

RESTORING HETEROGENEITY-BASED MANAGEMENT TO RANGELANDS FOR THE  
BENEFIT OF GRASSLAND BIRDS AND FLORAL RESOURCES

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**Title**

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**DOCTOR OF PHILOSOPHY**

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## ABSTRACT

Worldwide grassland loss necessitates careful consideration of management practices occurring on those grasslands that remain. Concerns with overgrazing in the early twentieth century led to overcorrection via uniform, moderate stocking. While these practices reversed some forms of rangeland degradation, they also suppressed variability in vegetation structure that is characteristic of native systems. Reduced heterogeneity resulted in biodiversity declines across many trophic levels. In an effort to restore heterogeneity, we reinstated the historic processes of fire and ungulate grazing. We studied the impacts to grassland birds and floral resources, as the Northern Plains are valuable landscapes for breeding grassland birds and both native and managed pollinators. We conducted our research at the Central Grasslands Research Extension Center in Streeter, North Dakota, USA. From 2017-2020, we evaluated grassland bird community composition, nest survival, and floral resource availability. We found that patch-burn and season-long grazing pastures had higher avian diversity than modified twice-over rotational grazing. Avian community composition was also sensitive to ecological site, topographic variability, and wetland area, suggesting that both the fire-grazing interaction and underlying inherent topographic variability maintain biodiversity. Species densities were sensitive to different sources of heterogeneity, with some responding to inherent landscape conditions and some responding to imposed grazing management. We found no differences in nest survival between grazing treatments for any of our 12 focal species despite treatment differences in vegetation and structural components associated with survival. Survival of five species was associated with vegetation structure, and one was associated with litter depth, smooth brome, and forb cover, respectively. We found higher nesting densities of three species (Chestnut-collared longspur, Northern pintail, Brewer's blackbird) in patch-burn pastures compared to season-long

pastures. All are associated with shorter, sparse vegetation. At a treatment scale, we found that patch-burn grazed pastures had shallower litter, less smooth brome, more forbs, and shorter vegetation structure than season-long pastures. Patch-burn grazing pastures increased floral resources across the majority of species. Patch-burn pastures had higher species richness, seasonal availability, and maximum abundance compared to season-long grazing. Our results broadly show the benefits of heterogeneity-based management on two important grassland guilds, birds and flowering plants.

## **ACKNOWLEDGEMENTS**

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## **DEDICATION**

I would like to dedicate this work to my mom, my dad, my sister Allison, my Aunt Annie and Uncle Jim, and my partner Maureen for helping me survive a crazy four years. Without you it would not have been possible.

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# **CHAPTER 1: EMBRACING SOURCES OF HETEROGENEITY IN RANGELAND BIRD MANAGEMENT**

## **Abstract**

Simplification of rangelands is a global threat to biodiversity. Historically, rangelands exhibited wide variation in vegetation structure, which provided habitat for wildlife with diverse requirements. Vegetation heterogeneity was the result of interactions between soil and topographic conditions (inherent heterogeneity) and spatiotemporally discrete disturbances such as fire and grazing (imposed heterogeneity). These interactive sources of heterogeneity have, until recently, been ignored, both in rangeland management and scientific study. Under an emerging paradigm that embraces sources of heterogeneity, the contributions of disturbance and topographic conditions to rangeland biodiversity remain largely unknown. Using the avian community, we assessed the effects of four imposed grazing strategies (patch-burn grazing with one or two seasons of fire, season-long grazing, and twice-over rotational grazing with variably stocked paddocks; imposed heterogeneity) and topographic conditions (wetland area, ecological site, topographic roughness; inherent heterogeneity) on vegetation structure, avian diversity, and avian species-specific densities. The effects of grazing management on vegetation structural heterogeneity varied from year to year, though it appears that patch-burn management generated heterogeneity and temporal stability in vegetation structure compared to season-long and modified twice-over rotational grazing. We also found that patch-burn and season-long grazing pastures had higher avian diversity than modified twice-over rotational grazing. Avian community composition was also sensitive to ecological site, topographic variability, and wetland area, suggesting that both the fire-grazing interaction and underlying inherent topographic variability maintain biodiversity. To better understand varied drivers of diversity,

we then focused on the densities of six grassland obligate species. Two species (savannah sparrow and bobolink) responded most strongly to inherent heterogeneity, achieving highest densities on loamy and sandy soils, respectively. Chestnut-collared longspur, clay-colored sparrow, and grasshopper sparrow densities were most sensitive to imposed management strategies. Chestnut-collared longspur densities were highest in pastures managed with interactive fire and grazing, while clay-colored sparrow densities were highest on pastures managed without fire. Grasshopper sparrow density was lowest in the modified twice-over rotational treatment. Finally, western meadowlarks did not respond to either source of heterogeneity. Conserving rangeland biodiversity in the future will require both managing for greater imposed heterogeneity and embracing existing variability on the landscape.

### **Introduction**

Simplification of rangelands due to human activities has resulted in broad biodiversity declines (Fuhlendorf et al. 2017). Causes of rangeland simplification include climate change, land conversion, energy development, invasive species, and alterations to historic disturbance processes (Fuhlendorf and Engle 2001, Belgacem and Louhaichi 2013, Cameron et al. 2014, Toledo et al. 2014, Kreuter et al. 2016). Broadly, these factors all mute the spatiotemporal variability that has been characteristic of rangeland systems. This natural variability was shaped historically by the interaction of inherent topoedaphic features and imposed disturbance regimes (Toombs et al. 2010), and is the scaffolding upon which rangeland biodiversity rests.

Inherent heterogeneity in rangelands is driven by geologic and topoedaphic variation, and can include factors such as soil type, local variability in topography, spatial and temporal variation in hydrological conditions, and landscape position (Briske 2000, Fuhlendorf et al. 2017). These baseline drivers of heterogeneity exist regardless of imposed management regimes.

For example, ecological site descriptions include geological, edaphic, and topographic characteristics such as soil depth, soil texture, and elevation, and are widely used to predict the occurrence and heterogeneity of vegetation communities (Mosely et al. 2010, Sedivec et al. 2021). The relationship between inherent heterogeneity and biodiversity is well-documented. For example, abiotic landscape diversity at large scales (geodiversity) has been used as a proxy for biodiversity conservation value, as sites with greater inherent heterogeneity are thought to have greater numbers of species present (Zarnetske et al. 2019). However, this is not the only major determinant of biodiversity. Though inherent heterogeneity provides an initial bottom-up constraint on potential site diversity, disturbance-driven, imposed heterogeneity adds an additional filter to species occurrences and dynamics (Briske 2000).

Grasslands evolved with imposed heterogeneity in the form of fire and grazing by large ungulates (Fuhlendorf et al. 2009). However, fire and grazing did not occur uniformly across the landscape, and interactions largely drove the occurrence and extent of these disturbance processes (Anderson 2006). Newly burned patches attract large ungulate grazers, which draws grazing pressure away from adjacent unburned patches, creating vegetation structural contrast and patch heterogeneity (Archibald et al. 2005). However, disturbance processes can also interact with inherent heterogeneity to drive overlying patterns in vegetation type. For example, domestic cattle graze more unevenly in landscapes with rugged terrain, creating heterogeneous structure (Raynor et al. 2021), while areas with a high degree of slope tend to have more rapid rates of fire spread, causing localized and predictable areas of short structure (Weise and Biging 1997). Alterations to fire and grazing regimes at broad scales have homogenized vegetation structure and decreased the number of available niches for rangeland wildlife (Wilgers and Horne 2006, Engle et al. 2008, Hovick et al. 2014). Many current rangeland livestock

management practices strive towards achieving uniform grazing pressure across the landscape resulting in a simplified vegetation structure (Fuhlendorf and Engle 2001). Through fire suppression and homogeneous grazing practices, humans have altered the distribution of vegetation structure on the landscape and subsequently the distribution and abundance of higher trophic levels (Fuhlendorf et al. 2010, Hovick et al. 2015).

Grassland birds present a unique opportunity to study the effects of rangeland heterogeneity on biodiversity, as they are readily observable, exhibit fidelity to particular vegetation structure, respond rapidly to disturbance, and are of conservation concern (Browder et al. 2002, Davis et al. 2020). Recent attempts to promote grassland bird conservation in working rangelands (i.e., rangelands managed with livestock grazing) have advocated for the creation of preferred vegetation structure for a wide variety of species by manipulating the distribution of domestic livestock through the use of discrete disturbances (Davis et al. 2016). In particular, patch-burn grazing has been shown to promote diversity and improve nesting success in certain grassland bird species, while also improving habitat for several species of conservation concern (Fuhlendorf et al. 2006, Hovick et al. 2014, 2015, Augustine and Derner 2015). However, in other cases, variability in vegetation structure resulting from inherent landscape heterogeneity seems to be sufficient at providing habitat for a diverse suite for grassland birds (Ranellucci et al. 2012). Disturbance-driven prescriptions have thus far focused on overriding inherent landscape heterogeneity, and therefore a need exists to increase our understanding of inherent and imposed heterogeneity drivers in tandem.

We still do not know the relative importance of imposed and inherent sources of heterogeneity in generating biodiversity as heterogeneous management regimes are restored to rangeland landscapes. A better understanding of these processes will assist land managers in



working landscapes. In this study, we 1) assess the capacity for four range management practices to create heterogeneous vegetation structure; 2) describe patterns of avian community assemblage in landscapes along a gradient of inherent and imposed heterogeneity; and 3) examine the interplay of grazing regimes and topographic variability as drivers of grassland bird density. Our robust experimental design allows us to answer these questions using a single cattle herd with identical stocking rates on a shared landscape. In general, we expect that heterogeneity imposed via patch-burn grazing will generate the highest amount of avian biodiversity by creating distinct and varied vegetation structure. However, we expect that the effects of inherent heterogeneity on vegetation structure will add nuance to these results.

## Methods

### Study Site

We conducted this study at the Central Grasslands Research Extension Center (hereafter CGREC), in Kidder and Stutsman Counties, North Dakota, USA (46°42'56"N, 99°27'08"W). The site is located in the Missouri Coteau ecoregion of the northern mixed-grass prairie. The grass community is dominated by invasive and native cool season grasses. Common native cool-season grasses include green needlegrass (*Nassella viridula*, USDA PLANTS 2021), western wheatgrass (*Pascopyrum smithii*, USDA PLANTS 2021), and needle-and-thread (*Heterostipa comata*, USDA PLANTS 2021). Common invasive grasses on site include Kentucky bluegrass (*Poa pratensis*, USDA PLANTS 2021) and smooth brome (*Bromus inermis*, USDA PLANTS 2021; Patton et al. 2007, Limb et al. 2018, Duquette et al. 2020). Western snowberry (*Symphoricarpos occidentalis*, USDA PLANTS 2021) is the dominant woody species at CGREC. Forb cover is diverse and includes western ragweed (*Ambrosia psilostachya*, USDA PLANTS 2021), prairie coneflower (*Ratibida columnifera*, USDA PLANTS 2021), goldenrod

(*Solidago spp.*, USDA PLANTS 2021), yarrow (*Achillea millifolium*, USDA PLANTS 2021), and Flodman's thistle (*Cirsium flodmanii*, USDA PLANTS 2021; Rogers et al. 2005, Limb et al. 2018, Duquette et al. 2020). The climate is characterized as temperate and experiences an average growing season (May 1 to September 1) precipitation of 28.6 cm and average growing season temperatures of 17.32 °C (1991–2020, North Dakota Agricultural Weather Network 2021). Conditions during the study period were as follows: 2017: 17.3 C, 22.6 cm; 2018: 18.6 C, 38.7 cm; 2019: 16.3 C, 33.4 cm ; 2020: 18.1 C, 20.4 cm. The study plots have a history of cattle grazing and limited areas of past short-term agriculture. Prior to this work, the study plots do not have a history of burning.

Our treatment structure includes four replicates of the following four treatments (65 ha pastures, 1040 ha total): (1) season-long grazing (SLG), (2) season-long grazing with dormant season patch-burning (one-fourth pasture burned late April–early May) at a 4-year return interval (PBG40), (3) season-long grazing with dormant season (one-eighth pasture burned late April–early May) and growing season (one-eighth pasture burned late August–late September) patch-burning at a 4-year return interval (PBG20) and, (4) a modified twice over rest-rotation treatment (MTRG; Figure 1.1). This final treatment attempted to impose vegetation heterogeneity using targeted grazing intensities in the absence of fire. We stocked cattle in the MTRG for varying lengths of time across four separate paddocks to achieve the desired amount of vegetation biomass removal (targeted grazing intensity). The stocking durations in the MTRG paddocks were 0 days (rested, 0% vegetation removal), 21 days (moderate, 20-40% vegetation removal), 50 days (full, 40-60% vegetation removal), and 77 days (heavy, 60-80% vegetation removal), divided between two intervals each year with 40 percent of the days grazed during the first rotation and 60 percent grazed during the second rotation. The targeted grazing intensity in each

paddock rotated from year to year (i.e., heavily stocked paddocks transitioned to rested paddock in the subsequent year, etc.) at a 4-year return interval.

