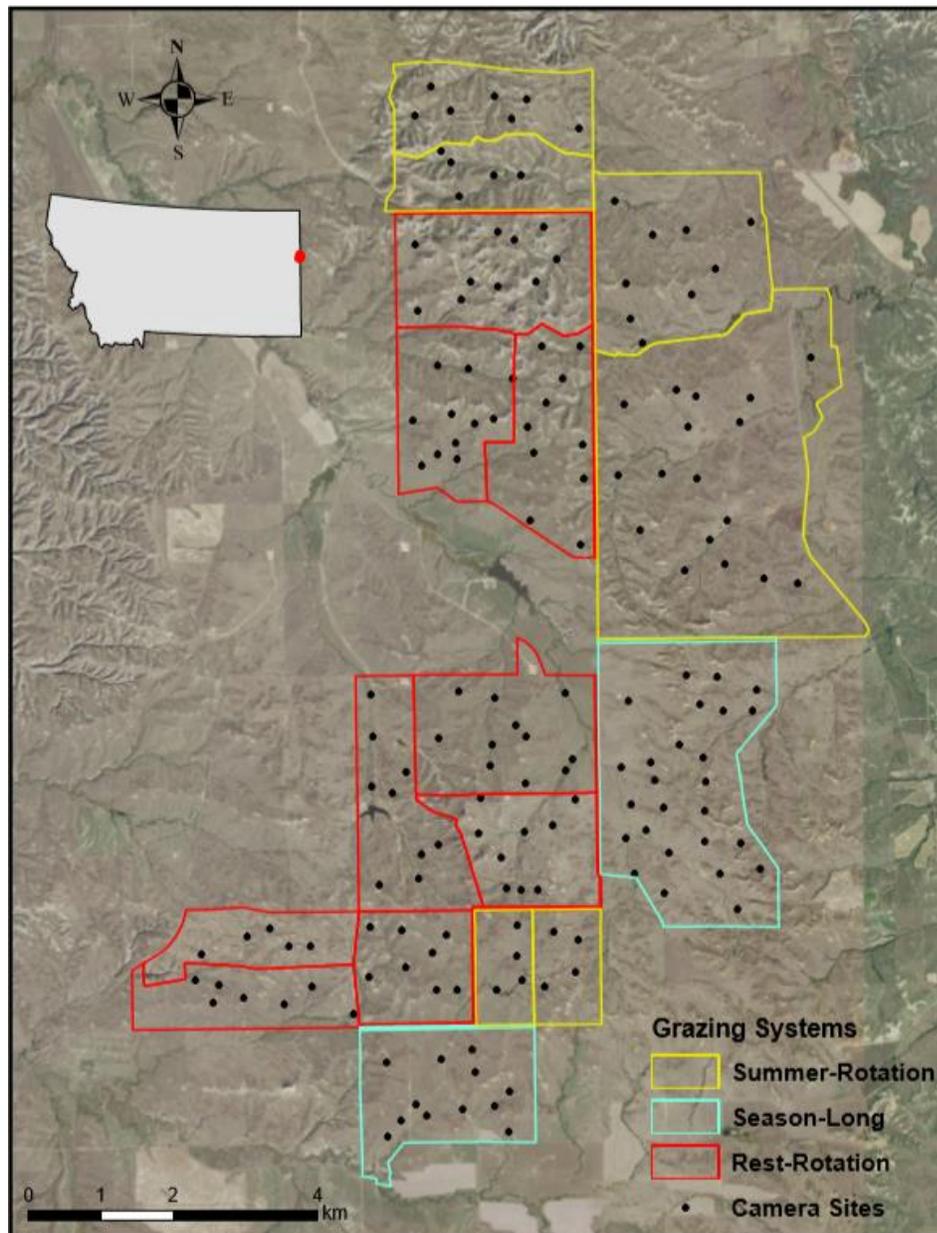


Figure 16. Study area in Richland County, Montana and McKenzie County, North Dakota, USA during 2016–17. Camera trap sites within pastures on the Montana FWP Upland Gamebird Enhancement Program project managed in a rest-rotation grazing system, and on adjacent pastures managed in season-long or summer-rotation grazing systems.

Cameras were programmed to be active 24 hours per day, with a two photo burst for each photographic event and a 1-minute delay between events. Cameras were motion-activated, so a photographic event occurred when the remote camera was triggered by the presence of a mesocarnivore. Date, time, and camera identity were recorded by the camera for each photographic event. Cameras were secured to tree trunks or mounted on metal stakes and positioned approximately 0.5 m above the ground. When present, cameras were faced toward game trails to maximize detections. The area in front of each camera was cleared of obstructive vegetation, and a scent or bait lure was placed 2 m in front of the camera. Lures were used to increase mesocarnivore detections, and in 2016, consisted of a combination of fatty acid scent disks (U.S. Department of Agriculture Pocatello Supply Depot, Pocatello, ID), trapping lure (Gusto; Minnesota Trapline Products, Inc., Penneck, MN), and/or sardines. Only trapping lure was used in 2017. All camera sites during each sampling period received the same lure. During each sampling period, camera sites were revisited weekly to replenish lures, swap memory cards, change camera batteries, and remove any new obstructive vegetation.

### **Habitat Evaluation**

My study site is an area of contiguous, native grassland managed for livestock grazing, resulting in relatively few areas of common edge habitats, with which mesocarnivores are typically associated. I identified 5 potential habitat edges within my study site, wooded coulees, roads and two-tracks, pasture fences, water features, and oil pads. I used ArcMap 10.4 to digitize each of these features within the study site using five band 1-m resolution aerial imagery from the National Agricultural Imagery Program

(NAIP) developed by the U.S. Farm Service Agency (ESRI 2011, v10.4). Data was obtained from Montana State Library GIS Clearinghouse and North Dakota GIS Hub Data Portal. I merged each of these features into a single 'edge' layer, and intersected this layer with buffered camera sites at 100-m, 500-m, and 1,000-m radial areas for analyses at multiple spatial scales (ESRI 2011, v10.4). I used the ArcMap 'Calculate Geometry' tool to estimate the total length of edge habitat associated at camera sites, and calculated edge density by dividing edge length by area at each of 100-m, 500-m, and 1,000-m spatial scales (ESRI 2011, v10.4). I used the ArcMap 'Near' tool to estimate the distance from each camera site to the nearest wooded coulee, pasture fence, road or two-track, water feature, or oil pad (ESRI 2011, v10.4).

Rangeland managers implement grazing systems based on the expected annual vegetative production of rangelands in an average year. I quantified rangeland production potential associated with each camera trap site using the Soil Survey Geographic database (SSURGO) ecological site data from the Natural Resources Conservation Service (NRCS) Web Soil Survey (NRCS 2017). NRCS defines rangeland production as "the amount of vegetation that can be expected to grow annually in a well-managed area that is supporting the potential natural plant community" (NRCS 2017). Previous researchers have found NRCS estimates of rangeland production potential based on the SSURGO ecological site data were reasonable estimates of true average rangeland productivity (Relyea et al. 2000). I calculated the weighted average rangeland production potential within 100 m of each camera trap site using the representative values (RV) of rangeland production for each ecological site type in the study area (Appendix B, Table B1),

effectively accounting for camera trap sites which encompassed multiple ecological sites. I used the representative values of rangeland production potential, as precipitation during the years prior to field work was approximately average, and the RV's are based on an average year's precipitation.

I interviewed landowners to gather cattle turn-out/turn-in dates and number of head stocked to calculate stocking rates for the pastures within my study area. These dates and numbers were validated by observation of when and approximately how many cattle were present in pastures during both grazing seasons. I calculated stocking rates within pastures based on an animal unit month (AUM), the amount of forage, measured on a dry weight basis, to feed a 1,000-lb cow-calf pair for a 30-day period (Holechek et al. 2011). The average cow-calf pair grazing on the pastures within my study area was approximately 1,400 lbs (635 kg) based on landowner interviews, so I accounted for this in my calculation of stocking rate. Typically, stocking rates consider all pastures within a multi-pasture grazing system, resulting in a single stocking rate for the system. I calculated the stocking rates of each individual pasture within the 3-pasture rest-rotation and 2-pasture summer-rotation grazing systems because I was interested in the indirect effects of livestock grazing on mesocarnivore occupancy through livestock alteration of vegetation structure. Stocking rates from the previous year's grazing season were used as a predictor of mesocarnivore occupancy, as residual vegetation from the previous year's grazing establishes habitat structure used by mesocarnivores for hunting and foraging activities during the grassland bird breeding season when I conducted camera trap surveys.

## **Statistical Analyses**

I evaluated the effects of edge density (100-m, 500-m, and 1,000-m scale) and distance to the nearest wooded coulee, road, fence, water, and oil pad on mesocarnivore occupancy. I also evaluated the management-level effects of rangeland production potential (100-m scale), stocking rate, and grazing system on mesocarnivore occupancy. The habitat variables were considered for their direct effect on mesocarnivore occupancy through habitat use, whereas the three management-level variables were considered for their indirect effect on mesocarnivore occupancy through the ability of livestock grazing to alter vegetation structure within rangelands. Rangeland production potential is included in the management-level model set because range managers consider the average production potential of rangelands when implementing grazing systems or manipulating livestock stocking rates.

I conducted all analyses in program R (R Core Team 2016) with use of packages ‘unmarked’ (Fiske and Chandler 2011) and ‘AICcmodavg’ (Mazerolle 2013) to identify specific effects on occupancy of mesocarnivores, where single-season occupancy modeling allowed for simultaneous estimation of detection probability and occupancy (MacKenzie et al. 2006). Accounting for imperfect detection is important to avoid bias in studies evaluating mesocarnivore occupancy using remote camera traps (Lesmeister et al. 2015). I used single-season occupancy modeling to increase the number of sites, as I was not interested in immigration or emigration from sites among years.

I used stepwise model selection techniques (backward selection) to identify the factors influencing mesocarnivore detection probability and occupancy, where I started

with a highly parameterized model and eliminated uninformative parameters based on their lack of influence on mesocarnivore detection probability or occupancy (Montgomery et al. 2012). Models related to mesocarnivore detection probability were fit prior to fitting models for local mesocarnivore occupancy. I pooled all mesocarnivore species for analyses due to low detection probabilities within each single species (MacKenzie et al. 2002). If a mesocarnivore was detected at a camera site during a sampling occasion, the site was considered occupied. Previous researchers have suggested, in grassland ecosystems with relatively high predator diversity, management actions to reduce grassland bird nest depredation may not prove successful if they do not consider the entire predator community (Renfrew and Ribic 2003, Pietz et al. 2012).

Prior to fitting occupancy models, I tested all covariates for multicollinearity, removing those which were highly correlated (Pearson's correlation estimate  $|r| > 0.6$ ) from further analyses. Edge density at 100-m and 500-m spatial scales were correlated ( $r = 0.66$ ), and edge density at 500-m and 1000-m scales were correlated ( $r = 0.77$ ). I removed edge density at the 500-m spatial scale from further analyses because it was correlated across the other two spatial scales (100-m and 1,000-m), and this metric assessed at two scales was uncorrelated. Edge density (100-m) and distance to nearest wooded coulee were correlated ( $r = -0.63$ ). I kept edge density and removed distance to the nearest coulee from analyses because mesocarnivores typically use habitat edges while hunting and foraging (Andr n 1995), and my metric of edge density includes wooded coulee, along with other habitat edges. For each variable included in detection and occupancy models, I evaluated whether a linear, quadratic, or pseudo-threshold

(pseudo-asymptotic) effect (Franklin et al. 2000) was best supported for its influence on mesocarnivore detection probability or occupancy.

Variables included in the detection probability model were year, cattle presence, visit, Julian day (134–201), and the amount of precipitation during each 5-day visit.

Variables included in the habitat model were cattle presence, edge density (100-m and 1,000-m spatial scales), and distance to nearest road or two-track, pasture fence, water feature, and oil pad. Once stepwise model selection was complete, I used Akaike's Information Criterion adjusted for finite samples ( $AIC_c$ ) to evaluate model support and identify important variables to include in the final detection or abundance model.

Supported models with large model weights ( $w_i$ ) and  $AIC_c$  values  $\leq 2$  from the best-fit model were considered parsimonious (Burnham et al. 2011). When a supported model differed from the best-fit model by a single parameter, I considered the additional parameter to be uninformative and excluded this parameter from inclusion in the final model (Arnold 2010). I built a candidate model set for the management-scale effects on mesocarnivore occupancy based on *a priori* hypotheses, which included additive effects, along with 2- and 3-way interactions (Table 5). Factors hypothesized to affect mesocarnivore occupancy at the management-level were grazing system, stocking rate, and rangeland production potential.

Table 5. Candidate model set for the management-level effects on mesocarnivore occupancy in eastern Montana during 2016–17.