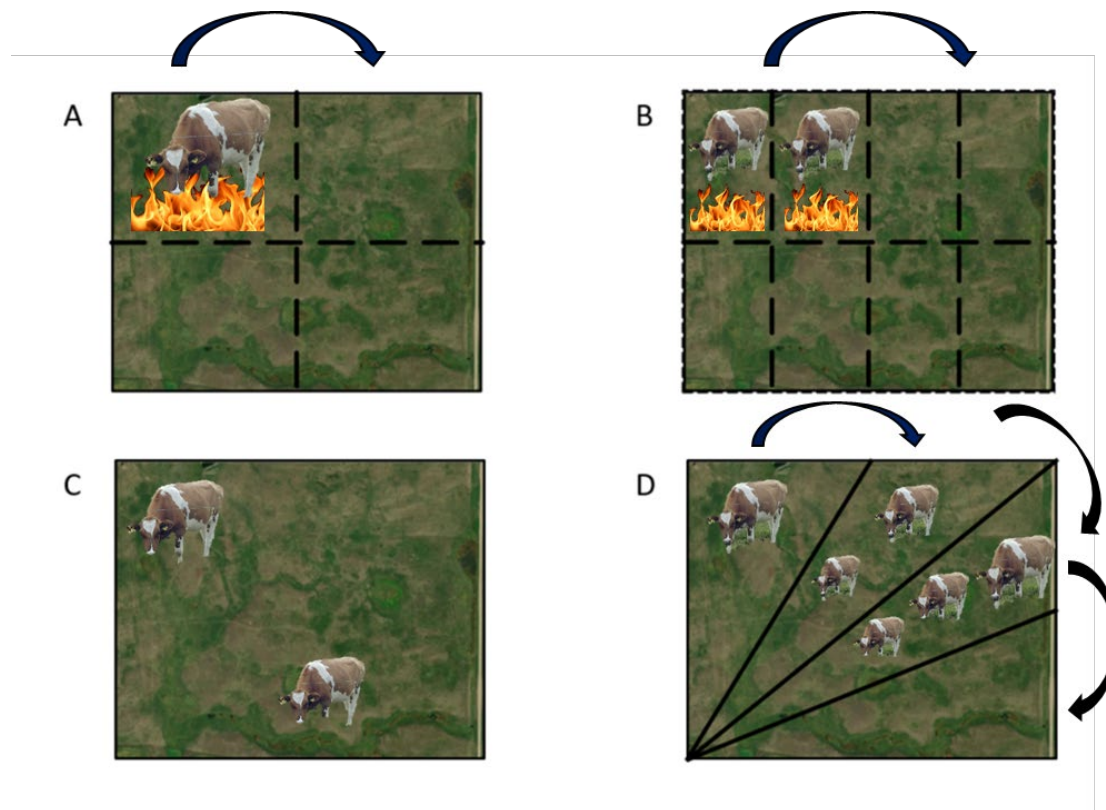


Figure 1.1. Treatments used to assess the influence of grazing management and sources of heterogeneity on avian species density and community composition at the Central Grasslands Research Extension Center near Streeter, North Dakota (2017-2020 for PBG20, PBG40, SLG, 2018-2020 for MTRG). A) Patch-burn grazing with dormant season fires (PBG40); B) Patch-burn grazing with dormant season and growing season fires (PBG20); C) Season-long grazing (SLG); D) Modified twice-over rotational grazing with variably-stocked paddocks (moderate, full, heavy, rested, MTRG). Dotted lines represent conceptual sub-pasture units while solid lines represent fencing. Arrows represent transitions from year to year.

The stocking rate was 2.26–2.31 Animal Unit Months/ha for all treatments over the four-year cycle; however, within a year the MTRG was stocked at 3.01-3.08 Animal Unit Months/ha. The stocking rate for all treatments was determined to achieve, on average across the pasture, a degree of utilization of 40 to 50 percent. In all treatments, we conducted biomass clippings in grazing exclosures at the end of each year to ensure that desired grazing intensities were achieved.

As this study marked the implementation of the patch-burn grazing treatment, the first burns were conducted in 2017 and fire was not applied to the entirety of each patch-burn pasture receiving a burned treatment until 2020. For the combination dormant and growing season patch burn grazing treatments, half of the growing season burns (two replicates) in 2018 and all of the growing season burns in 2019 were not performed due to weather constraints. We skipped these planned burns entirely as opposed to rescheduling them to preserve the area of high quality regrowth available in the pasture at one time so as not to dilute the grazer ‘magnet effect’ (i.e., grazer attraction to burned areas, Archibald et al. 2005). In addition, the modified twice over rest-rotation treatment was first implemented in 2018, so results incorporate only three years of this treatment.

### **Avian Surveys**

We monitored the breeding season avian community in each of our experimental pastures from June 1 to July 15 each year. In each sub-patch (1/8 of a 65-ha pasture) we conducted a 150 m line transect distance sampling survey four times during the season (384 surveys/year). We conducted surveys from ½ hour before sunrise until 4 hours after sunrise on days without rain or high wind speeds (> 20 kph) (Diefenbach et al. 2003, Pavlacky et al. 2017). Each time a bird was detected (auditory or visual), we recorded the species, sex, and behavior of the bird, as well as the individual’s perpendicular distance from the transect. Detections greater than 50 m from the transect were censored from analysis to preserve our ability to estimate the distance from observer of cryptic grassland species (Hovick et al. 2015).

### **Vegetation Monitoring**

We conducted vegetation surveys each year to quantify vegetation structural heterogeneity along each 150 m community transect. On each side of a transect, we measured the

percent canopy cover of vegetation using a 0.5 m<sup>2</sup> quadrat every 15 meters (20 frames/transect, offset by 15 m from community transect). Bare ground and litter cover were recorded using cover class category midpoints (0%, 3%, 15%, 38%, 63%, 85%, 98%). Additionally, at each plot we used a Robel pole to quantify visual obstruction in each cardinal from 4 m away at a height of 1 m (Robel 1970). We measured litter depth using a ruler in the northwest corner of each frame. Vegetation analysis focused on structural components (visual obstruction reading [VOR], litter depth, dead vegetation cover, and bare ground), as prior research has shown strong influence of vegetation structure on grassland bird community composition and nest success.

### **Quantifying Inherent and Imposed Heterogeneity**

We classified each transect according to its current management scheme (PBG40, PBG20, SLG, or MTRG) to capture imposed heterogeneity. To quantify inherent topographic variability around each transect, we calculated the variance of elevation in a 150 m by 150 m window around each transect (USGS GMTED 2010). We further characterized inherent landscape heterogeneity by determining the ecological site from the transect centroids (USDA Web Soil Survey) and quantifying the area of wetland in a 150 m by 150 m area around each transect using Copernicus imagery viewed through Google Earth (Copernicus Sentinel data 2017, processed by ESA). The presence of digitized wetlands were field-verified in subsequent years.

## **Data Analysis**

### **Vegetation Heterogeneity**

To verify that our imposed heterogeneity treatments were achieving desired objectives (generating heterogeneity in vegetation structure), we performed nonmetric dimensional scaling ordination using Bray-Curtis distance on structural variables (Kruskal 1964, Oksanen et al.

2007). We used the function *betadisper* in the *vegan* package to assess homogeneity of variances between grazing treatments (Oksanen et al. 2007) and used variance around group centroids within a treatment as a measure of its vegetation structural heterogeneity. We viewed treatments with a higher average distance to treatment centroid as being more structurally heterogeneous than grazing treatments with a shorter average distance to centroid (McGranahan et al. 2016, Londe et al. 2020).

### **Community Analysis**

We analyzed the relationship between the breeding bird community and sources of inherent and imposed heterogeneity using nonmetric dimensional scaling (NMDS) with the *vegan* package in the R statistical environment (Kruskal 1964, Oksanen et al. 2007). Because we assumed a closed breeding season community, we used the maximum count of each species out of all visits for each year for analysis. We employed Bray-Curtis dissimilarity and Wisconsin double standardization in the NMDS procedure (Field et al. 1982). We used permutational analysis of variance (PERMANOVA) to determine the significance of grazing treatment, ecological site, topographic variability, and wetland area in structuring the bird community (Oksanen et al. 2007, Duchardt et al. 2018). We assessed the significance of all two-way interactions between treatment and the inherent heterogeneity covariates listed above to determine if community differences between grazing treatments are dependent on inherent heterogeneity. PERMANOVA analysis was followed by post-hoc testing to determine differences in the community between factor levels. We decided to present community ordinations retaining all species even though resulting solutions have high stress values ( $\geq 0.20$ ). We felt that doing so aided in the interpretability of results, and we expected inherently high stress values due to the large size of our dataset (Dexter et al. 2018).

## **Diversity**

To aid in interpretation of community results, we supplemented these analyses with a linear mixed effects model to look at the effects of treatment on Shannon diversity with a random effect for transect (Bates et al. 2015). We assessed significance of this model using a likelihood ratio test and made pairwise contrasts of diversity between treatments using the R package *emmeans* (Lenth 2021). For all analyses, we centered continuous explanatory variables on their mean and scaled them by their standard deviation for ease of comparison.

## **Individual Species Density**

We used line transect distance sampling data to calculate detectability-adjusted density measurements for six grassland obligate birds (bobolink, *Dolichonyx oryzivorus*; chestnut-collared longspur, *Calcarius ornatus*; grasshopper sparrow, *Ammodramus savannarum*; savannah sparrow, *Passerculus sandwichensis*; clay-colored sparrow, *Spizella pallida*; western meadowlark, *Sturnella neglecta*) using the R package *unmarked* (Fiske and Chandler 2011, R Core Team 2021). We used an AIC model comparison framework to determine the relationship between sources of inherent and imposed heterogeneity and bird species' densities (Burnham and Anderson 2001). Our model set consisted entirely of univariate models, but if any models fell within 2 AICc units of the best-supported models, we assessed all additive and interactive combinations of variables in top models (Duchardt et al. 2018). In practice, the top model for each species received overwhelming model support, so there was no need to further investigate interactions between sources of inherent and imposed heterogeneity in species-specific models.

## Results

### Vegetation Heterogeneity

Differences in vegetation heterogeneity varied by year. In 2017, patch-burn and season-long grazing treatments had similar levels of structural heterogeneity (Figure 1.2). In 2018, season-long grazing had the highest amount of structural heterogeneity, followed by the dormant season-only patch burns, rotational grazing, and dormant and growing season patch burn treatments. In 2019, both patch-burns were the most heterogeneous, followed by season-long grazing and then the twice-over rotational grazing treatment (Figure 1.2). In 2020, rotationally grazed and patch-burn treatments were more structurally heterogeneous than the season-long treatment (Figure 1.2).

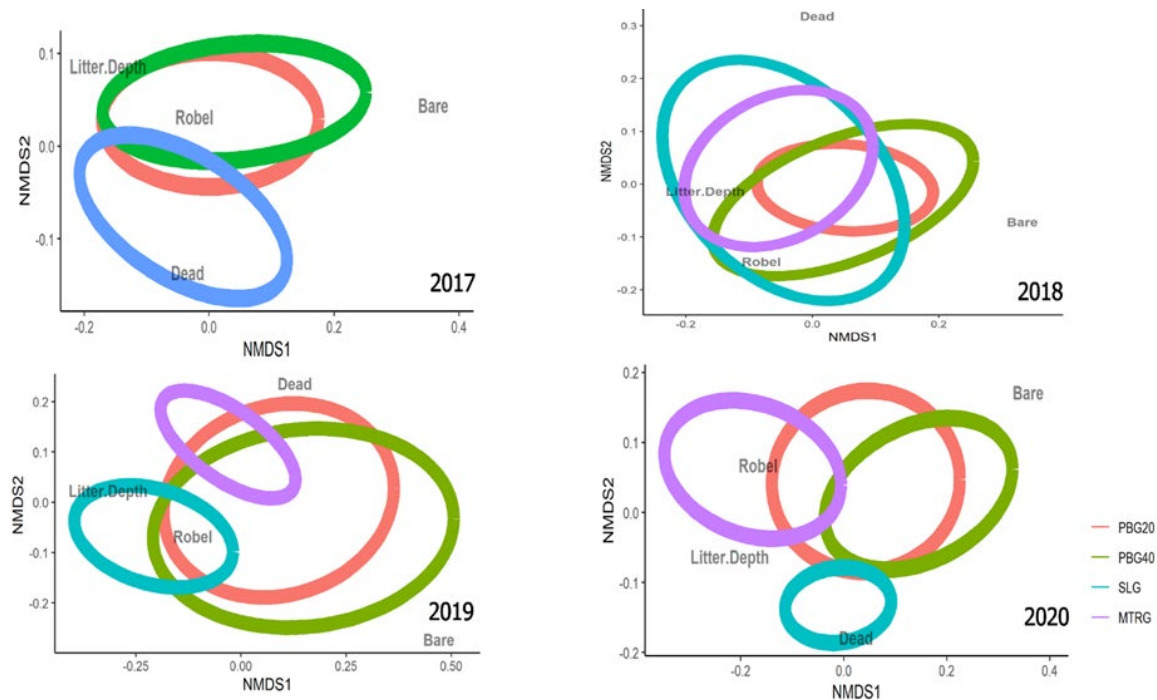


Figure 1.2. Nonmetric dimensional scaling (NMDS) of the vegetation structural variables at the Central Grasslands Research Extension Center near Streeter, North Dakota (2017-2020 for PBG20, PBG40, SLG, 2018-2020 for MTRG). Standard deviational ellipses represent grazing treatments; PBG20 = Patch-burn grazing with dormant season and growing season fires; PBG40 = Patch-burn grazing with dormant season fires; SLG = Season-long grazing; MTRG = Modified twice-over rotational grazing.