<b>Model</b>	<b>Description</b>
Null	Null Model
Mod1	Grazing System
Mod2	Stocking Rate
Mod3	Rangeland Production Potential
Mod4	Grazing System + Stocking Rate

Table 5. continued

<b>Model</b>	<b>Description</b>
Mod5	Grazing System + Rangeland Production Potential
Mod6	Stocking Rate + Rangeland Production Potential
Mod7	Grazing System + Stocking Rate + Rangeland Production Potential
Mod8	Grazing System $\times$ Stocking Rate
Mod9	Grazing System $\times$ Rangeland Production Potential
Mod10	Rangeland Production Potential $\times$ Stocking Rate
Mod11	Grazing System $\times$ Stocking Rate + Rangeland Production Potential
Mod12	Grazing System $\times$ Rangeland Production Potential + Stocking Rate
Mod13	Grazing System $\times$ Stocking Rate $\times$ Rangeland Production Potential

I assessed model fit for the best-fit model within habitat- and management-level analyses for mesocarnivores from 1,000 simulated datasets using the `mb.gof.test` function within `AICcmodavg` (Mazerolle 2013). Goodness-of-fit tests indicated  $\hat{c}$  estimates between 1.3 and 1.5, and p-values  $< 0.1$  for the most parsimonious models within each model set, providing evidence for potential overdispersion in the data. However, I identified the cause of lack-of-fit as two sites which had encounter histories of 11110, where the expected number of sites with this encounter history was 0.1, which substantially inflated the chi-square statistic. I temporarily removed these two sites with encounter histories 11110 from the analysis and re-ran the goodness-of-fit test, which resulted in  $\hat{c}$  estimates between 0.7 and 1.0, and p-values  $> 0.95$  for the most parsimonious models within each model set. These results indicated that the models adequately fit the data, and the original evidence for overdispersion was a result of two sites with unexpected encounter histories.

The best-fit model within habitat- and management-level analyses was used to generate predictions of mesocarnivore occupancy over the range of values for each variable, while holding other variables included in the best-fit model at their means.

When multiple models shared support ( $\Delta AIC_c$  values  $\leq 2$ ), model averaged estimates were used to generate predictions of mesocarnivore detection probability and occupancy.

## RESULTS

I recorded 178 mesocarnivore detections during 3,535 camera trap days at 164 remote camera sites located within 8 pastures managed for cattle grazing. I detected 5 species of mesocarnivores during camera trap surveys: American badger, coyote, raccoon, striped skunk, and weasel (*Mustela spp.*). Coyote was recorded at 69 of 164 camera sites, raccoon at 25 sites, American badger at 22 sites, striped skunk at 10 sites, and weasel at 4 sites. I recorded 4 species in pastures employing each of the three grazing systems: rest-rotation, summer-rotation, and season-long grazing systems. Striped skunk was not detected in season-long grazing systems, but weasel was only detected in season-long grazing systems.

### Detection

The average ( $\pm$  SE) probability of detecting a mesocarnivore at the study area was  $0.298 \pm 0.028$ . The top model describing mesocarnivore detection probability, with full support ( $AIC_c w_i = 0.71$ ), included the main effects of year, cattle presence, visit, Julian day, and total precipitation (Appendix H, Table H1). Detection probability was higher in 2016 than 2017, higher when cattle were present at a site, and lowest during visit 5 compared to visits 1 – 4 (Table 6). The probability of detection increased with Julian day, and showed a quadratic relationship with precipitation, where detection was lowest when precipitation during the visit was moderate (15 – 25 cm; Table 6).

Table 6. Standardized covariate estimates for the top mesocarnivore<sup>a</sup> models in eastern Montana during 2016–17.

	Estimates	
	$\beta$	SE
<b>Detection probability</b>		
Intercept	-0.76	0.30
Year, 2017	-0.46	0.25
Cattle presence, Yes	-0.49	0.25
Visit 2	-0.43	0.29
Visit 3	-0.25	0.31
Visit 4	0.26	0.31
Visit 5	-1.11	0.52
Julian day	0.22	0.14
Precipitation	-0.99	0.22
Precipitation <sup>2</sup>	0.37	0.10
<b>Occupancy, habitat</b>		
Intercept	4.02	1.70
Edge density (100 m)	3.66	2.05
Distance to road	2.89	1.16
Distance to fence	-1.92	0.64
Distance to water	0.58	0.42
<b>Occupancy, management</b>		
Intercept	4.06	2.24
Season-long Grazing	-3.54	2.49
Summer-rotation Grazing	-3.44	2.10
Stocking Rate	1.64	1.10

<sup>2</sup> Variable indicates support for a quadratic effect.

<sup>a</sup> Mesocarnivore models include detections of American badger, coyote, raccoon, striped skunk, and weasel.

## Habitat Conditions

After accounting for detection probability, four models shared support ( $\Delta\text{AIC}_c \leq 2.0$ ) for habitat effects on mesocarnivore occupancy (Appendix H, Table H1). Models including the main effects of edge density (100-m), distance to the nearest fence, and distance to the nearest road had the majority of support ( $w_i = 0.99$ ). The top habitat-level model describing occupancy of mesocarnivores included support for edge density (100-m), and distance to nearest road, fence, and water (Appendix H, Table H1). The probability of mesocarnivore occupancy increased with edge density (100-m;  $\beta = 3.66 \pm$

2.05) and distance to nearest road ( $\beta = 2.89 \pm 1.16$ ), and decreased sharply with distance to nearest fence ( $\beta = -1.92 \pm 0.64$ ; Figure 17). Distance to nearest water was also included in the top model, but the 95% CI for effect size overlapped 0 and the effect was considered non-informative.

### **Management-level**

Five models shared support ( $\Delta AIC_c \leq 2.0$ ) for management-level effects on mesocarnivore occupancy (Appendix H, Table H2). Models including the main effects of grazing system, stocking rate, or rangeland production potential had the majority of support ( $w_i = 0.67$ ). The top model included the main effects of grazing system and stocking rate ( $w_i = 0.24$ ), the next top model included the main effect of rangeland production potential ( $w_i = 0.13$ ), and the third supported model included the main effect of grazing system ( $w_i = 0.11$ ). Mesocarnivore occupancy was highest in rest-rotation grazing systems, followed by season-long ( $\beta = -3.54 \pm 2.49$ ) and summer-rotation systems ( $\beta = -3.44 \pm 2.10$ ), and the probability of mesocarnivore occupancy increased with stocking rate ( $\beta = 1.64 \pm 1.10$ ; Table 6, Figure 18).

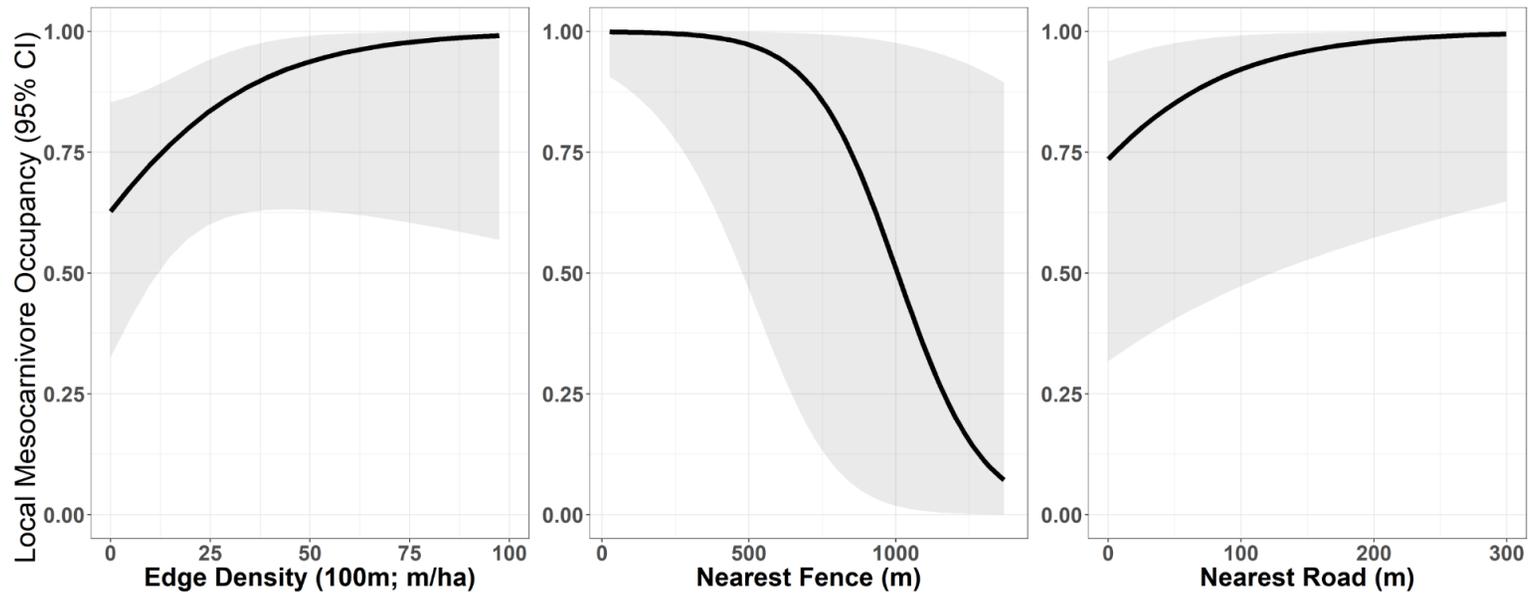


Figure 17. The top habitat model describing local occupancy of mesocarnivores in eastern Montana during 2016–17 included support for edge density (100-m), distance to nearest fence, and distance to nearest road. Distance to nearest water was also included in the top model, but the 95% CI for effect size overlapped 0 and the effect was considered non-informative.

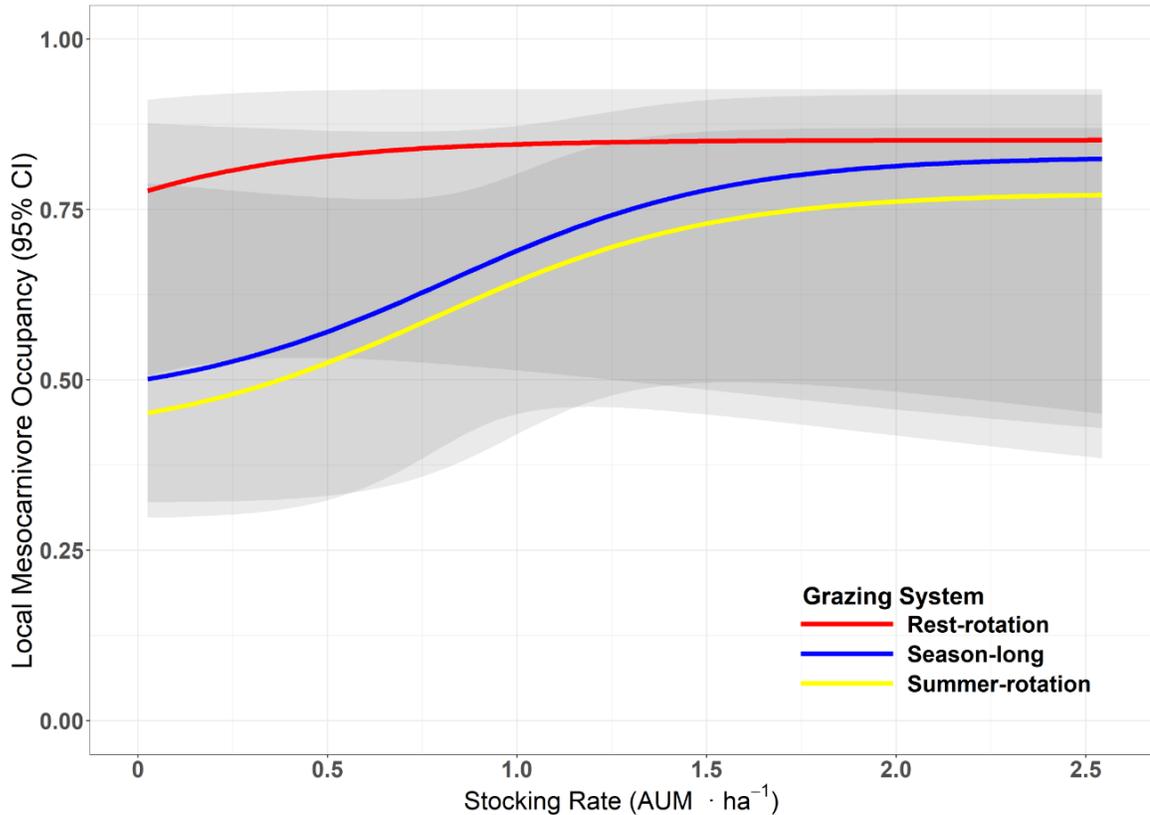


Figure 18. The top management-level model describing local occupancy of mesopredators in eastern Montana during 2016–17 included main effects of grazing system and stocking rate.

## DISCUSSION

Understanding changes in mesocarnivore ecology resulting from ‘mesopredator release’ has become a topic of recent concern in the field of wildlife conservation, as the removal of top predators from a system may accelerate local prey extinctions within biological communities (Borrvall and Ebenman 2006, Ritchie and Johnson 2009, Brashares et al. 2010). Effects of land management or land use are important considerations when evaluating mesocarnivore occupancy (Dijak and Thompson III 2000, Kuehl and Clark 2002). My evaluation of the effects of rangeland management practices on mesocarnivores in the northern mixed-grass prairie indicated that occupancy

of mesocarnivores was highest in rest-rotation grazing systems, followed by season-long and summer-rotation grazing systems. Assuming that hunting and foraging activities are related to site occupancy in my study area, mesocarnivores may occupy more sites within rest-rotation grazing systems potentially due to higher foraging success or prey availability (Fuller and Sievert 2001). Three possible explanations arise: 1) the vegetation structure created by rest-rotation grazing provides mesocarnivores with greater foraging efficiency, 2) increased fence density within rest-rotation grazing systems (Chapter 2; Appendix G, Table G1) facilitates higher mesocarnivore occupancy, or 3) rest-rotation grazing systems may support a greater abundance of prey, inherently resulting in more predators to exploit additional prey resources.

Vegetation structure in grassland ecosystems may influence mesocarnivore foraging efficiency (Bowman and Harris 1980, Crabtree et al. 1989). My analysis of vegetation conditions among grazing treatments within the rest-rotation grazing system showed that rest-rotation grazing created patch-size heterogeneity among treatments within the system (Chapter 2; Appendix G, Table G2). The grazed treatments within the rest-rotation grazing system also created distinct vegetation structure on the landscape when compared to adjacent pastures. I found that grazed pastures within the rest-rotation grazing system were characterized by lower residual grass height and density, lower litter depth, and higher bare ground coverage compared to the other two grazing systems within my study area. Previous researchers have suggested that predator foraging efficiency may be higher in areas of low vegetation height and density (Johnson and Temple 1990, Sutter and Ritchison 2005). Grazing systems with more intensive

manipulation of livestock, such as rest-rotation grazing, will typically result in more even forage utilization and lower within-pasture heterogeneity in vegetation structure as a result of reduced cattle forage selectivity (Coughenour 1991, Hart et al. 1993, Holechek et al. 2011). Mesocarnivores in my study area may have higher site occupancy in pastures managed with rest-rotation grazing due to increased foraging or hunting efficiency in a system which creates patch-size heterogeneity among pastures by reducing the amount of small-scale, within-pasture heterogeneity. Additionally, the overall shorter, sparser vegetation structure of pastures within the rest-rotation grazing system in my study area may facilitate increased mesocarnivore foraging efficiency.

Low livestock stocking rates (relative to the specific grassland ecosystem) typically result in higher cattle forage selectivity and higher within-pasture heterogeneity in vegetation structure, when compared to high stocking rates (Bailey et al. 1998, Fuhlendorf and Engle 2001, Toombs et al. 2010). I found mesocarnivore occupancy increased with stocking rate, and these results were consistent with previous research suggesting that livestock grazing may facilitate increased use by mesocarnivores (Gese and Thompson 2014). These results support the hypothesis that mesocarnivore foraging or hunting efficiency decreases in areas of rangeland dominated by small-scale, within-pasture heterogeneity, compared to large-scale patch-heterogeneity. However, these results also differ from previous research which has suggested that mesocarnivore activity declines with increasing livestock grazing intensity, potentially from decreased small mammal prey abundance associated with livestock grazing (Villar et al. 2013, Bylo et al. 2014). Likely due to the difficulty of surveying mesocarnivores, these studies used

burrow occurrence or scat counts as an index of mesocarnivore activity rather than techniques to estimate true occupancy or abundance, which may account for the inconsistencies among studies. Additionally, imperfect detection of burrows was not accounted for, but due to rigorous survey methods, assumed to be equal to 1.0. Other potential explanations for inconsistencies between my results and previous work include the absence of small mammal density data relative to grazing systems and mesocarnivore occupancy in my study, and the overall low-moderate stocking rates at my study area.

Strategies to restore patch-size structural heterogeneity to North American prairies have recently been promoted in rangeland management (Fuhlendorf et al. 2006, Fuhlendorf et al. 2012). Within the context of patch-heterogeneity based grazing management, researchers have shown that some mesocarnivores do not necessarily occupy those habitats with the highest prey abundance, suggesting that foraging efficiency may be more important than prey density (Ricketts 2016). In my study area, mesocarnivores appear to select vegetation conditions created by rest-rotation grazing systems over those of season-long or summer-rotation grazing systems. If heterogeneity in vegetation structure functions to decrease predator foraging efficiency as previous researchers have suggested (Bowman and Harris 1980, Crabtree et al. 1989, Martin 1993), the scale at which this occurs may not be at the patch-scale. My evaluation of vegetation conditions showed that the rest-rotation grazing systems within my study area created patch-heterogeneity in vegetation structure. However, I found occupancy of mesocarnivores was highest in rest-rotation grazing systems, indicating that heterogeneity at the patch-scale may not act to decrease predator foraging efficiency. Rather, small-

scale within-pasture heterogeneity created by higher livestock forage selectivity within the season-long or summer-rotation grazing systems may reduce predator foraging efficiency, relative to rest-rotation grazing in my study area.

The alternative to increased foraging efficiency explaining higher mesocarnivore occupancy is the potential for increased prey abundance in rest-rotation grazing systems to result in more predators to exploit additional prey resources. The typical goal of conservation-based livestock grazing systems which incorporate rotations or deferments from grazing, such as the rest-rotation grazing system, is to support grassland wildlife populations through livestock exclusion or extended periods of rest from livestock grazing (Krausman et al. 2009). However, there are numerous inconsistencies in the literature concerning the benefits of rotational or conservation-based grazing systems on wildlife populations or ecosystem functioning (Briske et al. 2008, Krausman et al. 2009, Roche et al. 2015). Thus, making generalizations to wildlife populations based on the type of grazing management being implemented is inappropriate. I found abundance of grassland birds was lowest in rest-rotation grazing systems, relative to season-long or summer-rotation systems. These results do not support the hypothesis that mesocarnivore occupancy is higher within rest-rotation grazing systems due to a higher prey availability. However, I have no data on abundance of small mammals, another main food resource of mesocarnivores. Previous researchers have found that patch-heterogeneity based rangeland management has a positive influence on community structure and species diversity of small mammals in prairie ecosystems (Ricketts and Sandercock 2016). However, occupancy of some mesocarnivores is not necessarily highest in areas of

greatest primary prey abundance (Ricketts 2016). Small mammal abundance is often lower in pastures grazed by livestock compared to ungrazed pastures, and abundance may decrease with increasing grazing intensity (Runge 2005, Schmidt et al. 2005, Evans et al. 2006, Bueno et al. 2011, Evans et al. 2015, Schieltz and Rubenstein 2016).

Mesocarnivore occupancy would likely not respond positively to increasing stocking rate if prey abundance was significantly lower in areas of high stocking rates, unless prey search efficiency is increased. Habitat structure may be a more important influence on occupancy of mesocarnivores than prey abundance, and the reduced small-scale, within-pasture heterogeneity created by higher stocking rates and by rest-rotation grazing systems in my study area may increase predator foraging or hunting efficiency.

In my analyses of the habitat variables which may influence mesocarnivore occupancy in northern mixed-grass prairie ecosystems, I found strong support for edge density (100-m), distance to nearest fence, and distance to nearest road. The positive relationship I found between mesocarnivore occupancy and edge density was not surprising, as predators typically forage and hunt along edges (Andrén 1995, Pedlar et al. 1997, Dijak and Thompson III 2000). I also found a positive relationship between mesocarnivore occupancy and distance to the nearest road or two-track, where areas further from roads had higher predicted site occupancy. This may be due to mesocarnivore avoidance of human presence, as previous researchers have found mesocarnivores avoid areas of high-traffic or human presence associated with oil development activities (Burr et al. 2017).

In agricultural landscapes, researchers have suggested that fencerows may be perceived as edge habitat, and that fences are often used as travel corridors for mesocarnivores (Pedlar et al. 1997). Additionally, previous researchers evaluating mesocarnivore occupancy using remote cameras in grassland habitats specifically selected camera trap locations along fencelines to maximize mesocarnivore detections, suggesting fences are associated with high mesocarnivore activity (Smith et al. 2017). Within contiguous rangeland landscapes such as that of my study area, I hypothesized that fences may represent effective habitat edges, potentially due to their physical structure and/or the difference in vegetation structure created by variable grazing regimes among pastures divided by fence. I found a negative relationship between mesocarnivore occupancy and distance to the nearest fence, which was consistent with my hypothesis and supported previous work in regard to mesocarnivore use of fencelines. In areas beyond 500 m from fences, predicted mesocarnivore site occupancy declined sharply. My results could have implications for mesocarnivore prey species occupying rangelands managed with multi-pasture rotational livestock grazing systems, such as rest-rotation or short-duration grazing systems. These more intensively managed grazing systems use fencing to divide larger pastures into multiple smaller pastures, effectively achieving the desired forage utilization of the range manager (Williams 1954, Hart et al. 1993). Adding more fence to the landscape may facilitate mesocarnivore occupancy and/or foraging efficiency in these areas, potentially reducing survival or reproductive output of grassland birds and small mammals, common mesocarnivore prey.

My research provides evidence for increased mesocarnivore occupancy in rangelands managed in rest-rotation grazing systems and rangelands managed with high stocking rates. Previous researchers have suggested that mesocarnivore nest depredation may often be opportunistic (Vickery et al. 1992a). As such, conservation-based rest-rotation grazing systems which support higher occupancy of mesocarnivores have the potential to facilitate unintended impacts on grassland bird nesting ecology in grassland ecosystems. This implication is based on the assumption that increased mesocarnivore site occupancy results in decreased grassland bird reproductive output or survival, which may depend upon a number of factors. However, recent work from the northern mixed-grass prairie found a negative correlation between nest survival of a ground-nesting obligate grassland bird, the sharp-tailed grouse (*Tympanuchus phasianellus*) and mesocarnivore occupancy (Burr et al. 2017). Further research is needed to relate mesocarnivore occupancy to grassland bird demographic and survival rates in the context of livestock grazing management.

## **MANAGEMENT IMPLICATIONS**

I found mesocarnivore occupancy was highest in rest-rotation grazing systems, followed by season-long and summer-rotation grazing systems. These results may be due to lower within-pasture heterogeneity, or overall shorter and sparser vegetation structure in rest-rotation grazing systems, resulting in increased mesocarnivore foraging or hunting efficiency. Additionally, the patch-heterogeneity in vegetation structure, along with increased fence density in rest-rotation grazing systems may function as perceived edge

habitat and increase mesocarnivore occupancy, as I found a strong negative relationship between mesopredator occupancy and distance to the nearest fence.

Previous researchers have suggested that livestock grazing intensity may have a negative effect on mesocarnivore habitat use (Villar et al. 2013, Bylo et al. 2014, Evans et al. 2015). I found a positive relationship between mesopredator occupancy and stocking rate, where occupancy was maximized at the highest stocking rates within my study area. However, stocking rates within my study were generally low to moderate, so habitat use of mesocarnivores may respond negatively to higher stocking rates than were included in my study. I cannot make inferences regarding the relationship between occupancy of mesopredators and higher livestock stocking rates, especially above 2.5 AUM · ha<sup>-1</sup>.

My results indicate that rest-rotation grazing systems, as well as livestock grazing management which employs relatively high stocking rates, may facilitate higher mesocarnivore occupancy. Nest depredation by mesocarnivores is often opportunistic, so management that facilitates increased mesocarnivore occupancy has the potential to negatively impact grassland bird reproductive output. However, mesocarnivore occupancy may not translate to negative effects on grassland bird demography relative to other grazing systems if nest or brood survival is higher in rest-rotation grazing systems, as previous researchers have suggested (Rice and Carter 1982). A demographic study comparing mesopredator occupancy to grassland bird fecundity within the context of grazing management practices in grassland ecosystems is needed confirm or deny the implication that grassland bird reproductive success is negatively impacted by increased

mesocarnivore occupancy in the northern mixed-grass prairie, and would support the implications of my results on grassland bird populations.

## CONCLUSIONS AND RECOMMENDATIONS

Grassland birds have experienced steeper population declines than any other avian guild during the past century (Knopf 1996, Brennan and Kuvlesky Jr 2005, Sauer et al. 2013). Breeding and wintering habitat historically dominated by contiguous, native grassland has undergone substantial degradation through widespread agricultural development and habitat fragmentation (Knopf 1994, Brennan and Kuvlesky Jr 2005, Askins et al. 2007). As a result, rangelands managed for livestock grazing constitute the majority of remaining grassland bird habitat (Knopf 1996, Davis et al. 2014). Unfortunately, conserving large tracts of grassland habitat, in itself, may not be sufficient to reverse grassland bird population trends (With et al. 2008). Proper management of remaining grassland habitat is necessary to incorporate within current grassland bird conservation efforts (With et al. 2008). Additionally, mesocarnivores as a guild have recently seen increased abundances and have undergone substantial range expansions in grassland ecosystems following extirpation of apex predators (Prugh et al. 2009). Mesocarnivores are a main predator of grassland birds and their nests (Rollins and Carroll 2001, Hovick et al. 2011, Pietz et al. 2012, Burr et al. 2017), and ‘mesopredator release’ has been attributed to population declines of birds and other mesocarnivore prey (Ritchie and Johnson 2009, Brashares et al. 2010). Therefore, understanding the effects of rangeland management on mesocarnivores is also an important consideration within grassland bird conservation efforts.