## Community Composition

Our final community analysis incorporated 64 species. Nonmetric dimensional scaling ordination converged on a three-dimensional solution with a stress of 0.20. Ecological site, treatment, topographic variance, and wetland area were significantly associated with differences in the bird community ( $P < 0.05$ , Table 1.1). In addition, ecological site and topographic variance had significant interactions with treatment ( $P < 0.05$ , Table 1.1). Communities on patch-burn grazed pastures differed from season-long and modified twice-over rotational grazing pastures, though there were no significant differences between patch-burn and non-patch-burn groups ( $P < 0.05$ , Figure 1.3). Communities differed between all ecological sites except for thin loamy and shallow gravel, very shallow and shallow gravel, and sandy and shallow gravel, which were similar to each other.

Table 1.1. PERMANOVA results of influences of inherent and topographic heterogeneity on grassland bird community structure at the Central Grasslands Research Extension Center near Streeter, North Dakota (2017-2020).

| <i>Term</i>                             | <i>Sum Sq</i> | <i>Mean Sq</i> | <i>Df</i> | <i>F</i> | <i>P</i> |
|---|---------------|----------------|-----------|----------|----------|
| <i>Ecological Site</i>                  | 3.47          | 0.87           | 4         | 3.63     | 0.001*** |
| <i>Treatment</i>                        | 7.88          | 2.63           | 3         | 10.99    | 0.001*** |
| <i>Topographic Variance</i>             | 0.73          | 0.73           | 1         | 3.04     | 0.004**  |
| <i>Wetland Area</i>                     | 1.88          | 1.88           | 1         | 7.86     | 0.001*** |
| <i>Ecological Site x Treatment</i>      | 2.99          | 0.43           | 7         | 1.79     | 0.001*** |
| <i>Topographic Variance x Treatment</i> | 1.15          | 0.38           | 3         | 1.61     | 0.023*   |
| <i>Wetland Area x Treatment</i>         | 0.88          | 0.29           | 3         | 1.20     | 0.250    |

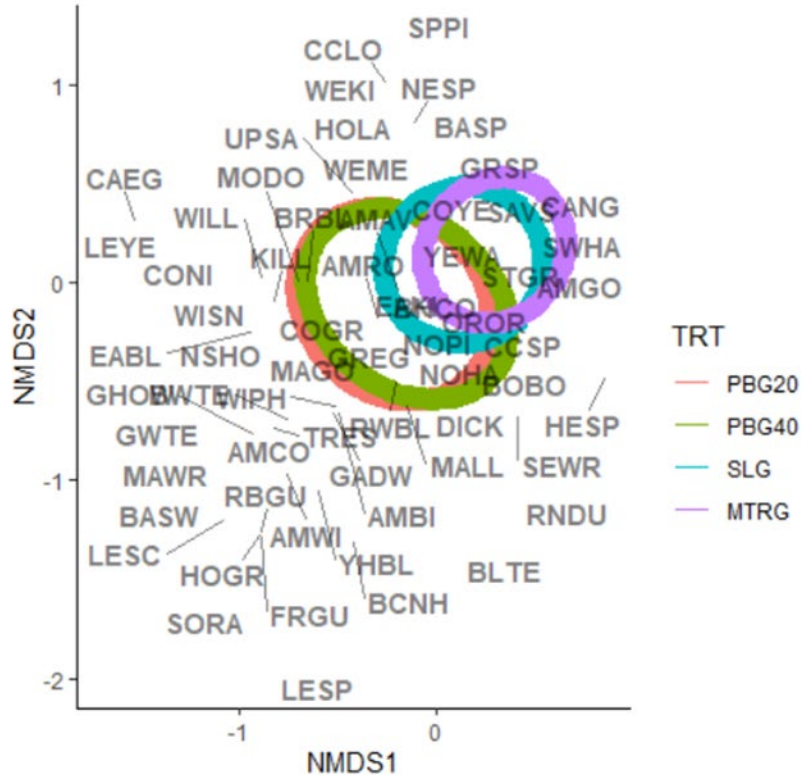


Figure 1.3. Nonmetric dimensional scaling (NMDS) of the breeding season bird community at the Central Grasslands Research Extension Center near Streeter, North Dakota (2017-2020 for PBG20, PBG40, SLG, 2018-2020 for MTRG). Standard deviational ellipses represent grazing treatments; PBG20 = Patch-burn grazing with dormant season and growing season fires; PBG40 = Patch-burn grazing with dormant season fires; SLG = Season-long grazing; MTRG = Modified twice-over rotational grazing.

### Diversity

Our best-supported model examining bird community diversity included treatment, though model fit was not improved by adding interactions with sources of inherent heterogeneity. When combining all years, modified twice-over rotational grazing pastures were less diverse than either the patch-burn treatments and season-long grazing treatment, but the patch-burn treatments and season-long treatments were not different from each other (Figure 1.4).

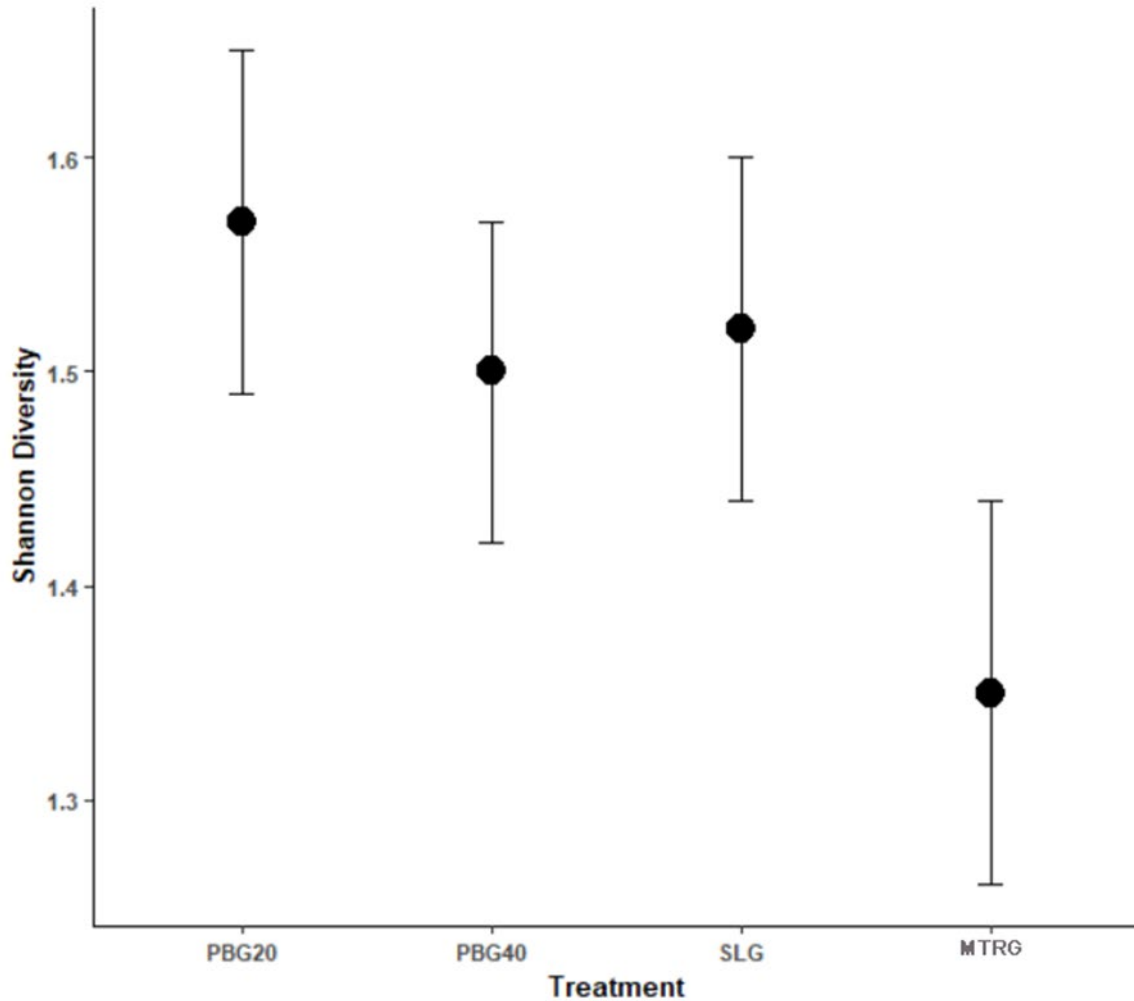


Figure 1.4. Shannon diversity of the breeding season avian community across four grazing treatments at the Central Grasslands Research Extension Center near Streeter, ND (2017-2020 for PBG20, PBG40, SLG, 2018-2020 for MTRG). Errors bars denote 95% confidence intervals.

### Individual Species Densities

Over four years of sampling, we detected 4894 individuals of 65 species. Two species responded most strongly to inherent heterogeneity, three species responded most strongly to imposed heterogeneity, and one species did not respond strongly to either driver at the studied scale.

Bobolink

In the best supported model, bobolink density varied by ecological site (Table 1.2).

Bobolinks achieved their highest densities on sandy and shallow-gravel sites, while loamy and thin loamy sites had the lowest densities (Figure 1.5). Densities did not vary significantly according to sources of imposed heterogeneity (i.e., grazing treatments, Figure 1.6).

Table 1.2. AIC model results of imposed and inherent heterogeneity factors on grassland bird density at the Central Grasslands Research Extension Center near Streeter, ND (2017-2020). Note that data was not collected on the MTRG grazing treatment in 2017.

| <i>Species</i>                    | <b>Variable</b>         | <b>k</b> | <b>ΔAIC</b> | <b>cumWt</b> |
|-----------------------------------|-------------------------|----------|-------------|--------------|
| <i>Bobolink</i>                   | <b>Ecological Site</b>  | <b>7</b> | <b>0.00</b> | <b>1.00</b>  |
|                                   | Treatment               | 6        | 11.47       | 1.00         |
|                                   | Null                    | 3        | 16.81       | 1.00         |
|                                   | Wetland Area            | 4        | 17.41       | 1.00         |
|                                   | Topographic Variability | 4        | 18.47       | 1.00         |
| <i>Chestnut-collared Longspur</i> | <b>Treatment</b>        | <b>7</b> | <b>0.00</b> | <b>1.00</b>  |
|                                   | Ecological Site         | 8        | 37.79       | 1.00         |
|                                   | Wetland Area            | 5        | 43.70       | 1.00         |
|                                   | Null                    | 4        | 47.69       | 1.00         |
|                                   | Topographic Variability | 5        | 48.99       | 1.00         |
| <i>Clay-Colored Sparrow</i>       | <b>Treatment</b>        | <b>6</b> | <b>0.00</b> | <b>1.00</b>  |
|                                   | Ecological Site         | 7        | 112.35      | 1.00         |
|                                   | Wetland Area            | 4        | 124.88      | 1.00         |
|                                   | Topographic Variability | 4        | 141.43      | 1.00         |
|                                   | Null                    | 3        | 143.54      | 1.00         |
| <i>Savannah Sparrow</i>           | <b>Ecological Site</b>  | <b>7</b> | <b>0.00</b> | <b>1.00</b>  |
|                                   | Wetland Area            | 4        | 20.44       | 1.00         |
|                                   | Topographic Variability | 4        | 24.36       | 1.00         |
|                                   | Null                    | 3        | 24.69       | 1.00         |
|                                   | Treatment               | 6        | 27.13       | 1.00         |
| <i>Western Meadowlark</i>         | <b>Treatment</b>        | <b>6</b> | <b>0.00</b> | <b>1.00</b>  |
|                                   | Ecological Site         | 7        | 32.72       | 1.00         |
|                                   | Null                    | 3        | 34.64       | 1.00         |
|                                   | Wetland Area            | 4        | 35.64       | 1.00         |
|                                   | Topographic Variability | 4        | 36.61       | 1.00         |
| <i>Grasshopper Sparrow</i>        | <b>Treatment</b>        | <b>7</b> | <b>0.00</b> | <b>1.00</b>  |
|                                   | Ecological Site         | 8        | 14.54       | 1.00         |
|                                   | Wetland Area            | 5        | 19.16       | 1.00         |
|                                   | Null                    | 4        | 10.90       | 1.00         |
|                                   | Topographic Variability | 5        | 22.90       | 1.00         |