Grassland ecosystems in the shortgrass, tallgrass, and mixed-grass prairie regions of North America were historically heterogeneous landscapes dominated by frequent, yet

sporadic disturbance from bison grazing and natural or Native American induced wildfire (Pyne 1993, Kay 1998, Knapp et al. 1999). Rangeland management practices which restore this patchy heterogeneity in vegetation structure within grassland ecosystems, such as patch-burn grazing, have proven ecologically beneficial for numerous wildlife taxa native to these habitats, including grassland birds (Fuhlendorf et al. 2006, Coppedge et al. 2008, McNew et al. 2015, Ricketts and Sandercock 2016, Winder et al. 2018). The rest-rotation grazing system may have a similar effect on grassland wildlife, conceptually creating patch-heterogeneity in rangeland vegetation structure with the use of fence and strategic manipulation of livestock grazing among pastures within the system (Hagen et al. 2004, Derner et al. 2009, Toombs et al. 2010). However, little information exists regarding the effects of rest-rotation grazing on grassland wildlife, or the ability of this system to create the patch-heterogeneity in vegetation structure which effectively mimics historical grassland disturbance.

Research in the field of avian ecology has recently focused on understanding grassland bird habitat selection and demography in the context of variable land management practices, annual precipitation, and rangeland productivity within prairie ecosystems (Golding and Dreitz 2017, Lipsey and Naugle 2017). In the northern mixed-grass prairie, precipitation may have a more significant influence on vegetation structure and composition than livestock grazing management (Vermeire et al. 2008). Grassland birds have responded positively to the patch-heterogeneity created through grazing management practices which utilize pyric-herbivory (i.e., patch-burn grazing). The absence of fire in the northern mixed-grass prairie conceptually justifies implementation

of an intensive, conservation-based livestock grazing system (i.e., rest-rotation grazing) to overcome effects of variable annual precipitation and restore patch-heterogeneity in grassland vegetation structure.

My research evaluated the effects of livestock grazing management on the abundance of grassland birds and occupancy of mesocarnivores in the northern mixed-grass prairie, specifically comparing rest-rotation grazing to more commonly implemented grazing systems, season-long and summer-rotation grazing. My objectives were to 1) evaluate how species-specific abundances and community composition of grassland birds were affected by livestock grazing management in the context of site-specific rangeland production potential, 2) evaluate how occupancy of mesocarnivores was affected by livestock grazing management in the context of site-specific rangeland production potential, 3) estimate the importance of habitat conditions and vegetation characteristics for grassland birds and mesocarnivores, as mediated by livestock grazing management, 4) evaluate the effectiveness of rest-rotation grazing to create patch-heterogeneity in rangeland vegetation structure, and 5) provide management recommendations to agencies and private landowners for improving grassland bird habitat quality, and for reducing the potential impacts of mesocarnivore depredation of grassland birds and their nests in northern mixed-grass prairie ecosystems.

My analysis of vegetation conditions among treatments within the rest-rotation grazing system showed that this system created patch-size heterogeneity in rangeland vegetation structure among treatments, as conceptualized by previous researchers (Hagen et al. 2004, With et al. 2008, Toombs et al. 2010). Pastures deferred from grazing the

previous year had significantly ( $p < 0.05$ ) higher visual obstruction, residual grass height, and litter depth, and significantly lower bare ground than the two grazed treatments, and the post-seed ripe grazing treatment had significantly lower residual grass coverage than the other two treatments.

The rest-rotation grazing systems in my study area also created patches of distinct vegetation structure when compared to adjacent pastures in two more commonly employed grazing systems, season-long and summer-rotation grazing. I found that grazed pastures within the rest-rotation grazing system were characterized by lower residual grass height and density, lower litter depth, and higher bare ground coverage compared to the other two grazing systems within my study area. However, it appears the rest-rotation grazing systems within my study area failed to create structurally distinct vegetation conditions for species which require dense-grass habitats, when compared to adjacent pastures managed under the two other grazing systems. Results from my assessment of vegetation conditions were supported by the relationship I found between abundance of grasshopper sparrows, the dense-grass representative in my study, and grazing system, where season-long grazing systems supported the highest overall abundance of grasshopper sparrows. Evaluating the effects of grazing systems on the ecology of other dense-grass species in the northern mixed-grass prairie is necessary to support the implications of my results to this guild of grassland birds.

Hypothetically, pastures within the rest-rotation grazing system which experienced rest from livestock grazing during the previous grazing season should be characterized by the tallest, densest herbaceous vegetation structure, relative to adjacent

grazed pastures. However, average residual grass coverage was higher and bare ground coverage was lower in season-long and summer-rotation grazing systems than the rested treatment within the rest-rotation grazing system. Average litter depth between the rested treatment of the rest-rotation grazing system and the season-long grazing system was similar. As a result, the only structurally distinct grassland habitat that the rest-rotation grazing system appeared to create, relative to the other two grazing systems in my study area, were patches of short, sparse vegetation with high bare ground and low litter depth. These findings may contribute to the reason I did not find evidence that grassland bird community composition differed among treatments within the rest-rotation grazing system, or among grazing systems, and may indicate that the distinction among patches in terms of vegetation structure was not adequate for exhibition of species-specific habitat selection in my study area.

At the management-level, I found evidence for an effect of livestock grazing system and stocking rate on abundance of grassland birds and occupancy of mesocarnivores within my study area. Abundance of grasshopper sparrow ( $\beta = -0.10 \pm 0.03$ ), western meadowlark ( $\beta = -0.09 \pm 0.03$ ), and all grassland-associated species ( $\beta = -0.06 \pm 0.02$ ) showed a negative relationship with increasing stocking rate, and the effect was similar among grazing systems. Occupancy of mesocarnivores showed a positive relationship with increasing stocking rate ( $\beta = 1.64 \pm 1.10$ ). Within my study area in the northern mixed-grass prairie, low stocking rates ( $0 - 1 \text{ AUM} \cdot \text{ha}^{-1}$ ) appear to support overall higher abundances of grassland birds, and facilitate lower occupancy of mesocarnivores.

I found species-specific responses of grassland birds to livestock grazing management differ even at small spatial extents, and may be mediated by rangeland production. Two grassland obligate species, grasshopper sparrow and western meadowlark, showed support for an interaction between grazing system and rangeland production potential. Abundance of grasshopper sparrow, a dense-grass representative in my study area, showed a positive relationship with increasing rangeland production potential in season-long grazing systems, while a quadratic response was supported in summer-rotation and rest-rotation grazing systems, where abundance was maximized at intermediate estimates of production potential. Abundance of western meadowlark, typically a generalist species, was highest in summer-rotation grazing systems in sites of low rangeland production potential ( $<1,000 \text{ kg} \cdot \text{ha}^{-1}$ ) and lowest in summer-rotation systems in sites of high production potential ( $>1,500 \text{ kg} \cdot \text{ha}^{-1}$ ), while the effect was similar between rest-rotation and season-long grazing systems. The vesper sparrow, a sparse-grass representative in my study area, showed support for an effect of grazing system, where abundance was highest in summer-rotation grazing systems, followed by rest-rotation and season-long grazing systems.

A caveat to making management recommendations based on estimates of abundance is the potential dissociation between abundance and demography (Van Horne 1983, Bock and Jones 2004). However, estimates of avian abundances within native landscapes that are characterized by light human disturbance likely make reliable indices of habitat quality (Bock and Jones 2004). Habitats characterized by greater alteration from their native form have a higher probability of functioning as ecological sinks, where

disturbed habitats appear desirable and are selected by more individuals, but these individuals ultimately experience lower reproductive output (Van Horne 1983). Further research is needed to evaluate the effects of livestock grazing management on the demography of grassland birds in northern mixed-grass prairie ecosystems.

Occupancy of mesocarnivores was highest in rest-rotation grazing systems, followed by season-long and summer-rotation systems. Previous researchers have suggested that predator foraging efficiency may be higher in areas of low vegetation height and density (Johnson and Temple 1990, Sutter and Ritchison 2005). Grazing systems with more intensive manipulation of livestock, such as rest-rotation grazing, will result in even forage utilization and lower within-pasture heterogeneity in vegetation structure as a result of reduced cattle forage selectivity (Coughenour 1991, Hart et al. 1993, Holechek et al. 2011). Mesocarnivores in my study area may have higher site occupancy in pastures managed with rest-rotation grazing due to increased foraging or hunting efficiency in a system which creates patch-size heterogeneity among pastures by reducing the amount of small-scale, within-pasture heterogeneity. Additionally, the overall shorter, sparser vegetation structure of pastures within the rest-rotation grazing system in my study area may facilitate increased mesocarnivore foraging efficiency.

My research provides an evaluation of the effects of livestock grazing management, specifically grazing system type and stocking rate, on the ecology of grassland birds and mesocarnivores in northern mixed grass prairie rangelands of northeastern Montana. Overall, I did not find support for a noticeable benefit of rest-rotation grazing on abundance or diversity of grassland birds relative to two more

commonly employed grazing systems, season-long and summer-rotation grazing. Significant interactions between grazing management and local rangeland productivity may severely limit our ability to recommend general management practices to benefit grassland bird populations, or even specific species, on rangelands managed for livestock production. Thus, regional or distribution-wide guidelines for livestock grazing management are inappropriate in terms of grassland bird conservation efforts. Rather, efforts for conserving grassland birds on rangelands in the northern mixed-grass prairie should identify specific conservation goals and management should occur at the local, individual pasture scale.

I found evidence that occupancy of mesocarnivores is higher in rest-rotation grazing systems, relative to season-long and summer-rotation grazing systems. Grassland bird nest depredation is often opportunistic (Vickery et al. 1992a), so higher mesocarnivore occupancy has the potential to negatively impact grassland bird reproductive output if occupancy and avian nest depredation are correlated, as previous research has suggested (Burr et al. 2017). Further research is necessary to evaluate the demographic responses of grassland birds to livestock grazing systems and stocking rates, especially in the context of variable rangeland production potential and mesocarnivore occupancy.

My research was conducted during two years of average precipitation conditions. Further research may be necessary to evaluate the effects of rest-rotation livestock grazing on grassland bird ecology in years of drought conditions. However, if my results are applicable during years of average and extreme precipitation and weather conditions,

allocating funds to establish conservations easements which keep grassland ecosystems from further human development, rather than for the implementation of rest-rotation grazing systems would be more beneficial for the conservation of grassland birds in the northern mixed-grass prairie.

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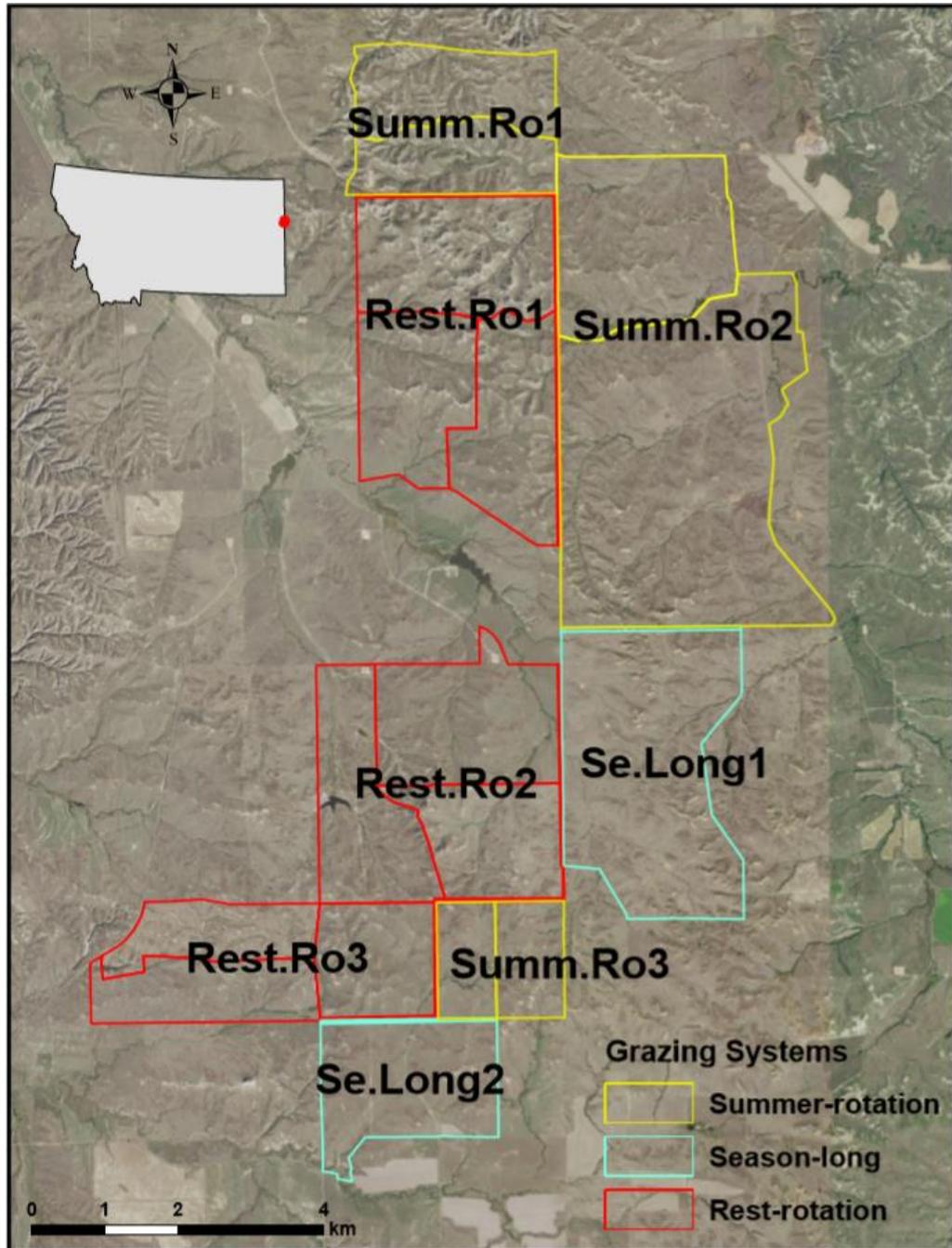
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APPENDICES

APPENDIX A

PASTURE LOCATIONS WITHIN THE STUDY AREA

Figure A1. Pasture locations in eastern Montana during 2016–17.



APPENDIX B

ECOLOGICAL SITES AND ASSOCIATED RANGELAND PRODUCTION  
POTENTIAL VALUES WITHIN THE STUDY AREA

Table B1. Total areas of each ecological site and associated values of rangeland production potential on 8 pastures in eastern Montana and western North Dakota during 2016–17. Representative values of production potential are based on Soil Survey Geographic Database (SSURGO) ecological site data from the Natural Resources Conservation Service (NRCS) Web Soil Survey.

<b>Ecological Site Description</b>	<b>Representative Value<sup>1</sup></b>	<b>Total Area<sup>2</sup></b>
Wetland	6613	0.08
Wet Meadow	3923	0.25
Loamy Overflow	3587	47.38
Sandy Terrace	3363	1.56
Loamy Terrace	3250	22.93
Saline Lowland	2802	14.70
Sands	2802	86.27
Closed Depression	2690	0.05
Loamy	2690	688.0
Sandy	2690	114.48
Clayey	2130	132.08
Limy Sands	2018	6.44
Limy Residual	1905	1817.25
Claypan	1681	87.40
Shallow Loamy	1569	1189.01
Shallow Sandy	1569	32.59
Clayey-Steep	1233	588.33
Thin Loamy	1121	125.16
Shallow Clayey	1009	24.36
Badlands Fan	897	1119.20
Thin Claypan	897	27.19
Very Shallow	897	160.01
Badland	0	402.67
Non-site <sup>3</sup>	0	20.95
Rock Outcrop	0	17.73

<sup>1</sup> Representative Value (RV) defined as the rangeland production ( $\text{kg} \cdot \text{ha}^{-1}$ ) during a year with average precipitation.

<sup>2</sup> Total area (hectares) of each ecological site and associated value of rangeland production potential within the study area.

<sup>3</sup> Open water classified as Non-site.

APPENDIX C

GRASSLAND BIRD SPECIES LIST

Table C1. Bird species observed during 2016 and 2017 avian point count surveys at 610 sites on 8 pastures managed for livestock grazing in eastern Montana.

4-letter Code	Common Name	Scientific Name
AMCR	American Crow	<i>Corvus brachyrhynchos</i>
AMGO	American Goldfinch	<i>Carduelis tristis</i>
AMKE	American Kestrel	<i>Falco sparverius</i>
AMRO	American Robin	<i>Turdus migratorius</i>
AMWI	American Widgeon	<i>Anas americana</i>
BAIS*	Baird's Sparrow	<i>Ammodramus bairdii</i>
BANS	Bank Swallow	<i>Riparia riparia</i>
BAOR	Baltimore Oriole	<i>Icterus galbula</i>
BARS	Barn Swallow	<i>Hirundo rustica</i>
BBMA	Black-billed Magpie	<i>Pica hudsonia</i>
BEKI	Belted Kingfisher	<i>Megaceryle alcyon</i>
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>
BHGR	Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>
BOBO*	Bobolink	<i>Dolichonyx oryzivorus</i>
BRBL	Brewer's Blackbird	<i>Euphagus cyanocephalus</i>
BRSP*	Brewer's Sparrow	<i>Spizella breweri</i>
BRTH	Brown Thrasher	<i>Toxostoma rufum</i>
BUOR	Bullock's Oriole	<i>Icterus bullockii</i>
CAGO	Canada Goose	<i>Branta canadensis</i>
CCSP*	Clay-colored Sparrow	<i>Spizella pallida</i>
CEDW	Cedar Waxwing	<i>Bombycilla cedrorum</i>
CHSP*	Chipping Sparrow	<i>Spizella passerina</i>
CLSW	Cliff Swallow	<i>Petrochelidon pyrrhonota</i>
COGR	Common Grackle	<i>Quiscalus quiscula</i>
CONI*	Common Nighthawk	<i>Chordeiles minor</i>
COYE*	Common Yellowthroat	<i>Geothlypis trichas</i>
EABL*	Eastern Bluebird	<i>Sialia sialis</i>
EAKI*	Eastern Kingbird	<i>Tyrannus tyrannus</i>
EUST	European Starling	<i>Sturnus vulgaris</i>
FISP*	Field Sparrow	<i>Spizella pusilla</i>
GRCA	Gray Catbird	<i>Dumetella carolinensis</i>
GRSP*	Grasshopper Sparrow	<i>Ammodramus savannarum</i>
HAWO	Hairy Woodpecker	<i>Leuconotopicus villosus</i>
HOLA*	Horned Lark	<i>Eremophila alpestris</i>
HOWR	House Wren	<i>Troglodytes aedon</i>
KILL*	Killdeer	<i>Charadrius vociferus</i>
LARB*	Lark Bunting	<i>Calamospiza melanocorys</i>

Table C1. continued

4-letter Code	Common Name	Scientific Name
LASP*	Lark Sparrow	<i>Chondestes grammacus</i>
LEFL	Least Flycatcher	<i>Empidonax minimus</i>
LOSH*	Loggerhead Shrike	<i>Lanius ludovicianus</i>
MAGO*	Marbled Godwit	<i>Limosa fedoa</i>
MALL	Mallard	<i>Anas platyrhynchos</i>
MOBL*	Mountain Bluebird	<i>Sialia currucoides</i>
MODO*	Mourning Dove	<i>Zenaida macroura</i>
NOFL	Northern Flicker	<i>Colaptes auratus</i>
NOHA*	Northern Harrier	<i>Circus hudsonius</i>
NRWS	Northern Rough-Winged Swallow	<i>Stelgidopteryx serripennis</i>
OROR	Orchard Oriole	<i>Icterus spurius</i>
PRFA*	Prairie Falcon	<i>Falco mexicanus</i>
RNEP*	Ring-necked Pheasant	<i>Phasianus colchicus</i>
ROPI	Rock Pigeon	<i>Columba livia</i>
ROWR	Rock Wren	<i>Salpinctes obsoletus</i>
RTHA	Red-tailed Hawk	<i>Buteo jamaicensis</i>
RWBL*	Red-winged Blackbird	<i>Agelaius phoeniceus</i>
SAPH*	Say's Phoebe	<i>Sayornis saya</i>
SPPI*	Sprague's Pipit	<i>Anthus spragueii</i>
SPTO	Spotted Towhee	<i>Pipilo maculatus</i>
STGR*	Sharp-tailed Grouse	<i>Tympanuchus phasianellus</i>
TRES	Tree Swallow	<i>Hirundo nigricans</i>
UPSA*	Upland Sandpiper	<i>Bartramia longicauda</i>
VESP*	Vesper Sparrow	<i>Pooecetes gramineus</i>
WEKI*	Western Kingbird	<i>Tyrannus verticalis</i>
WEME*	Western Meadowlark	<i>Sturnella neglecta</i>
WEWP	Western Wood-Pewee	<i>Contopus sordidulus</i>
WIFL	Willow Flycatcher	<i>Empidonax traillii</i>
YBCH	Yellow-breasted Chat	<i>Icteria virens</i>
YHBL*	Yellow-headed Blackbird	<i>Xanthocephalus xanthocephalus</i>
YWAR	Yellow Warbler	<i>Dendroica petechia</i>

\*Indicates grassland-associated species. 4-letter codes based on American Ornithological Society's (AOS) checklist of North American birds.

APPENDIX D

MODEL SELECTION RESULTS DESCRIBING SUPPORT FOR EFFECTS ON  
GRASSLAND BIRD DETECTION PROBABILITY AND LOCAL ABUNDANCE

Table D1. Support for candidate models predicting observation-level effects on grassland bird detection probability in eastern Montana during 2016-17. Included are the effects of year, observer, Julian day, time of day, wind speed, slope, shrub cover, and shrub height. The number of parameters (K), AIC<sub>c</sub> values, ΔAIC<sub>c</sub> values, model weights ( $w_i$ ), and cumulative model weights (Cum  $w_i$ ) are reported.

Model	K	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$w_i$	Cum $w_i$
<b>Grasshopper Sparrow</b>					
Day <sup>2</sup> + Time + Slope <sup>2</sup> + Shrub Height <sup>2</sup>	9	4378.75	0.00	0.54	0.54
Day <sup>2</sup> + Time + Slope <sup>2</sup> + Shrub Height <sup>2</sup> + Observer	11	4380.93	2.17	0.18	0.72
Day <sup>2</sup> + Time + Slope <sup>2</sup>	7	4381.06	2.31	0.17	0.89
Day <sup>2</sup> + Time + Slope <sup>2</sup> + Shrub Height <sup>2</sup> + Observer + Wind	12	4382.82	4.07	0.07	0.96
Day <sup>2</sup> + Time + Slope <sup>2</sup> + Shrub Height <sup>2</sup> + Observer + Wind + Year	13	4384.75	6.00	0.03	0.99
Null Model	2	4450.64	71.88	0.00	1.00
<b>Vesper Sparrow</b>					
Year + Day <sup>2</sup> + Wind	6	3054.34	0.00	0.44	0.44
Year + Day <sup>2</sup> + Wind + Shrub Height	7	3055.69	1.35	0.22	0.67
Year + Day <sup>2</sup> + Wind + Shrub Height + Shrub Cover	8	3056.49	2.15	0.15	0.82
Year + Wind	4	3057.93	3.60	0.07	0.89
Year + Day <sup>2</sup> + Wind + Shrub Height + Shrub Cover + Slope	9	3058.22	3.88	0.06	0.95
Year + Day <sup>2</sup> + Wind + Shrub Height + Shrub Cover + Slope + Time	10	3060.16	5.82	0.02	0.98
Null Model	2	3071.97	17.63	0.00	1.00
<b>Western Meadowlark</b>					
Year + Day + ln(Wind) + Slope	6	4898.46	0.00	0.50	0.50
Year + Day + Slope	5	4899.35	0.89	0.32	0.82
Year + Day + ln(Wind) + Slope + Observer	8	4901.46	3.00	0.11	0.93
Year + Day + ln(Wind) + Slope + Observer + Shrub Cover	9	4903.42	4.96	0.04	0.97
Year + Day + ln(Wind) + Slope + Observer + Shrub Cover + Time	10	4905.40	6.94	0.02	0.99
Null Model	2	4965.84	67.37	0.00	1.00

Table D1. continued

<b>Model</b>	<b>K</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b>w<sub>i</sub></b>	<b>Cum w<sub>i</sub></b>
<b>Grassland-Associated Species</b>					
Year + Observer + Day <sup>2</sup> + Time + ln(Wind) + Slope	10	7352.04	0.00	0.47	0.47
Year + Observer + Day <sup>2</sup> + Time + ln(Wind) + Slope + Shrub Height	11	7353.25	1.21	0.26	0.72
Year + Day <sup>2</sup> + Time + ln(Wind) + Slope	8	7354.19	2.14	0.16	0.88
Year + Observer + Day <sup>2</sup> + Time + ln(Wind) + Slope + Shrub Height + Shrub Cover	12	7355.19	3.15	0.10	0.98
Year + Time + ln(Wind) + Slope	6	7358.50	6.46	0.02	1.00
Null Model	2	7464.29	112.24	0.00	1.00

<sup>2</sup> Variable indicates support for a quadratic effect.

ln(variable) indicates support for a pseudo-threshold effect.