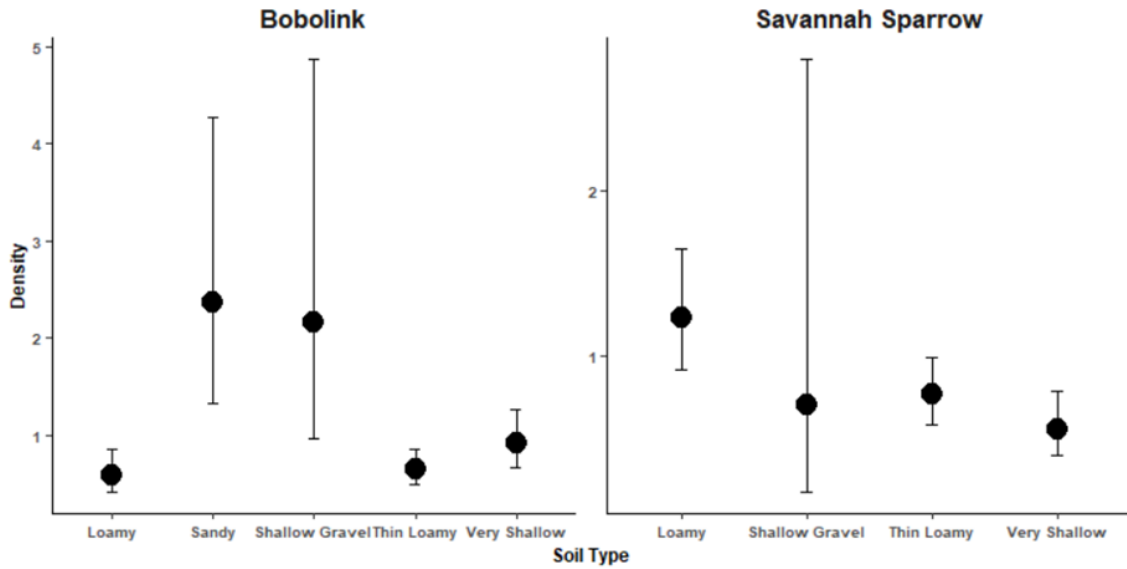


Figure 1.5. Predicted density (individuals/ha) of grassland birds across ecological sites at the Central Grasslands Research Extension Center near Streeter, ND (2017-2020). Only species with ecological site as the best-supported model are presented.

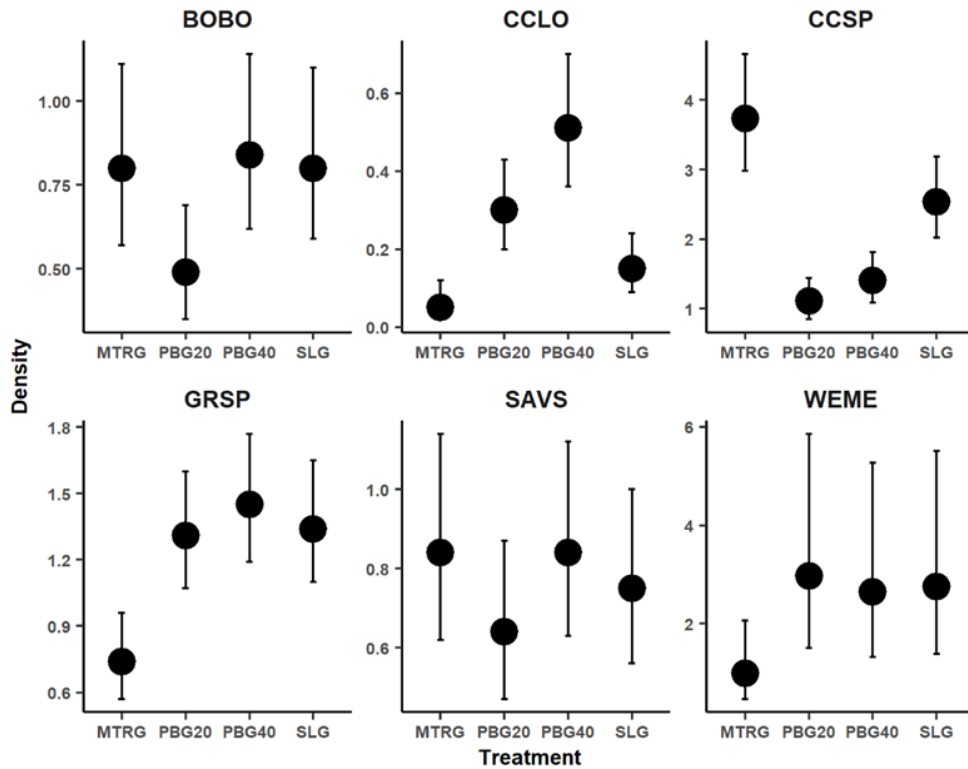


Figure 1.6. Predicted density (individuals/ha) of grassland birds across grazing treatments at the Central Grasslands Research Extension Center near Streeter, ND (2017-2020 for PBG20, PBG40, SLG, 2018-2020 for MTRG).

### Chestnut-collared Longspur

The imposed heterogeneity model was the best-supported, with higher densities in the patch-burn treatments compared to the modified twice-over rotational grazing treatment (Table 1.2, Figure 1.6). Densities in the dormant season fire only patch-burn treatment were also higher than the season-long pastures but did not differ between season-long and patch-burning with dormant and growing season fires (Figure 1.6).

### Clay-colored Sparrow

The imposed heterogeneity model was the best-supported, with highest densities occurring in the season-long grazing and modified twice-over rotational grazing pastures (Table 1.2, Figure 1.6). The lowest densities occurred on the patch-burn pastures, which did not differ from each other (Figure 1.6). Inherent heterogeneity sources did not explain variation in density (Table 1.2).

### Savannah Sparrow

Ecological site (inherent heterogeneity) was the best-supported model, with lower densities in shallow sites compared to loamy sites (Table 1.2, Figure 1.5).

### Western Meadowlark

Imposed heterogeneity (grazing treatment) was the best-supported model, though densities did not vary significantly between treatments (i.e., 95% confidence intervals overlapped 0, Table 1.2, Figure 1.6).

### Grasshopper Sparrow

The imposed heterogeneity model was best-supported, with lower densities in the modified-twice over rotational treatment compared to the other three treatments (Table 1.2, Figure 1.6).

## Discussion

Our results show that rangeland heterogeneity is structured by a combination of inherent and imposed sources. Grassland bird community composition will vary due to grazing management, ecological site, wetland area, and topographic complexity; while the sources of heterogeneity that maximize densities varied by species. This study supports a growing body of work suggesting that range management must consider both applied grazing management strategies and existing sources of heterogeneity (Ahlering and Merkord 2016, Porensky 2021). While it may be tempting to reduce the complexity of rangeland systems to pithy and universally-applicable principles, rangeland species evolved in heterogeneous systems, ensuring that biodiversity and complexity are inherently linked (Fuhlendorf et al. 2017).

Grazing management has recently advocated the creation of diverse vegetation structure through techniques such as patch-burn grazing (Toombs et al. 2010, Hovick et al. 2015), though the incorporation of inherent heterogeneity into our understanding has been delayed. However, we show that each is important in structuring grassland bird communities. Ecological site, topographic variance, and wetland area all structured communities along with grazing regime. However, sources of inherent heterogeneity did not interact with avian diversity in a meaningful way in our models. Similarly to previous research, our results show that the effects of grazing management on grassland bird communities are context dependent, varying based on inherent heterogeneity (Ahlering and Merkord 2016, Duchardt et a. 2018).

Though we found comparable levels of avian diversity in both patch-burn treatments and the season-long grazing treatments, modified twice-over rotational grazing had the lowest diversity of all grazing treatments. Our study employed variably-stocked paddocks as an attempt to mimic the rotating disturbance of patch-burn grazing without the use of fire, but results

indicate that this objective was unsuccessful, as least to date with only two years of treatment effect. It is possible that further years of study would allow vegetation contrast to develop, though theory and initial results do not suggest so. In contrast to our patch burning where four years are needed for disturbance to directly affect the entire pasture, all levels of stocking are performed on the modified twice-over rotational grazing treatment after the first year of study. Rotational grazing pastures may also create an ecological trap for grassland birds due to the timing of disturbance (Ranellucci et al. 2012). In a patch-burn system, the timing of disturbance allows for the creation of vegetation structural heterogeneity before grassland birds arrive to select territories, whereas in a twice-over rotational grazing system, grazing-mediated changes to vegetation structure take place once breeding territories are established in some cells. Therefore, even if variably-stocked rotational grazing pastures generate sufficient structural heterogeneity, it may be within a temporal frame that is incompatible with the breeding ecology of many grassland birds.

In addition to community differences, we found variability in responses to the grazing treatments by species. Four of our six focal species responded most strongly to grazing treatment (imposed heterogeneity), while the density of two species was best explained by ecological site (inherent heterogeneity). Because western meadowlark did not respond strongly to grazing system or sources of inherent heterogeneity, it is likely that they are responding to heterogeneity at finer scales than those captured by our analysis. In more arid rangelands, western meadowlarks have been found to respond negatively to patch-burn management and rest-rotation grazing (Augustine and Derner 2015, Golding and Dreitz 2017). In such cases, management may need to occur at larger scales and consider the context of the surrounding landscapes.



Variability in vegetation structure is likely the mechanism by which sources of heterogeneity structure grassland bird diversity and density (Augustine and Derner 2015, Hovick et al. 2015). Structural heterogeneity varied from year to year in all treatments, though some were more stable than others. However, due to the recent implementation of the patch-burn treatment, we feel that our results may be conservative with respect to the ability of patch-burn management to generate avian diversity. Over time, structural heterogeneity in patch-burn treatments increased as more of the landscape was burned, consistent with prior findings (Duchardt et al. 2016). Vegetation heterogeneity in the PBG20 treatment developed more slowly, but this may be because we did not conduct half of the growing season burns in 2018 and all in 2019. Season-long grazing became less structurally heterogeneous over time relative to the patch-burn treatment, while twice-over rotational grazing displayed no clear pattern from year to year. Continued data collection on the treatments during the second round of patch-burning will provide a more complete assessment of the ability of patch-burn and variably-stocked rotational grazing to create structural heterogeneity. However, our initial data suggests that patch-burn grazing also creates temporal stability in heterogeneity over time, consistent with previous research (Hovick et al. 2015).

### **Conclusion**

Our results show that both patch-burn and season-long grazing are successful at generating avian biodiversity compared to modified twice-over rotational grazing. Despite lower overall diversity, modified twice-over rotational grazing did benefit clay colored sparrows, a shrub specialist. However, certain species such as bobolink and savannah sparrow are more responsive to site characteristics, so managers should take care to employ diversity-generating management strategies on compatible ecological sites. In addition, despite the fact that our patch-

burn treatments were still in their infancy, it seems that patch-burn structural heterogeneity may be more temporally stable over time, in contrast to season-long systems. Our results further suggest that variably-stocked rotational grazing systems are not a suitable substitute for the fire-grazing interaction for generating avian biodiversity, at least during the initial stages of the treatment. Based on the results of this study, we advocate practicing any grazing strategy that consistently develops vegetation structural heterogeneity to support a diverse suite of grassland avifauna, while also incorporating landscape context into management planning.

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## **CHAPTER 2: SPATIALLY DISCRETE DISTURBANCE PROCESSES ENHANCE GRASSLAND FLORAL RESOURCES**

### **Abstract**

Grasslands provide floral resources for managed and wild pollinators. The floral resource have declined over the past few decades due to alterations in historic disturbance regimes such as fire and grazing. Fire and grazing historically occurred interactively; so the uniform application of these disturbances may be a detriment to pollinators and the resources they depend on. We investigated the impacts of spatiotemporally varying fire and grazing versus traditional management on floral resource abundance and diversity in mixed-grass prairie. We aimed to capture the ability of fire to stimulate flowering while also sheltering flower heads from grazing pressure by directing cattle away from regenerating forbs in unburned portions of the landscape. Over two years, we surveyed 1,238,241 ramets of 160 species. We found positive effects of patch-burn grazing on total seasonal flower abundance, maximum abundance, and species richness compared to traditional management. Results provide a potential mechanism for enhancing biodiversity and pollination services in grasslands.

### **Introduction**

Agricultural intensification has resulted in widespread declines in pollinators and their habitat due to a multitude of factors, including increased pesticide use and floral resource decline (Goulson et al. 2015, Jachuła et al. 2021, Raven and Wagner 2021). Although many commercially important plants depend upon pollinators, crop monocultures do not provide sufficient resources to pollinator species on their own (Jachuła et al. 2018). On the contrary, diverse native pollinator communities are highly correlated with diverse floral resource assemblages (Potts et al. 2003a, Kral-O'Brien et al. 2021). This interdependency means that it is

essential to promote floral resources in grassland patches in agricultural landscapes for the benefit of both native and managed pollinators.

Management can potentially promote floral resources, but not all practices are equal. Fire suppression, even-aged forest management, and uniform grazing have homogenized vegetation structure and composition to the detriment of floral resource availability (Dumont et al. 2011, Lettow et al. 2014, Mallinger et al. 2016, Ponisio et al. 2016). These management practices alter natural disturbance regimes, resulting in a decrease in biodiversity (Fuhlendorf and Engle 2001). The restoration of the natural disturbances of fire and grazing has been used to promote floral resources in grassland habitats (Black et al. 2011), though the wholesale and individual application of each may not be sufficient. Wildfire and ungulate grazing were historically interactive processes, and the interaction of the two is needed to produce the desired ecological effects (Fuhlendorf and Engle 2001).

Though fire is usually deleterious to floral resource availability immediately following a burn, species richness and floral abundance rebound over time and can exceed comparable unburned areas (Potts et al. 2003b, Mola and Williams 2018). Fire disturbance can also stimulate flowering in grassland plants, though responses are species-specific (Fidelis and Blanco 2014, Pilon et al. 2018, Wagenius et al. 2020). Flowering increases can be immediate following fire or delayed until the following season (Hinman and Brewer 2007). Because of this, unburned areas are important for sustaining plant/pollinator interactions in burned landscapes as complete burns can temporarily deplete grasslands of floral resources (Peralta et al. 2017, Adedaja et al. 2019). Similarly, heavy or undirected animal grazing can decrease floral resources through livestock selectivity for forbs, but a total absence of grazing can decrease floral resources by favoring graminoids (Carvell 2002, Yoshihara et al. 2008, Buckles and Harmon-Threatt 2019, Cutter et al.



2021). In both cases, floral resources benefit from both focal disturbances and refuge from disturbance, suggesting that a patchy disturbance regime might be beneficial for flower abundance and diversity.

Patch-burn grazing combines focal fire and grazing disturbance on the landscape to generate heterogeneity (Fuhlendorf and Engle 2004). Each year, a portion of the landscape is burned, resulting in high-quality regrowth that is selected by grazers, which in turn maintain low vegetation structure and greater forage quality in burned areas through grazing action (Archibald et al. 2005, McGranahan et al. 2014). Due to this “magnet effect”, animals focus grazing activity on burned portions of the landscape that have already experienced floral resource depletions from fire. Unburned areas are thereby sheltered from grazing pressure, protecting flower heads from livestock herbivory (Helzer and Steuter 2005). Direct comparisons of patch-burn grazing versus other management strategies with regard to floral resources are limited in number, but research shows that patch-burn grazing can increase the abundance of flowers of key pollinator species while reducing flower herbivory (Helzer and Steuter 2005, Moranz et al. 2014).

In this study, we evaluated the effects of spatially discrete disturbance versus traditional management on grassland floral resource diversity and abundance. Specifically, we compare total seasonal floral resources, maximum floral abundance, and species richness between patch-burning with varying degrees of spatial heterogeneity and season-long grazing. By using generalized additive models (GAMs) to fit flower phenology curves over the course of the growing season, we were able to directly consider total seasonal floral availability to the pollinator community. This method accounts for both abundance and constancy, two factors that are essential for providing floral resources for a diverse pollinator assemblage. We hypothesize that patch-burn grazing will generate more diverse and abundant floral resources in native

rangelands by balancing the flower-stimulating effects of fire with refuge from grazing pressure. Because of the close connection between pollinators and floral resource diversity and availability, results will inform pollinator conservation in native grasslands while potentially enhancing pollination services of wild and commercially important plants.

## **Materials and Methods**

### **Study Site**

We conducted our assessment of floral resource abundance at the Central Grasslands Research Extension Center in southcentral North Dakota, USA (99°25'W, 42°42'N, 586 m). The site is located in the Prairie Pothole Region of the northern mixed-grass prairie. Vegetation cover is dominated by invasive cool season grasses such as Kentucky bluegrass (*Poa pratensis*, USDA PLANTS 2021) and smooth brome (*Bromus inermis*, USDA PLANTS 2021) interspersed with native grasses that include green needlegrass (*Nassella viridula*, USDA PLANTS 2021), western wheatgrass (*Pascopyrum smithii*, USDA PLANTS 2021), and needle-and-thread grass (*Heterostipa comata*, USDA PLANTS 2021; Patton et al. 2007, Limb et al. 2018, Duquette et al. 2020). Common forbs include goldenrod (*Solidago spp.*, USDA PLANTS 2021), milkweed (*Asclepias spp.*, USDA PLANTS 2021), and thistle (*Cirsium spp.*, USDA PLANTS 2021; Rogers et al. 2005, Limb et al. 2018, Duquette et al. 2020). At the start of our study, a concurrent project verified that the plant communities were similar across study pastures within treatments (Hamel 2021). The study site receives an average growing season precipitation of 28.6 cm and average growing season temperatures of 17.3 °C (May 1 to September 1, 1991–2020; North Dakota Agricultural Weather Network 2021). Growing season average temperatures during the study were 18.6 C and 16.3 C, and growing season precipitation 38.7 cm and 33.4 cm in 2018

and 2019, respectively. Study pastures have a history of cattle grazing and small-scale short-term agriculture.

Our treatment structure consists of four replicates of three treatments (65 ha pastures, 780 ha total): (1) season-long grazing (cattle stocked mid-May through late-October for 158 days; SLG), (2) season-long grazing with dormant season patch-burning (one-fourth pasture burned late April through early May; PBG40), (3) season-long grazing with dormant season (one-eighth pasture burned late April through early May) and growing season (one-eighth pasture burned late August through early September) patch-burning (PBG20). Fire return intervals for patch burn treatments were four years. Prior to the implementation of patch-burning for our study, pastures had no known history of burning. Treatments were stocked with Angus crossbred cow/calf pairs to achieve an average full use grazing stocking rate (40-50 percent degree of disappearance) across all pastures and treatments (2.26–2.31 Animal Unit Months/ha). Due to weather constraints, we did not conduct the late growing season burns in half of the replicates in 2018.

### **Floral Resource Surveys**

We used 300 m belt transects to assess the expression of floral resources in the three grazing treatments (Cutter et al. 2021). In 2018 and 2019, we conducted weekly surveys in each 1/8 pasture (4 replicates x 3 treatments x 8 transects = 96 surveys/week). Surveys occurred from May 20 to September 1 each year. Though floral resources were still being expressed in pastures after this date, we reasoned that our survey period captured the majority of floral resources and encompassed most of the flight season for many pollinators, while also avoiding the confounding effects of conducting growing season burns during data collection. We counted ramets (independent plant unit, could include a member of a clone) of all species within 1 m of the transect. We considered flowers to be available if at least one flower had anthers visible (Fründ

et al. 2010). Species relying on wind dispersal, such as *Artemisia spp.*, were censored from analysis to focus our results on implications for pollinator conservation.

## **Analysis**

To model total seasonal floral resource availability over the course of the growing season, we employed GAMs using the R package *mgcv* (Wood 2011, R Core Team 2021). GAMs are commonly used to model phenological data as they handle flexible, nonlinear relationships (Timberlake et al. 2019, Stenkovski et al. 2020). We modeled  $\log(\text{ramet count} + 1)$  as a function of week and grazing treatment using a global smoothing term with individual effects and individual smoothing penalties (Pedersen et al. 2019). This formulation balances detecting differences in phenological patterns between treatments and sharing information between floral resource expressions at a common site.

We predicted phenology curves for each treatment using fitted GAM models to measure differences in floral resources between treatments. Resulting predicted response values were used to integrate the area under the growing season phenology curve. To obtain 95% confidence intervals for our estimates, we generated 10,000 posterior prediction sequences from weeks 1 to 15 for each grazing treatment using fitted model coefficients and their Bayesian covariance matrix and calculated an AUC for each (Wood 2017). We used the MASS package to simulate draws from a multivariate normal distribution (Venables and Ripley 2002). We considered differences in total seasonal floral resources between grazing treatments to be significant if 95% confidence intervals did not overlap.

We then modeled differences in maximum floral abundance between treatments by species and overall ramet count (all species combined). We ran negative binomial generalized linear models using the MASS package with maximum count as the independent variable, and

grazing treatment and year as explanatory variables with pasture as a random effect (Venables and Ripley 2002). For models with a significant treatment effect ( $p < 0.05$ ), we assessed pairwise differences using the *emmeans* package (Lenth 2021). We used a similar procedure to evaluate species richness between treatments, summing the total number of species in each transect in each year and running a model with year and grazing treatment as explanatory variables.

## Results

Over two years of sampling, we detected 1,238,241 ramets of 160 species. For species-specific analyses, we focused on 36 species making up 95% of observations.

### Total Seasonal Floral Resources

Total seasonal floral resources differed between patch-burn and SLG treatments for 32 species, while four species (purple milkvetch, *Astragalus agrestis*, USDA PLANTS; shy wallflower; *Erysimum inconspicuum*, USDA PLANTS; blue lettuce, *Lactuca tatarica*, USDA PLANTS; and western snowberry, *Symphoricarpos occidentalis*, USDA PLANTS) displayed no differences between treatments (Figure 2.1). Of the 32 species with differences between treatments, 29 had higher total seasonal resources in at least one of the patch-burn treatments (PBG20 and PBG40) compared to the SLG treatment (Figure 2.1). Of these, 13 had higher abundances in the PBG20 treatment (compared to zero with higher abundances in the PBG40 treatment, Figure 2.1). Total floral resource abundance of all 160 species combined was highest in the PBG20 treatment and lowest in the SLG treatment (SLG; Figure 2.2). Differences in total seasonal resources between the patch-burned and SLG treatments were more pronounced in the second half of the growing season (Figure 2.2). PBG20 pastures consistently had more total floral resources compared to PBG40 pastures, but these differences peaked around midseason and diminished over time (Figure 2.2).

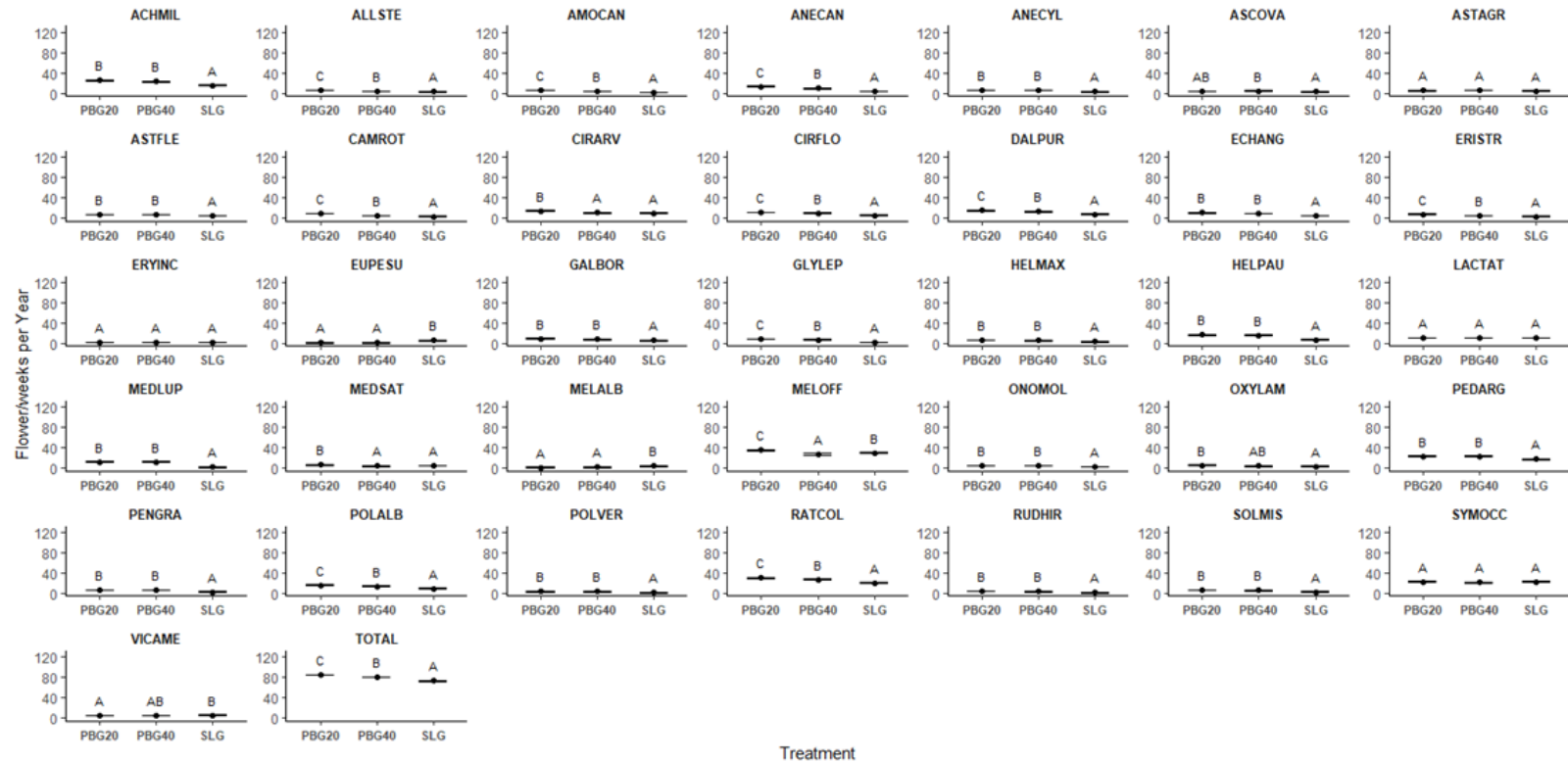


Figure 2.1. Comparisons of total seasonal floral abundance between three grassland management treatments in 2018 and 2019 at the Central Grasslands Research Extension Center near Streeter, North Dakota, USA. These 36 species represent 95% of observations. Estimates are derived from area under the curve estimates of generalized additive models (GAMs) for weekly flower counts. Letters denote statistically significant differences ( $p \leq 0.05$ ). See Supplement 1 for abbreviations. PBG20 = Patch-burn grazing with dormant season and growing season burns; PBG40 = Patch-burn grazing with dormant season burns; SLG = Season-long grazing