Table D2. Support for candidate models predicting local habitat-level effects on grassland bird abundance in eastern Montana during 2016-17. Included are the effects of visual obstruction (VOR), standard deviation of VOR (sdVOR), residual grass height, residual grass coverage, forb coverage, litter depth, bare ground coverage, shrub cover, shrub height, and wooded coulee area. The number of parameters (K), AIC<sub>c</sub> values, ΔAIC<sub>c</sub> values, model weights (*w<sub>i</sub>*), and cumulative model weights (Cum *w<sub>i</sub>*) are reported.

<b>Model</b>	<b>K</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b><i>w<sub>i</sub></i></b>	<b>Cum <i>w<sub>i</sub></i></b>
<b>Grasshopper Sparrow</b>					
Residual Height <sup>2</sup> + Litter Depth <sup>2</sup> + Bare Ground <sup>2</sup> + Shrub Cover + ln(Coulee Area)	17	4146.30	0.00	0.35	0.35
Residual Height <sup>2</sup> + Litter Depth <sup>2</sup> + Bare Ground <sup>2</sup> + Shrub Cover + ln(Coulee Area) + Shrub Height	18	4146.75	0.45	0.28	0.63
Residual Height <sup>2</sup> + Litter Depth <sup>2</sup> + Bare Ground <sup>2</sup> + Shrub Cover + ln(Coulee Area) + Shrub Height + ln(Residual)	19	4147.65	1.35	0.18	0.81
Residual Height <sup>2</sup> + Litter Depth <sup>2</sup> + Bare Ground <sup>2</sup> + Shrub Cover + ln(Coulee Area) + Shrub Height + ln(Residual) + Forb	20	4149.18	2.88	0.08	0.90
Residual Height <sup>2</sup> + Litter Depth <sup>2</sup> + Shrub Cover + ln(Coulee Area)	15	4149.86	3.56	0.06	0.96
Residual Height <sup>2</sup> + Litter Depth <sup>2</sup> + Bare Ground <sup>2</sup> + Shrub Cover + ln(Coulee Area) + Shrub Height + ln(Residual) + Forb + sdVOR	21	4150.82	4.52	0.04	0.99
Null Model	2	4450.64	304.34	0.00	1.00
<b>Vesper Sparrow</b>					
VOR + Forb + Litter Depth + Bare Ground + ln(Shrub Cover)	11	3026.26	0.00	0.25	0.25
VOR + Forb + Litter Depth + Bare Ground + ln(Shrub Cover) + Residual Height	12	3026.84	0.58	0.19	0.43
VOR + Litter Depth + Bare Ground + ln(Shrub Cover)	10	3027.24	0.99	0.15	0.59
VOR + Forb + Litter Depth + Bare Ground + ln(Shrub Cover) + Residual Height + Residual	13	3027.25	0.99	0.15	0.74
VOR + Forb + Litter Depth + Bare Ground + ln(Shrub Cover) + Residual Height + Residual + Coulee Area	14	3028.05	1.79	0.10	0.84
Litter Depth + Bare Ground + ln(Shrub Cover)	9	3028.26	2.01	0.09	0.93
VOR + Forb + Litter Depth + Bare Ground + ln(Shrub Cover) + Residual Height + Residual + Coulee Area + sdVOR	15	3029.92	3.66	0.04	0.97
Null Model	2	3071.97	45.71	0.00	1.00

Table D2. continued

Model	K	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	Cum w <sub>i</sub>
<b>Western Meadowlark</b>					
VOR + Residual + ln(Litter Depth) + Bare Ground + ln(Forb)	11	4830.19	0.00	0.32	0.32
VOR + Residual + ln(Litter Depth) + Bare Ground + ln(Forb) + Residual Height	12	4831.26	1.07	0.19	0.51
VOR + Residual + ln(Litter Depth) + Bare Ground + ln(Forb) + Residual Height + Shrub Cover	13	4831.36	1.17	0.18	0.68
VOR + Residual + ln(Litter Depth) + ln(Forb)	10	4831.52	1.33	0.16	0.85
VOR + Residual + ln(Litter Depth) + Bare Ground + ln(Forb) + Residual Height + Shrub Cover + sdVOR	14	4832.78	2.59	0.09	0.94
VOR + Residual + ln(Litter Depth) + Bare Ground + ln(Forb) + Residual Height + Shrub Cover + sdVOR + Coulee Area	15	4834.44	4.25	0.04	0.97
Null Model	2	4965.84	135.65	0.00	1.00
<b>Grassland-Associated Species</b>					
VOR + Residual + Litter Depth <sup>2</sup> + Forb + ln(Coulee Area)	16	7290.83	0.00	0.35	0.35
VOR + Residual + Litter Depth <sup>2</sup> + Forb + ln(Coulee Area) + Shrub Height	17	7291.27	0.44	0.28	0.62
VOR + Litter Depth <sup>2</sup> + Forb + ln(Coulee Area)	15	7292.42	1.59	0.16	0.78
VOR + Residual + Litter Depth <sup>2</sup> + Forb + ln(Coulee Area) + sdVOR	18	7292.63	1.80	0.14	0.92
VOR + Residual + Litter Depth <sup>2</sup> + Forb + ln(Coulee Area) + sdVOR + Bare Ground	19	7294.59	3.77	0.05	0.97
VOR + Residual + Litter Depth <sup>2</sup> + Forb + ln(Coulee Area) + sdVOR + Bare Ground + Shrub Cover	20	7296.57	5.74	0.02	0.99
Null Model	2	7464.29	173.46	0.00	1.00

<sup>2</sup> Variable indicates support for a quadratic effect.

ln(variable) indicates support for a pseudo-threshold effect.

Table D3. Support for candidate models predicting landscape-level effects on grassland bird abundance in eastern Montana during 2016-17. Included are the effects of wooded coulee area (500-m and 1,000-m scales) and fence density (500-m and 1,000-m scales). The number of parameters (K), AIC<sub>c</sub> values, ΔAIC<sub>c</sub> values, model weights ( $w_i$ ), and cumulative model weights (Cum  $w_i$ ) are reported.

<b>Model</b>	<b>K</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b><math>w_i</math></b>	<b>Cum <math>w_i</math></b>
<b>Grasshopper Sparrow</b>					
Coulee Area <sup>2</sup> (1,000 m) + ln(Fence Density; 500 m)	12	4297.63	0.00	0.95	0.95
Coulee Area <sup>2</sup> (1,000 m)	11	4303.69	6.06	0.05	1.00
Null Model	9	4378.75	81.12	0.00	1.00
<b>Vesper Sparrow</b>					
ln(Coulee Area; 1,000 m) + Fence Density (1,000 m)	8	3044.03	0.00	0.57	0.57
ln(Coulee Area; 1,000 m)	7	3044.59	0.56	0.43	1.00
Null Model	6	3054.34	10.31	0.00	1.00
<b>Western Meadowlark</b>					
Coulee Area (1,000 m)	7	4896.91	0.00	0.52	0.52
Coulee Area (1,000 m) + Fence Density (500 m)	8	4898.41	1.49	0.24	0.76
Null Model	6	4898.46	1.55	0.24	1.00
<b>Grassland-Associated Species</b>					
ln(Coulee Area; 500 m) + Fence Density (1,000 m)	12	7347.19	0.00	0.72	0.72
Fence Density (1,000 m)	11	7349.59	2.40	0.22	0.94
Null Model	10	7352.04	4.85	0.06	1.00

<sup>2</sup> Variable indicates support for a quadratic effect.

ln(variable) indicates support for a pseudo-threshold effect.

Table D4. Support for candidate models predicting management-level effects on grassland bird abundance in eastern Montana during 2016-17. Included are the effects of grazing system, stocking rate, and rangeland production potential. The number of parameters (K), AIC<sub>c</sub> values, ΔAIC<sub>c</sub> values, model weights (*w<sub>i</sub>*), and cumulative model weights (Cum *w<sub>i</sub>*) are reported.

<b>Model</b>	<b>K</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b><i>w<sub>i</sub></i></b>	<b>Cum <i>w<sub>i</sub></i></b>
<b>Grasshopper Sparrow</b>					
Grazing System × Rangeland Production Potential <sup>2</sup> + Stocking Rate	16	4168.27	0.00	0.85	0.85
Rangeland Production Potential <sup>2</sup> + Stocking Rate	12	4173.01	4.73	0.08	0.93
Grazing System + Rangeland Production Potential <sup>2</sup> + Stocking Rate	14	4174.25	5.98	0.04	0.98
Grazing System × Stocking Rate + Rangeland Production Potential <sup>2</sup>	14	4175.95	7.67	0.02	1.00
Null Model	9	4378.75	210.48	0.00	1.00
<b>Vesper Sparrow</b>					
Grazing System + Rangeland Production Potential	9	3035.42	0.00	0.61	0.61
Grazing System + Rangeland Production Potential + Stocking Rate	10	3036.67	1.25	0.33	0.93
Rangeland Production Potential	7	3042.53	7.11	0.02	0.95
Grazing System × Rangeland Production Potential	9	3042.99	7.57	0.01	0.96
Stocking Rate + Rangeland Production Potential	8	3043.03	7.61	0.01	0.98
Grazing System	8	3043.92	8.50	0.01	0.99
Null Model	6	3054.34	18.92	0.00	1.00
<b>Western Meadowlark</b>					
ln(Stocking Rate) + ln(Rangeland Production Potential)	8	4880.16	0.00	0.57	0.57
Grazing System × ln(Rangeland Production Potential) + ln(Stocking Rate)	10	4881.91	1.75	0.24	0.81
Grazing System + ln(Rangeland Production Potential) + ln(Stocking Rate)	10	4884.05	3.89	0.08	0.89
Grazing System × ln(Stocking Rate)+ ln(Rangeland Production Potential)	10	4884.11	3.95	0.08	0.97
ln(Stocking Rate)	7	4888.71	8.56	0.01	0.98
ln(Rangeland Production Potential)	7	4889.30	9.17	0.01	0.99
Null Model	6	4898.46	18.31	0.00	1.00

Table D4. continued

<b>Model</b>	<b>K</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b>w<sub>i</sub></b>	<b>Cum w<sub>i</sub></b>
<b>Grassland-Associated Species</b>					
Grazing System + Rangeland Production Potential + Stocking Rate	14	7338.12	0.00	0.35	0.35
Grazing System + Stocking Rate	13	7338.48	0.36	0.29	0.64
Rangeland Production Potential + Stocking Rate	12	7339.54	1.42	0.17	0.81
Stocking Rate	11	7340.56	2.45	0.10	0.91
Grazing System × Stocking Rate + Rangeland Production Potential	14	7342.47	4.36	0.04	0.95
Grazing System × Rangeland Production Potential + Stocking Rate	14	7343.30	5.18	0.03	0.98
Null Model	10	7352.04	13.93	0.00	1.00

<sup>2</sup> Variable indicates support for a quadratic effect.

ln(variable) indicates support for a pseudo-threshold effect.

APPENDIX E

PREDICTIONS OF GRASSLAND BIRD DETECTION PROBABILITIES

Figure E1. Variables influencing detection probabilities of grasshopper sparrows in eastern Montana during 2016-17 were Julian day, time of day, slope, and shrub height.