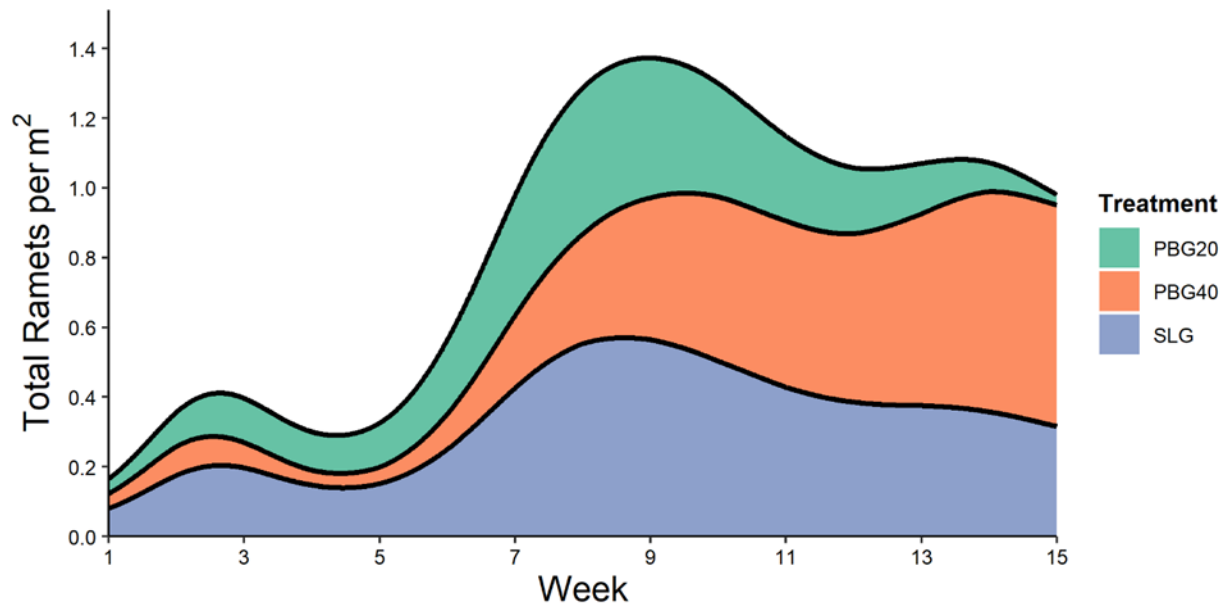


Figure 2.2. Whole season floral abundances for three management treatments from 5/21 to 9/1 in 2018 and 2019 at the Central Grasslands Research Extension Center near Streeter, North Dakota, USA derived from GAM models. PBG20 = Patch-burn grazing with dormant season and growing season burns; PBG40 = Patch-burn grazing with dormant season burns; SLG = Season-long grazing

### Maximum Floral Abundance

Thirty-two of the thirty-six species displayed differences in maximum abundance by treatment (Figure 2.3). All but one of these species (Leafy spurge, *Euphorbia esula*, a noxious weed, USDA PLANTS) differed between the SLG treatment and at least one of the patch-burn treatments (Figure 2.3). Twenty-nine species had the highest total resource abundance in the PBG20 treatment (Figure 2.3). Maximum ramet counts across all 160 species were highest in the PBG20 treatment and lowest in the SLG treatment (Figure 2.3).

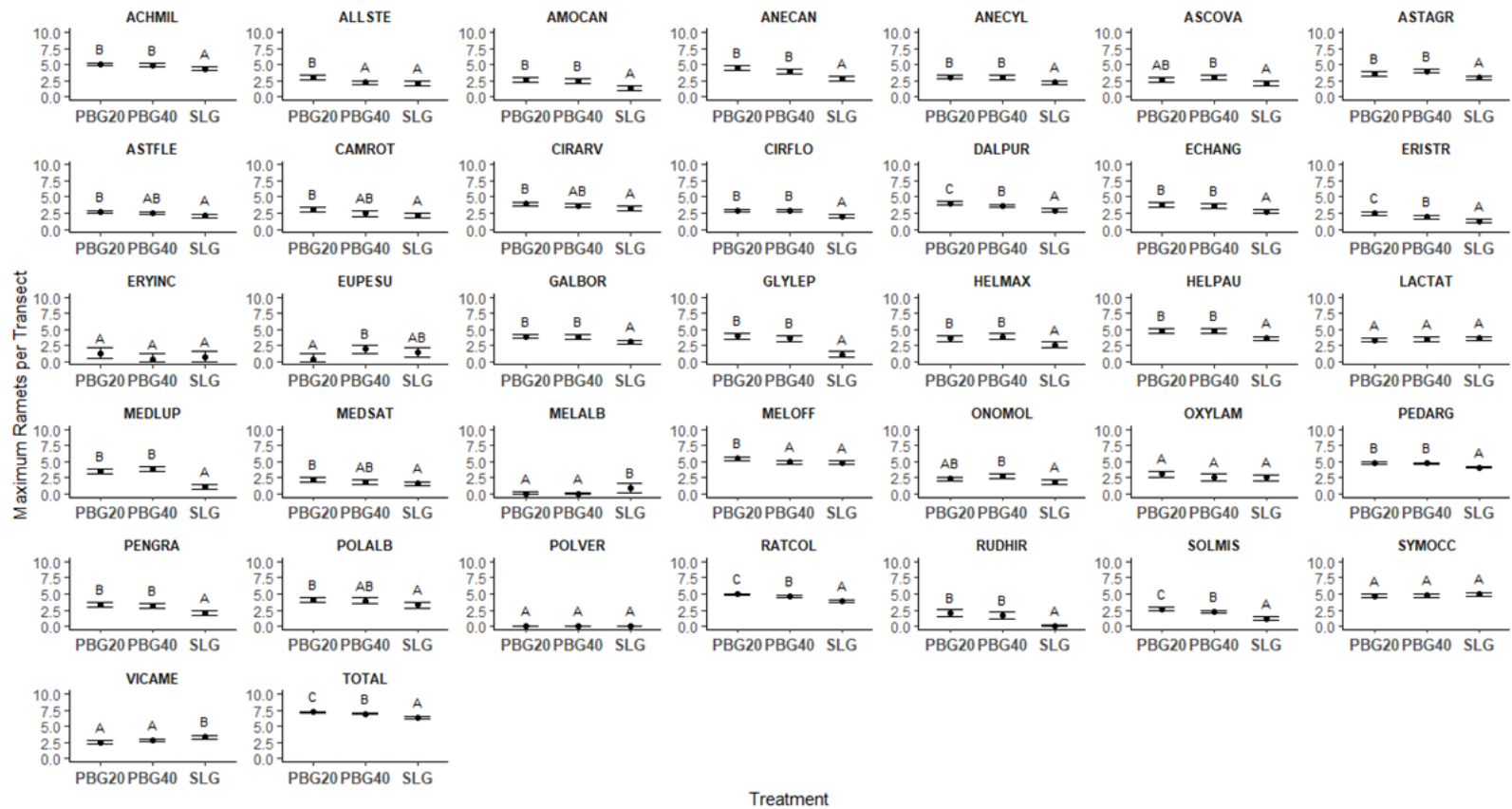


Figure 2.3. Comparisons of maximum floral abundances between three management treatments in 2018 and 2019 at the Central Grasslands Research Extension Center near Streeter, North Dakota, USA. Letters denote statistically significant differences ( $p \leq 0.05$ ). See Supplement 1 for abbreviations. PBG20 = Patch-burn grazing with dormant season and growing season burns; PBG40 = Patch-burn grazing with dormant season burns; SLG = Season-long grazing



## Species Richness

Annual species richness was highest in the PBG20 treatment and lowest in the SLG treatment (Figure 2.4).

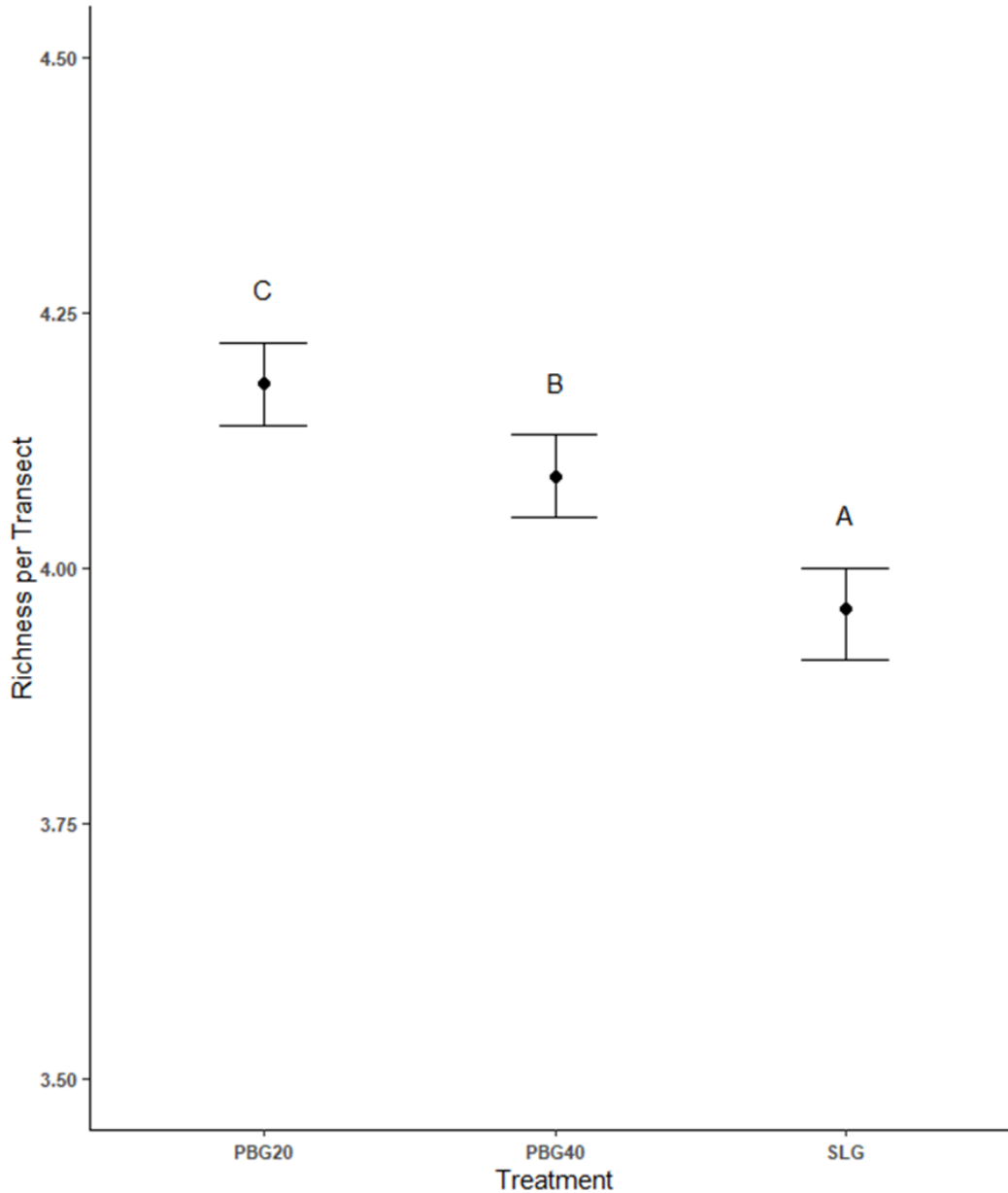


Figure 2.4. Comparisons of per-transect species richness between three management treatments in 2018 and 2019 at the Central Grasslands Research Extension Center near Streeter, North Dakota, USA. Letters denote statistically significant differences ( $p \leq 0.05$ ). PBG20 = Patch-burn grazing with dormant season and growing season burns; PBG40 = Patch-burn grazing with dormant season burns; SLG = Season-long grazing

## Discussion

As population expansion and land-use change diminish the extent of unconverted natural landscapes, the potential value of remaining natural areas and working lands as pollinator habitat only increases (Black et al. 2011). It is therefore important to consider strategies to bolster floral resources in intact grasslands. Our novel analytical approach comparing grazing management practices across the growing season clearly shows benefits of patch-burn grazing on floral resource diversity and abundance. Furthermore, benefits to floral resources increased across our treatments as heterogeneity increased (i.e., patch-burning with two seasons of fire usually outperformed patch-burning with one season of fire, and both had higher seasonal richness and abundance than season-long grazing).

Changes to floral resources likely translate into changes to ecosystem processes and services. Higher abundance of floral resources in grasslands has been linked to both higher pollinator diversity and abundance (Heithaus 1974, Banaszak 1996, Steffan-Dewenter and Tschardt 1997, Potts et al. 2003a), while more abundant floral resources have been linked to enhanced provisioning of crop pollination services in neighboring fields (Orford et al. 2016). Demonstrated benefits to floral resources from patch-burn grazing contribute to a growing body of work showing that periodic disturbances can be a net positive influence on grassland pollinators (Ponisio et al. 2016, Carbone et al. 2019, Galbraith et al. 2019).

We found that patch-burning with two seasons of fire often achieved more beneficial outcomes than patch-burning with one season of fire. Here, we propose two potential mechanisms for these differences. Our first explanation regards potential seasonal differences in the effects of fire on floral resources. Differences in the effects of dormant and growing season fires on flower expression depend on the seasonality of the species in question (i.e., species with

a late summer phenology often benefit more from spring fire in the year following a burn; Towne and Kemp 2003, Towne and Craine 2014). As floral richness tends to increase throughout the growing season, growing season fires may benefit a larger amount of species by promoting those with a later phenology, potentially explaining our results. However, two years of data limits our ability to compare burn seasonality directly. A second potential explanation is that differences in burn sizes (8.1 ha in PBG20 vs 16.2 ha in PBG40) affect rates of flower herbivory via differences in livestock distribution. Growing season burns create late-season high quality forage for livestock, and may prevent “spillover” of grazing animals later in the season due to maturing plants in dormant season burns (Sensenig et al. 2010, Allred et al. 2011). Future study should investigate these hypotheses to elucidate mechanisms of the effect of burn season on floral resource abundance and diversity.

Our study design prevented us from assessing the effects of patch-burn grazing on intraplant floral resource changes, as well as on late season floral resources. However, anecdotal evidence and previous research suggest that our results may be conservative. To survey at a high spatiotemporal intensity, we counted flowering ramets and did not collect information on the number of flowers per plant. It is possible that increases in ramets from patch-burn management could be moderated by decreases in the average number of flowers per plant. However, prior research indicates that this is likely not the case, as studies have found mostly positive or neutral effects of fire on per-plant floral resources (Lesica 1999, Wroblewski and Kauffman 2003). This, combined with the fact that at the patch level forbs in patch-burn grazed pastures should receive less grazing pressure in subsequent years following a burn year (Helzer and Steuter 2005), means that plant-level floral resources should be equivalent or greater in patch-burn pastures.

It is important to note that our results are likely the result of changes in expression of existing species. We would not expect comparable diversity benefits from patch-burn grazing to occur in species-poor grasslands, at least over similar timescales. For grasslands with present but suppressed forbs, patch-burn grazing is likely a preferred alternative to methods such as over-seeding of diverse seed mixes, which are expensive and have long restoration timelines (Török et al. 2010). Patch-burn grazing also avoids the use of nonlocal seed sources which, although essential to global grassland restoration initiatives, may be maladapted to site conditions or low in genetic diversity (Zinnen et al. 2021). While likely not a substitute for restoration activities in species-poor grasslands, patch-burn grazing may be an important tool for enhancing pollinator resources where forbs exist but are not currently expressed.

Landscape fragmentation and land use intensification is jeopardizing the flowers that pollinators depend on. The conservation of biodiversity and the continued provisioning of pollination services depends on season-long access to diverse and abundant floral resources. Our results show consistently greater flower availability, diversity, and peak abundance in rangelands managed with patch-burn grazing. We also show that benefits of this heterogeneity-based management increased with greater levels of heterogeneity (two smaller burns at two times vs. one larger burn). Conservation of pollinators in the future will depend on maximizing resources in working landscapes, and by embracing historic disturbance regimes, we provide key habitat requirements for diverse pollinator assemblages.

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## **CHAPTER 3: PATCH-BURN GRAZING BENEFITS NESTING OF SHORT-VEGETATION SPECIALISTS IN THE NORTHERN GREAT PLAINS**

### **Abstract**

Worldwide grassland loss necessitates careful consideration of management practices occurring on those remaining grasslands. Concerns with overgrazing in the early twentieth century led to overcorrection via uniform, moderate stocking. While these practices reversed some forms of rangeland degradation, they also suppressed the variability in vegetation structure that is characteristic of native systems. This reduced heterogeneity resulted in declines in guilds relying on diverse vegetation structure, such as grassland birds. In an effort to restore heterogeneity, we reinstated the historic processes of fire and ungulate grazing. We studied the impacts to grassland bird nest survival and density compared to traditional season-long grazing. We conducted our research at the Central Grasslands Research Extension Center near Streeter, North Dakota, USA. From 2017-2020, we monitored 1975 nests from 30 species. Of the 12 focal species, we found no differences in nest survival between grazing treatments despite treatment-level differences in vegetation and structural components associated with nest survival. Survival of five species was associated with vegetation structure (height or visual obstruction) and one associated with litter depth, smooth brome, and forb cover; respectively. We found higher densities of three species (Chestnut-collared longspur, Northern pintail, Brewer's blackbird) in patch-burn grazing pastures compared to season-long grazing pastures. All three were associated with shorter, sparse vegetation and two (Chestnut-collared longspur, Northern pintail) are of local concern. At a treatment scale, we found that patch-burn grazed pastures had shallower litter, less smooth brome, more forbs, and shorter vegetation structure than season-long pastures. These results show the value of patch-burn grazing at generating vegetation structure for

grassland birds. The Prairie Pothole Region of the Northern Great Plains has experienced invasion by non-native sod-forming grasses and a multidecadal period of above average precipitation. As a result, sparse vegetation is at a premium, necessitating conservation strategies to provide nesting areas with short, sparse vegetation.

### **Introduction**

Modern human activities have resulted in a loss of the majority of grasslands, with concurrent steep declines in the species that depend on them (Ceballos et al. 2010). As a result, many conservation programs have focused on preserving grassland habitat, as well as reverting other land uses back into grassland (Lark 2020, Adkins et al 2021). Just as important as restoration activities on former and degraded grasslands are the management decisions that occur on those that remain. Livestock grazing on grasslands is a dominant practice affecting the majority of grassland ecosystems worldwide (Holechek et al. 1998, Evans et al. 2015). As a result, the impacts of grazing management decisions on grassland biota warrant careful consideration and scrutiny.

Fundamental decisions in grazing management such as stocking rate and choice of grazing system influence both grassland vegetation structure and composition (Lwiwski et al. 2015, Scasta et al. 2016). Past decisions involving chronic overstocking of rangelands resulted in practices designed to promote even grazing pressure across the landscape (Toombs et al. 2010). While these grazing strategies have accomplished the important objective of reducing erosion and improving rangeland condition, they also have fostered a fear of both bare ground and localized “overuse” of pastures, resulting in declines in rangeland structural diversity (Toombs et al. 2010). Under this paradigm of even use, vegetation structure is homogenized resulting in the loss of both sparsely vegetated open areas and dense patches with deep litter (Fuhlendorf et al.

2012). Simplified vegetation structure in grasslands has been shown to reduce the number of available niches for many guilds of rangeland wildlife, including small mammals, arthropods, and grassland birds (Krausman et al. 2009, Doxon et al. 2011, Lwiwski et al. 2015, Ricketts and Sandercock 2016, Herrero-Jáuregui and Oesterheld 2018).

Grassland birds are highly sensitive to vegetation structure, with widely-varying preferences across species (Hovick et al. 2014, 2015). Some, such as Smith's longspur (*Calcarius pictus*) are specialists of open areas with short-statured vegetation, while others, such as Le Conte's sparrow (*Ammodramus leconteii*) require dense stands (Hovick et al. 2014). Still other taxa, such as prairie chickens (*Tympanuchus spp.*), rely on several different vegetation structure types to carry out their life histories, with preferences for both dense nesting cover and open areas for brood foraging (Fuhlendorf et al. 2017, Winder et al. 2017). Declines in grassland bird diversity have been attributed in part to grazing practices that promote even grazing pressure on the landscape (Duchardt et al. 2016). This even grazing pressure promotes homogeneous vegetation structure at intermediate height and density (Fuhlendorf and Engle 2001). As such, much contemporary rangeland conservation management advocates the creation and maintenance of heterogeneous vegetation structure to provide for a suite of grassland bird species with diverse breeding requirements.

Reproductive output of grassland birds is a key metric for evaluating the success of conservation activities (Davis et al. 2016), as previous research shows a consistent relationship between avian reproductive success and adult densities (Bock and Jones 2004). Choice of nest site can be thought of as a series of trade-offs between concealment, ease of escape, foraging opportunities, and shelter from the environment, with different species making different choices (Davis 2005, Fogarty et al. 2017, Duquette et al. 2020). Aside from direct predation risk,

vegetation structure may predispose nesting birds to parasitism from species such as brown-headed cowbirds (*Molothrus ater*), which can result in decreased survival (Lorenzana and Sealy 1999). Vegetation structure can also mediate nest survival through exposure to thermal stress (Carroll et al. 2015, Hovick et al. 2015). Finally, partitioning of preferred nest sites among coexisting species may serve to reduce predation pressure (i.e., predation pressure is higher when nesting in the same area as sympatric species; Martin 1996). All of these factors influence whether a nest will successfully fledge offspring but are not the only way that grazing management can mediate grassland bird reproductive output. Aside from direct effects on nest survival, the influence of grassland management on grassland bird nesting output may be indirect and mediated by nest density.

Nest survival and nesting densities interact to shape grassland bird production on a landscape. Since nesting grassland birds appear to demonstrate selectivity based on habitat characteristics, nest survival at a pasture scale may not be reflective of management even when management practices alter vegetation structure (Carroll et al. 2017). However, grassland bird nest densities may change when management alters overall vegetation conditions. For example, if nest survival is unrelated to density and all birds choosing to nest at a site can choose nesting structure that will maximize nest survival, then site level nesting output would be mediated by density. Therefore, management decisions creating heterogeneous environments should maximize community level nesting output by generating structure for a wide range of species with a similarly broad range of structural preferences.

We evaluate the effects of heterogeneity-based management on grassland bird nesting in this study. Specifically, we determined the influence of patch-burn grazing versus season-long grazing on 1) grassland bird nest success; 2) grassland bird nest density; and 3) vegetation

structure and composition. Results will inform conservation of grassland bird species and shed additional light on the complex dynamics relating grassland management to avian conservation objectives. A growing body of research on grazing management and nesting birds has generated diverse and nuanced results, and proper generalization will require data in the context of many systems. As rangeland management recognizes the need to embrace site specificity and variability in management, further study will allow for precise and effective grassland bird management recommendations.

## Methods

### Study Site

We quantified nest survival between grazing treatments at the Central Grasslands Research Extension Center (hereafter CGREC) located in southcentral North Dakota, USA. The CGREC is located in the Prairie Pothole Region of the northern mixed-grass prairie. Though the grass community is dominated by nonnative cool season grasses (Kentucky bluegrass, *Poa pratensis*, USDA PLANTS 2021; smooth brome, *Bromus inermis*, USDA PLANTS 2021), native grasses such as western wheatgrass (*Pascopyrum smithii*, USDA PLANTS 2021) and green needlegrass (*Nassella viridula*, USDA PLANTS 2021) are relatively common (Duquette et al. 2020). The diverse forb community includes milkweed (*Asclepias spp.*, USDA PLANTS 2021), goldenrod (*Solidago spp.*, USDA PLANTS 2021), and echinacea (*Echinacea angustifolia*, USDA PLANTS 2021); while western snowberry is the most common woody plant (*Symphoricarpos occidentalis*, USDA PLANTS 2021; Duquette et al. 2020). Study pastures do not have a prior history of management using fire but have underwent prior grazing and limited temporary farming. The climate is characterized as temperate, and growing season (May 1 to

September 1) conditions during the study period were as follows: 2017: 17.3 C, 22.6 cm; 2018: 18.6 C, 38.7 cm; 2019: 16.3 C, 33.4 cm; 2020: 18.1 C, 20.4 cm.