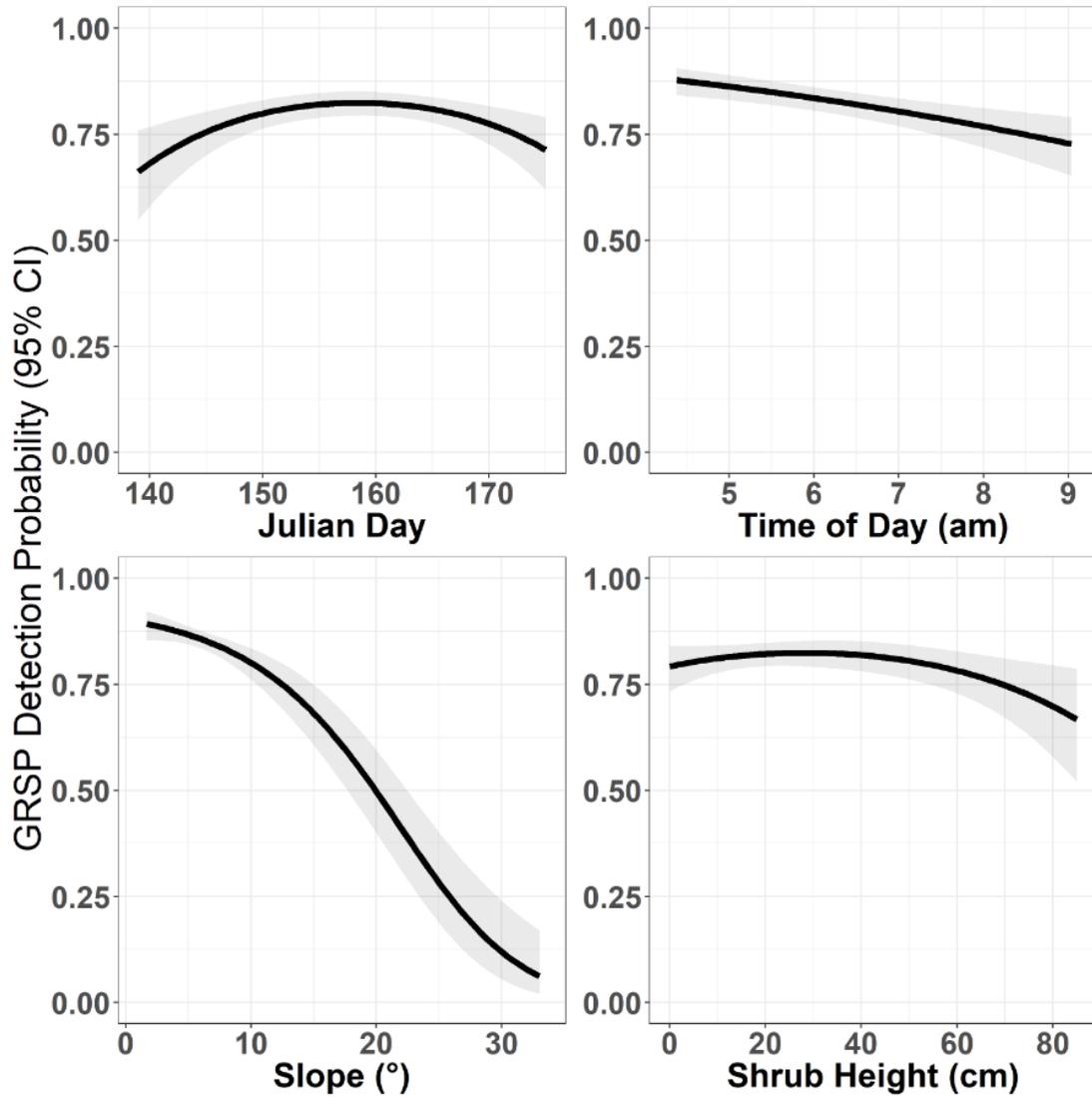


Figure E2. Variables influencing detection probabilities of vesper sparrows in eastern Montana during 2016-17 were year, Julian day, and wind speed.

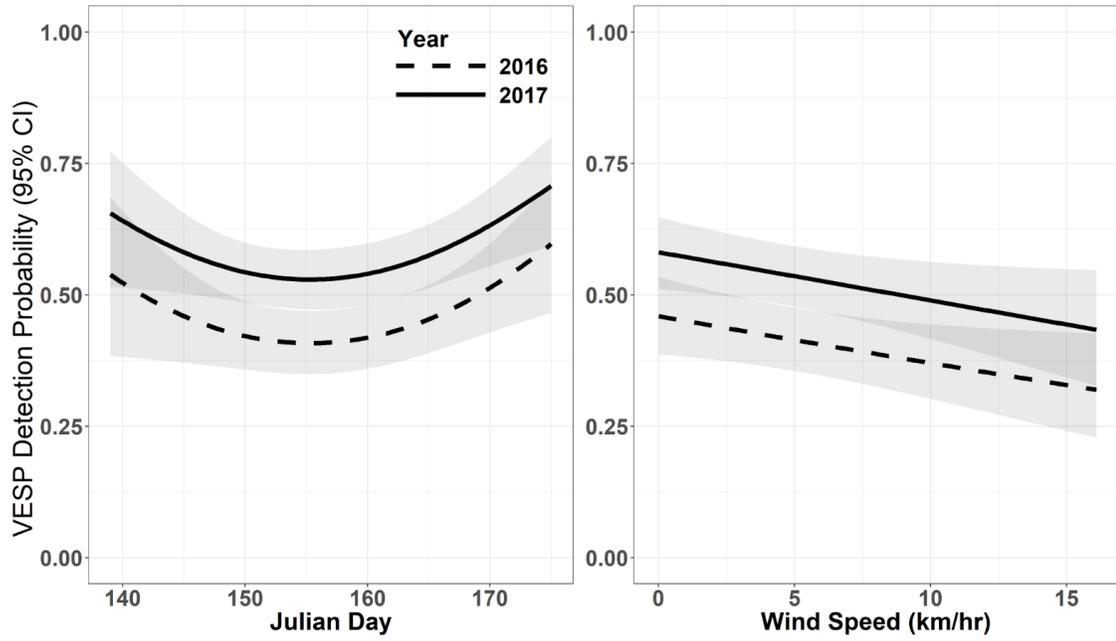


Figure E3. Variables influencing detection probabilities of western meadowlark in eastern Montana during 2016-17 were year, Julian day, and time of day.

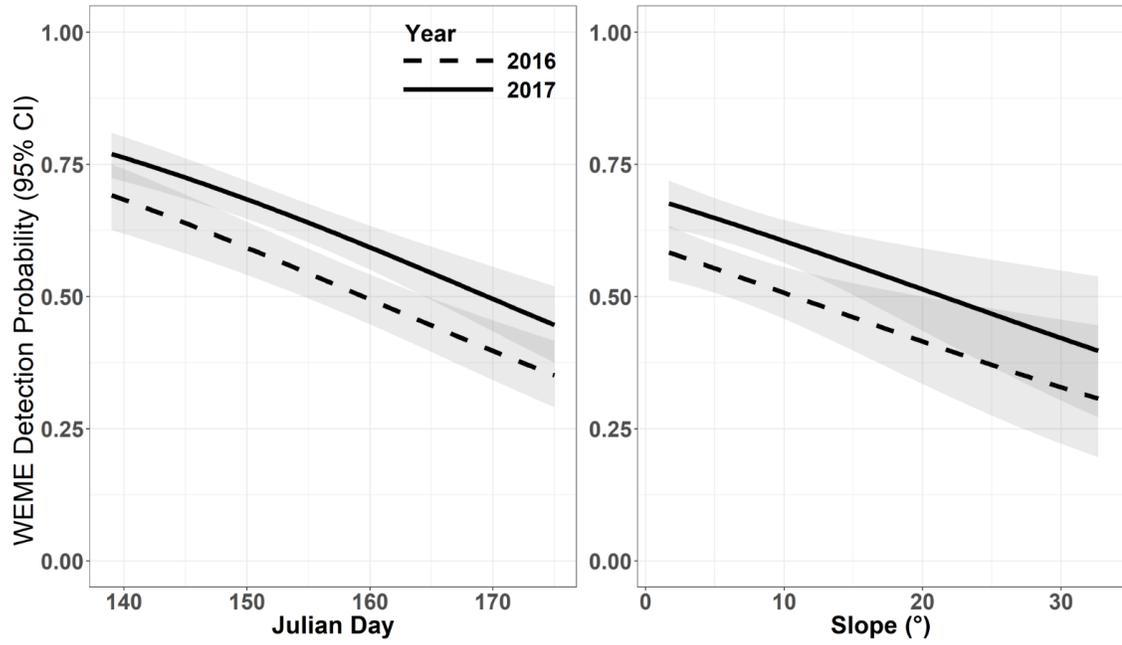
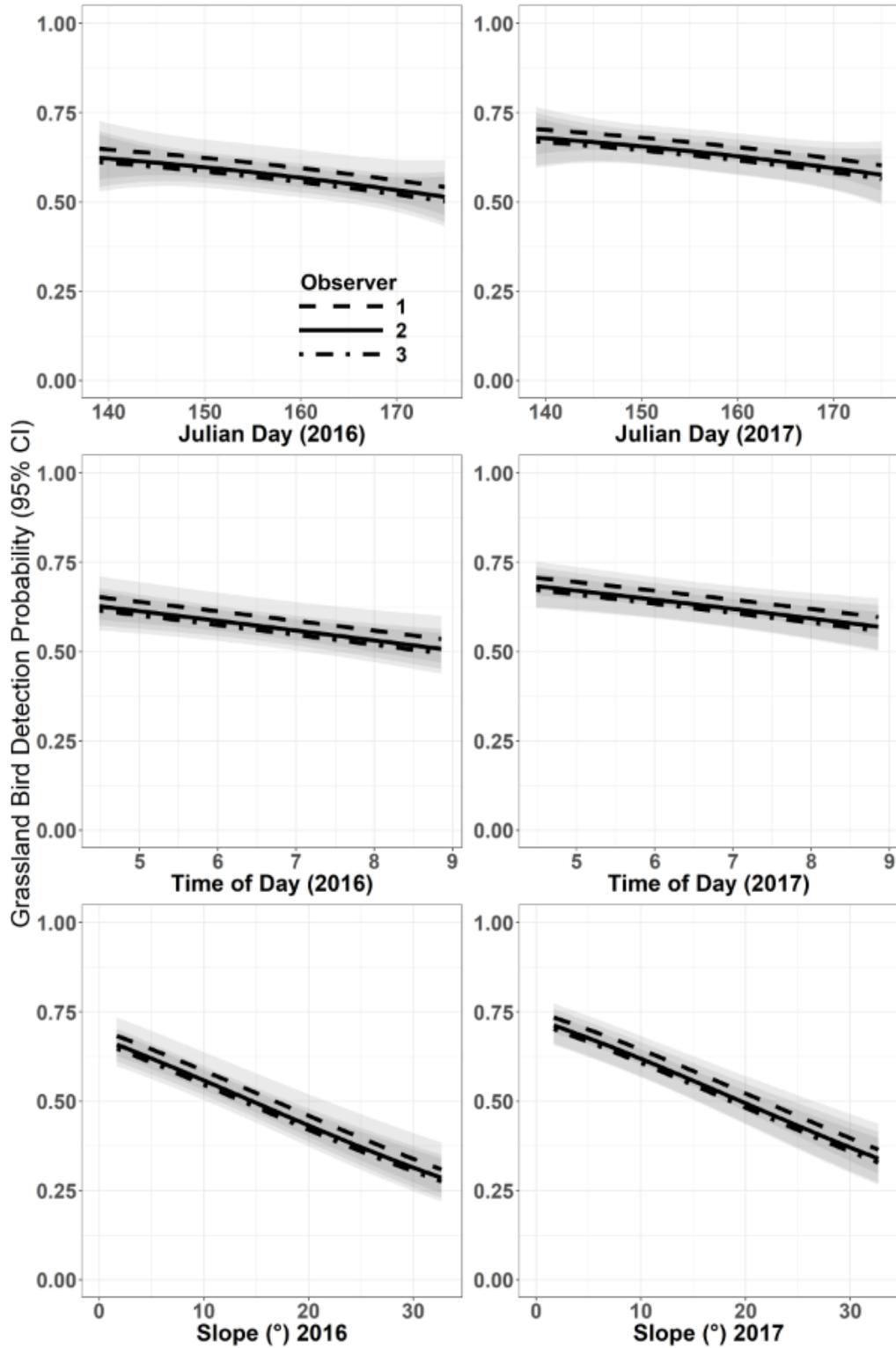


Figure E4. Variables influencing detection probabilities of grassland-associated species in eastern Montana during 2016-17 were year, observer, Julian day, time, and slope.



APPENDIX F

STANDARDIZED COVARIATE ESTIAMTES FOR THE TOP MODELS OF  
GRASSLAND BIRD DETECTION PROBABILITY AND ABUNDANCE

Table F1. Standardized covariate estimates for the top models of three focal species and all grassland-associated species combined in eastern Montana, 2016–17.

	Grasshopper Sparrow		Vesper Sparrow		Western Meadowlark		All Grassland Birds	
	$\beta$	SE	$\beta$	SE	$\beta$	SE	$\beta$	SE
<b>Detection probability</b>								
Intercept	1.542	0.010	-0.367	0.127	0.080	0.096	0.418	0.113
Year, 2017			0.490	0.142	0.391	0.106	0.250	0.084
Observer2							-0.110	0.093
Observer3							-0.160	0.069
Day	0.040	0.055	0.069	0.072	-0.326	0.051	-0.104	0.037
Day <sup>2</sup>	-0.161	0.046	0.139	0.057			-0.007	0.030
Time	-0.224	0.059					-0.118	0.037
Time <sup>2</sup>								
Slope	-0.524	0.112			-0.188	0.056	-0.258	0.031
Slope <sup>2</sup>	-0.076	0.039						
Shrub height	0.032	0.071						
Shrub height <sup>2</sup>	-0.065	0.031						
Wind speed			-0.149	0.071				
ln(Wind speed)					-0.079	0.047	-0.076	0.034
<b>Abundance, local habitat<sup>a</sup></b>								
Intercept	0.859	0.043	0.047	0.055	0.968	0.039	2.185	0.030
Residual grass coverage					-0.113	0.036	-0.036	0.019
Residual grass coverage <sup>2</sup>								
Residual grass height	0.051	0.037						
Residual grass height <sup>2</sup>	-0.054	0.021						
Litter depth	0.199	0.043	0.113	0.053			0.145	0.022
Litter depth <sup>2</sup>	-0.053	0.017					-0.041	0.010
ln(Litter depth)					0.224	0.050		
Bare ground	-0.112	0.042	0.179	0.054	-0.078	0.043		
Bare ground <sup>2</sup>	-0.064	0.028						
Shrub cover	-0.102	0.040						
ln(Wooded coulee)	-0.336	0.038					0.050	0.016

Table F1. continued

	Grasshopper Sparrow		Vesper Sparrow		Western Meadowlark		All Grassland Birds	
	$\beta$	SE	$\beta$	SE	$\beta$	SE	$\beta$	SE
VOR			-0.105	0.054	-0.156	0.035	-0.049	0.018
Forb			0.078	0.045			0.046	0.016
ln(Forb)					0.091	0.030		
ln(Shrub cover)			0.169	0.053				
<b>Abundance, landscape habitat</b>								
Intercept	0.946	0.039	0.056	0.054	1.018	0.038	2.159	0.028
Wooded coulee (1000 m)	-0.123	0.037			-0.053	0.028		
Wooded coulee <sup>2</sup> (1000 m)	-0.172	0.035						
ln(Wooded coulee 500 m)							0.033	0.016
ln(Wooded coulee 1000 m)			0.165	0.047				
Fence density (1000 m)			-0.071	0.045			-0.034	0.015
ln(Fence density; 500 m)	-0.077	0.027						
<b>Abundance, management</b>								
Intercept	0.866	0.039	0.018	0.072	1.011	0.038	2.133	0.034
Season-long grazing			-0.160	0.138			0.013	0.046
Summer-rotation grazing			0.247	0.097			0.079	0.035
Stocking rate	-0.104	0.030					-0.056	0.017
Stocking rate <sup>2</sup>								
ln(Stocking rate)					-0.087	0.025		
Rangeland production potential			-0.151	0.046			0.029	0.019
ln(Rangeland production potential)					0.106	0.033		
Season-long x Range production potential	0.246	0.109						
Summer-rotation x Range production potential	0.597	0.077						

Table F1. continued

	Grasshopper Sparrow		Vesper Sparrow		Western Meadowlark		All Grassland Birds	
	$\beta$	SE	$\beta$	SE	$\beta$	SE	$\beta$	SE
Rest-rotation x Range production potential	0.378	0.050						
Season-long x Range production potential <sup>2</sup>	-0.019	0.066						
Summer-rotation x Range production potential <sup>2</sup>	-0.298	0.076						
Rest-rotation x Range production potential <sup>2</sup>	-0.182	0.035						

<sup>a</sup> Abbreviations: VOR, visual obstruction reading.

<sup>2</sup> Variable indicates support for a quadratic effect.

ln(variable) indicates support for a pseudo-asymptotic effect.

APPENDIX G

LOCAL VEGETATION CONDITIONS AMONG GRAZING SYSTEMS AND  
AMONG TREATMENTS WITHIN REST-ROTATION GRAZING SYSTEMS

Table G1. Local vegetation conditions among three grazing systems in eastern Montana during 2016–17. Mean, standard error, minimum and maximum values presented for each variable. *P*-values reported for Kruskal-Wallis Test of significance among the three grazing systems.

	Season-long (n = 120)				Rest-rotation (n = 300)				Summer-rotation (n = 190)				K-W Test <sup>a</sup>
	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	<i>p</i> -value
Visual obstruction (VOR)	0.92	0.05	0.0	2.5	0.90	0.04	0.07	5.0	0.95	0.04	0.07	5.1	0.366
Standard deviation of VOR	0.61	0.04	0.0	3.4	0.75	0.04	0.18	4.6	0.72	0.04	0.18	4.6	0.314
% Residual grass coverage	47.6	1.5	8.3	83.5	37.7**	0.93	3.0	81.2	42.1**	1.2	3.3	81.3	0.000
Residual grass height (cm)	14.4	0.47	3.5	32.5	13.3	0.26	3.5	30.9	13.7	0.31	4.7	26.1	0.285
% Forb coverage	10.3	0.38	1.3	19.3	11.0	0.32	1.8	53.2	9.8**RR	0.32	0.67	26.3	0.052
Litter depth (cm)	1.6	0.07	0.40	4.3	1.3*SL	0.04	0.0	5.1	1.4	0.05	0.23	3.4	0.002
% Bare ground coverage	15.5	1.1	0.0	71.2	22.4**	0.81	0.33	85.3	19.8**	0.96	0.17	68.8	0.000
Shrub cover	3.5	0.57	0.0	48.5	6.4*SL	0.55	0.0	69.0	6.2*SL	0.62	0.0	44.8	0.000
Shrub height (cm)	18.5	1.2	0.0	59.3	25.2*SL	0.95	0.0	85.0	26.5*SL	1.1	0.0	76.7	0.000
% Wooded coulee (100-m)	0.52	0.21	0.0	16.9	1.8*SL	0.25	0.0	26.3	1.9*SL	0.33	0.0	24.5	0.000
% Wooded coulee (500-m)	0.81	0.10	0.0	4.5	2.0**	0.09	0.0	6.9	2.4**	0.14	0.0	11.1	0.000
% Wooded coulee (1000-m)	1.4	0.08	0.04	3.7	2.0**	0.06	0.52	4.8	2.6**	0.10	0.89	7.5	0.000
Fence density (m · ha <sup>-1</sup> ; 500-m)	6.3	0.60	0.0	22.1	10.5**	0.41	0.0	30.3	8.3**	0.53	0.0	28.4	0.000

Table G1. continued

	Season-long (n = 120)				Rest-rotation (n = 300)				Summer-rotation (n = 190)				K-W Test <sup>a</sup>
	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	<i>p</i> -value
Fence density (m · ha <sup>-1</sup> ; 1000-m)	8.7	0.36	0.0	20.0	12.9**	0.24	4.8	26.4	9.4**RR	0.39	0.0	17.9	0.000
Stocking rate (AUM · ha <sup>-1</sup> )	1.3	0.02	0.77	1.5	0.92*	0.05	0.0	2.5	0.97*	0.02	0.23	1.4	0.000
Rangeland production potential (kg · ha <sup>-1</sup> )	1789	29	1027	2608	1372**	27	197	2625	1518**	26	616	2389	0.000

<sup>a</sup> Abbreviations: K-W Test, Kruskal-Wallis Test of significance.

\*<sup>SL</sup> Indicates covariate value is significantly lower or higher ( $p < 0.05$ ) relative to season-long grazing systems.

\*<sup>RR</sup> Indicates covariate value is significantly lower or higher ( $p < 0.05$ ) relative to rest-rotation grazing systems.

\*\* Indicates covariate value is significantly lower or higher ( $p < 0.05$ ) than that of both the other grazing systems.

Table G2. Local vegetation conditions among the three treatments within rest-rotation grazing systems in eastern Montana during 2016–17. Mean, standard error, minimum and maximum values presented for each variable. *P*-values reported for Kruskal-Wallis Test of significance among the three treatments.

	Growing Season (n = 102)				Post Seed-ripe (n = 96)				Rested (n = 102)				K-W Test <sup>a</sup>
	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	<i>p</i> -value
Visual obstruction (VOR)	0.80	0.06	0.07	5.0	0.94	0.08	0.07	4.3	0.98**	0.04	0.10	3.1	0.000
Standard deviation of VOR	0.75	0.08	0.18	4.6	0.84	0.08	0.18	4.3	0.67	0.05	0.18	3.3	0.274
% Residual grass coverage	40.3	1.9	3.0	81.2	32.5**	1.3	9.7	71.2	39.9	1.5	7.5	74.5	0.001
Residual grass height (cm)	12.4	0.42	5.0	30.9	11.8	0.50	3.5	24.5	15.8**	0.34	6.7	25.5	0.000
% Forb coverage	10.9	0.69	2.2	53.2	10.7	0.46	2.0	21.0	11.5* <sup>G</sup>	0.45	1.8	24.2	0.102
Litter depth (cm)	1.3	0.06	0.0	3.1	1.2	0.06	0.45	4.2	1.6**	0.08	0.33	5.1	0.000
% Bare ground coverage	24.7	1.5	0.50	85.3	24.2	1.4	1.3	72.0	18.3**	1.2	0.33	70.7	0.001
Shrub cover	5.9	0.91	0.0	69.0	8.0**	0.98	0.0	53.8	5.5	0.97	0.0	52.7	0.005
Shrub height (cm)	26.6	1.7	0.0	85.0	27.3	1.8	0.0	74.9	21.9* <sup>G</sup>	1.4	0.0	70.8	0.071
% Wooded coulee (100-m)	2.1	0.48	0.0	26.3	2.2	0.48	0.0	26.3	1.2	0.30	0.0	14.3	0.154

Table G2. continued

	Growing Season (n = 102)				Post Seed-ripe (n = 96)				Rested (n = 102)				K-W Test <sup>a</sup>
	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	<i>p</i> -value
Stocking rate (AUM · ha <sup>-1</sup> )	1.3	0.05	0.80	2.3	1.5**	0.06	0.91	2.5	0.0**	0.0	0.0	0.0	0.000
Rangeland production potential (kg · ha <sup>-1</sup> )	1307	49	197	2605	1297	45	197	2148	1510**	39	696	2625	0.003

<sup>a</sup> Abbreviations: K-W Test, Kruskal-Wallis Test of significance.

\*<sup>G</sup> Indicates covariate value is significantly lower or higher ( $p < 0.05$ ) relative to the growing season treatment.

\*\* Indicates covariate value is significantly lower or higher ( $p < 0.05$ ) than that of both the other treatments.

APPENDIX H

MODEL SELECTION RESULTS DESCRIBING SUPPORT FOR EFFECTS ON  
MESOCARNIVORE DETECTION PROBABILITY AND LOCAL OCCUPANCY

Table H1. Support for candidate models predicting observation-level effects on mesopredator detection probability and habitat-level effects on mesopredator occupancy in eastern Montana during 2016-17. Effects on detection probability include year, cattle presence, visit, Julian day, and precipitation. Effects on occupancy at the habitat-level include cattle presence, edge density (100-m and 1,000-m scales), and distance to the nearest road, fence, water, and oil pad. The number of parameters (K), AIC<sub>c</sub> values, ΔAIC<sub>c</sub> values, model weights ( $w_i$ ), and cumulative model weights (Cum  $w_i$ ) are reported.

Model	K	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$w_i$	Cum $w_i$
<b>Detection</b>					
Precipitation <sup>2</sup> + Date + Cattle + Year + Visit	11	734.48	0.00	0.71	0.71
Precipitation <sup>2</sup> + Date + Cattle + Year	7	737.74	3.26	0.14	0.85
Precipitation <sup>2</sup> + Date + Cattle	6	738.83	4.35	0.08	0.94
Precipitation <sup>2</sup> + Date	5	740.45	5.98	0.04	0.97
Precipitation <sup>2</sup>	4	740.95	6.47	0.03	1.00
Null Model	2	754.55	20.08	0.00	1.00
<b>Occupancy, habitat-level</b>					
Edge Density (100-m) + Road + Fence + Water	15	713.35	0.00	0.28	0.28
Edge Density (100-m) + Road + Fence + Water + Edge Density (1,000-m)	16	713.39	0.05	0.28	0.56
Edge Density (100-m) + Road + Fence	14	713.62	0.27	0.25	0.81
Edge Density (100-m) + Road + Fence + Water + Edge Density (1,000-m) + Oil	17	714.93	1.58	0.13	0.94
Edge Density (100-m) + Road + Fence + Water + Edge Density (1,000-m) + Oil + Cattle	18	716.71	3.36	0.05	0.99
Null Model	11	734.48	21.13	0.00	1.00

<sup>2</sup> Variable indicates support for a quadratic effect.

ln(variable) indicates support for a pseudo-threshold effect.

Table H2. Support for candidate models predicting management-level effects on mesocarnivore occupancy in eastern Montana during 2016-17. Included are the effects of grazing system, stocking rate, and rangeland production potential. The number of parameters (K), AIC<sub>c</sub> values, ΔAIC<sub>c</sub> values, model weights ( $w_i$ ), and cumulative model weights (Cum  $w_i$ ) are reported.

<b>Model</b>	<b>K</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b><math>w_i</math></b>	<b>Cum <math>w_i</math></b>
Grazing System + Stocking Rate	14	730.99	0.00	0.24	0.24
Rangeland Production Potential <sup>2</sup>	13	732.19	1.20	0.13	0.37
Grazing System	13	732.60	1.61	0.11	0.48
Rangeland Production Potential <sup>2</sup> × Stocking Rate	13	732.88	1.89	0.09	0.58
Grazing System + Rangeland Production Potential <sup>2</sup>	15	732.99	2.00	0.09	0.66
Grazing System × Stocking Rate + Rangeland Production Potential <sup>2</sup>	16	733.65	2.66	0.06	0.73
Stocking Rate + Rangeland Production Potential <sup>2</sup>	14	734.04	3.05	0.05	0.78
Grazing System × Stocking Rate	14	734.27	3.28	0.05	0.83
Grazing System + Stocking Rate + Rangeland Production Potential <sup>2</sup>	16	734.37	3.38	0.05	0.87
Null Model	11	734.48	3.49	0.04	0.91

<sup>2</sup> Variable indicates support for a quadratic effect.