### **Treatment Structure**

Our treatment structure includes two variations on patch burn grazing and season-long grazing without fire (four replicates of 65 ha pastures per treatment, 1040 ha total). One patch-burn treatment consists of 16.2 ha dormant season burns (late-April through early-May) at a 4-year return interval (PBG40). The other consists of 8.1 ha dormant season and 8.1 ha growing season burns (mid-August to early-September) at a 4-year return interval (PBG20). The PBG20 treatment was designed to provide a midseason boost in livestock forage quality while allowing us also to investigate the effects of reduced patch size and greater heterogeneity. A full-use grazing (40-50 percent degree of disappearance) stocking rate using Angus crossbred cow/calf pairs was applied on a pasture-wide basis at 2.26–2.31 Animal Unit Months/ha and maintained across all pastures and treatments for a grazing season of mid-May through late-October. We did not perform half of growing season fires (two patches) in 2018 and all growing season fires (four patches) in 2019 due to unfavorable weather conditions.

### **Nest Searching and Monitoring**

Each year (2017-2020) from approximately 600 h to 1200 h from May 20<sup>th</sup> to July 15<sup>th</sup>, we searched pastures for grassland bird nests using systematic rope-dragging. We aimed to revisit each patch every two weeks over this interval. Two people pulled a 30m rope with regularly spaced bunches of aluminum cans through 4 ha plots in each 8.1 ha patch (eight plots/pasture; Hovick et al. 2012). Upon flushing a bird from the rope, we performed a detailed search of the immediate area. After finding a nest, we flagged the area 5 m north and 5 m south of the nest and recorded the UTM to aid in monitoring. When we did not find a nest but observed



scolding behavior from flushed birds, we flagged the area and returned within three days to attempt to locate a nest again (Winter et al. 2003). Upon discovering a nest, we assessed clutch size and candled two eggs of the host species (Lokemoen and Kofford 1996). For passerines, we also assessed parasitism by brown-headed cowbirds (*Molothrus ater*). We returned to nests every 2-4 days to assess fates and considered nests successful if at least one host individual fledged. Signs indicating successful nests in passerines included nearby parental scolding behavior and feeding activities, while waterfowl and shorebird nests were considered successful if we detected the presence of chicks, shells with intact membranes, or eggshell chips from pipping activities (Hovick et al. 2012, Hovick and Miller 2013, Ludlow and Davis 2018). We also included incidentally located nests in monitoring and analysis. Occasionally, we found nests that never contained host eggs during monitoring. These were excluded from survival but not density analysis.

### **Vegetation Monitoring**

We standardized vegetation monitoring to the actual or expected fledging date of all nests to assess the effects of vegetation structural characteristics on nest survival (Hovick et al. 2012). This allowed us to avoid biasing vegetation measurements for failed nests while also minimizing human disturbances to active nests (McConnell et al. 2017). At each nest, we estimated canopy cover of vegetation functional groups using a 0.5 x 1.0 m quadrat and cover class category midpoints (0%, 3%, 15%, 38%, 63%, 85%, 98%). We separated Kentucky bluegrass and smooth brome from remaining grasses due to their unique structural characteristics and non-native status (Duquette et al. 2020, USDA PLANTS 2021). We also measured litter depth, maximum vegetation height, bare ground extent, and litter cover at the nest. As a further measure of vegetation structure, we took nest site visual obstruction readings (VOR) in each cardinal

direction from 1 m above the ground at a distance of 4 m (Robel et al. 1970). These measures all served to quantify vegetation structure, as structure has been shown to be important in grassland bird breeding habitat (Davis et al. 2020).

We also assessed vegetation characteristics between treatments at the patch level. By doing so, we were able to quantify the direct effects of each grazing treatment on key vegetation structural attributes mediating nest survival. In each experimental pasture we distributed eight 150 m transects to coincide with each 8.1 ha burn patch. On each side, we placed a 0.5 m<sup>2</sup> frame every 15 m (20 frames/transect) and quantified vegetation using the same method as above. This additional vegetation data allowed us to compare structural and compositional components at nests to patch-level values.

## **Analysis**

### *Nest Survival*

All survival analyses were performed using mixed-effects logistic exposure models with the *lme4* package (Bates et al. 2015, Shew et al. 2019, R Core Team 2021). Each interval between nest checks constituted an exposure period, and all survival models included a random effect for nest identification. For the final monitoring interval at each nest, the fate was determined to occur halfway through the interval unless evidence suggested otherwise (e.g. a duck nest was in the process of hatching on the final check). Continuous covariates were scaled to one standard deviation and centered around their mean prior to analysis to improve model fit (Shew et al. 2019).

Our nest survival analyses were undertaken with several objectives. To separate purely inferential analyses from more exploratory ones, we first performed likelihood ratio tests for each species, evaluating support for survival models containing grazing treatment over the null

model (Rahmig et al. 2009). We then performed an exploratory analysis with the objective of determining relationships between vegetation structural variables and nest survival. For each species, we evaluated a set containing univariate models of vegetation functional groupings and measures of structure (i.e., litter depth, VOR, bare ground, litter cover, and vegetation height). For passerines, we also included a model containing a categorical covariate for Brown-headed cowbird parasitism. Models within 2 AICc of the best model were viewed as having support (Burnham and Anderson 2001). If a model was within 2 AICc units of the null model, we considered it to be uninformative (Arnold 2010). Before conducting vegetation analyses, we checked for multicollinearity in vegetation variables using a correlation coefficient of 0.7 as a cutoff.

### Nest Densities

We compared nest densities between pastures in each treatment. To do so, we corrected the apparent density in each pasture to account for already depredated (and thus less detectable) nests using the following formula:

$$Density = \frac{N}{DSR^a * A}$$

Where  $N$  is the number of nests found,  $DSR$  is the constant daily survival rate as calculated from our logistic exposure models,  $a$  is the average age of nests upon discovery in days, and  $A$  is the area of each pasture in hectares (Arnold et al. 2007). For each species considered, this equation adds the number of nests to each pasture that are expected to have been depredated before nest dragging occurred. Adjusted densities violated assumptions of normality, so to assess differences between treatments we employed a Kruskal-Wallis test and a post-hoc pairwise Wilcoxon rank sum test with a Bonferroni-Holmes correction for multiple comparisons (Hollander and Wolfe 1973, Saville 1990).

## Vegetation Structure

After identifying key vegetation and structural variables associated with nest survival, we evaluated differences in these factors between treatments. We performed mixed-effects models using Transect identification as a random effect, and treatment and year as fixed effects. Since our vegetation cover variables followed a right-skewed distribution, we used an inverse gamma link function and added a constant of 0.001 to all values to accommodate zeroes. We assessed post-hoc differences in vegetation and structural components using estimated marginal means in the *emmeans* package (Lenth, 2018).

## Results

We discovered 1975 nests from 30 species over the four-year study period (Table 3.1). For analysis, we focused on the 12 species with over 30 nests (Northern pintail, *Anas acuta*; Mallard, *Anas platyrhynchos*; Blue-winged teal, *Spatula discors*; Northern shoveler, *Spatula clypeata*; Gadwall, *Mareca strepera*; Brewer's blackbird, *Euphagus cyanocephalus*; Chestnut-collared longspur, *Calcarius ornatus*; Clay-colored sparrow, *Spizella pallida*; Western meadowlark, *Sturnella neglecta*; Grasshopper sparrow, *Ammodramus savannarum*; Savannah sparrow, *Passerculus sandwichensis*; Mourning dove, *Zenaida macroura*). We excluded Red-winged blackbirds (*Agelaius phoeniceus*) as most nests were encountered incidentally on the border of wetlands and we did not feel like wetland vegetation structure was reflective of grazing treatments.

Table 3.1. Nest totals by treatment from 2017 to 2020 at the Central Grasslands Research Extension Center near Streeter, North Dakota. Treatment abbreviations are as follows: PBG20, Patch-burn grazing with dormant and growing season fires; PBG40, Patch-burn grazing with dormant season fires; SLG, Season-long grazing.

| Species                    | PBG20 | PBG40 | SLG |
|----------------------------|-------|-------|-----|
| American Bittern           | 0     | 0     | 2   |
| American Wigeon            | 6     | 4     | 13  |
| Gadwall                    | 39    | 28    | 55  |
| Bobolink                   | 1     | 1     | 6   |
| Brewer's Blackbird         | 49    | 70    | 3   |
| Blue-winged Teal           | 164   | 91    | 128 |
| Canada Goose               | 0     | 0     | 3   |
| Chestnut-collared Longspur | 36    | 33    | 3   |
| Clay-colored Sparrow       | 70    | 102   | 121 |
| Common Nighthawk           | 14    | 6     | 0   |
| Eastern Kingbird           | 0     | 0     | 2   |
| Grasshopper Sparrow        | 31    | 22    | 18  |
| Green-winged Teal          | 1     | 0     | 0   |
| Horned Lark                | 2     | 3     | 0   |
| Killdeer                   | 10    | 3     | 0   |
| Lesser Scaup               | 0     | 2     | 4   |
| Marbled Godwit             | 3     | 3     | 0   |
| Mallard                    | 34    | 19    | 20  |
| Mourning Dove              | 34    | 15    | 39  |
| Northern Pintail           | 52    | 51    | 37  |
| Northern Shoveler          | 27    | 33    | 20  |
| Wilson's Phalarope         | 5     | 3     | 0   |
| Red-winged Blackbird       | 15    | 15    | 10  |
| Savannah Sparrow           | 13    | 18    | 14  |
| Sharp-tailed Grouse        | 3     | 6     | 3   |
| Upland Sandpiper           | 10    | 4     | 5   |
| Western Meadowlark         | 100   | 93    | 82  |
| Willet                     | 7     | 6     | 1   |
| Wilson's Snipe             | 14    | 9     | 5   |
| Yellow-headed Blackbird    | 1     | 0     | 0   |
|                            | 741   | 640   | 594 |
| Total                      | 1975  |       |     |

## Nest Survival

Nest survival was not different between treatments ( $p > 0.05$ ) for all 12 bird species considered. However, the survival of some species was associated with vegetation and structural variables that are influenced by fire and grazing disturbances (Table 3.2). Vegetation height was positively associated with nest survival in Brewer’s blackbirds and Clay-colored sparrows (Fig. 3.1). However, Northern pintail and Western meadowlark nest survival decreased with taller vegetation (Fig. 3.1). Savannah sparrow survival decreased with increasing litter depth (Fig. 3.1). Brewer’s blackbird nest survival increased with vegetation obstruction (Fig. 3.1). Mallard and Chestnut-collared longspur survival increased with smooth brome and forb cover, respectively (Fig. 3.1). Mourning dove, Blue-winged teal, Grasshopper sparrow, Gadwall, and Northern shoveler survival was not associated with vegetation and structural variables at the scale measured.

Table 3.2. Model outputs for vegetation and structural components affecting nest survival of 12 species of grassland birds at the Central Grasslands Research Extension Center near Streeter, North Dakota from 2017-2020. Only models with a  $\Delta\text{AICc} \leq 2$  are presented. We do not present models when best models are within 2  $\Delta\text{AICc}$  of the null model. Best-supported models are in bold.

| Species                    | Model                    | $\Delta\text{AICc}$ | K | $W$  |
|----------------------------|--------------------------|---------------------|---|------|
| Northern Pintail           | <b>Vegetation Height</b> | <b>0</b>            | 3 | 0.54 |
|                            | Bare                     | 1.94                | 3 | 0.20 |
| Mallard                    | <b>Smooth Brome</b>      | <b>0</b>            | 3 | 0.38 |
|                            | Bare                     | 1.36                | 3 | 0.19 |
| Blue-winged Teal           | <i>Null</i>              | 0                   | 2 | 0.16 |
| Brewer’s Blackbird         | <b>VOR</b>               | <b>0</b>            | 3 | 0.6  |
|                            | <b>Vegetation Height</b> | <b>1.43</b>         | 3 | 0.29 |
| Chestnut-collared Longspur | <b>Forb</b>              | <b>0</b>            | 3 | 0.68 |
| Clay-colored Sparrow       | <b>Vegetation Height</b> | <b>0</b>            | 3 | 0.79 |
| Western Meadowlark         | <b>Vegetation Height</b> | <b>0</b>            | 3 | 0.97 |
| Grasshopper Sparrow        | <i>Null</i>              |                     |   |      |
| Northern Shoveler          | <i>Null</i>              |                     |   |      |
| Savannah Sparrow           | <b>Litter Depth</b>      | <b>0</b>            | 3 | 0.88 |
| Gadwall                    | <i>Null</i>              |                     |   |      |
| Mourning Dove              | <i>Null</i>              |                     |   |      |

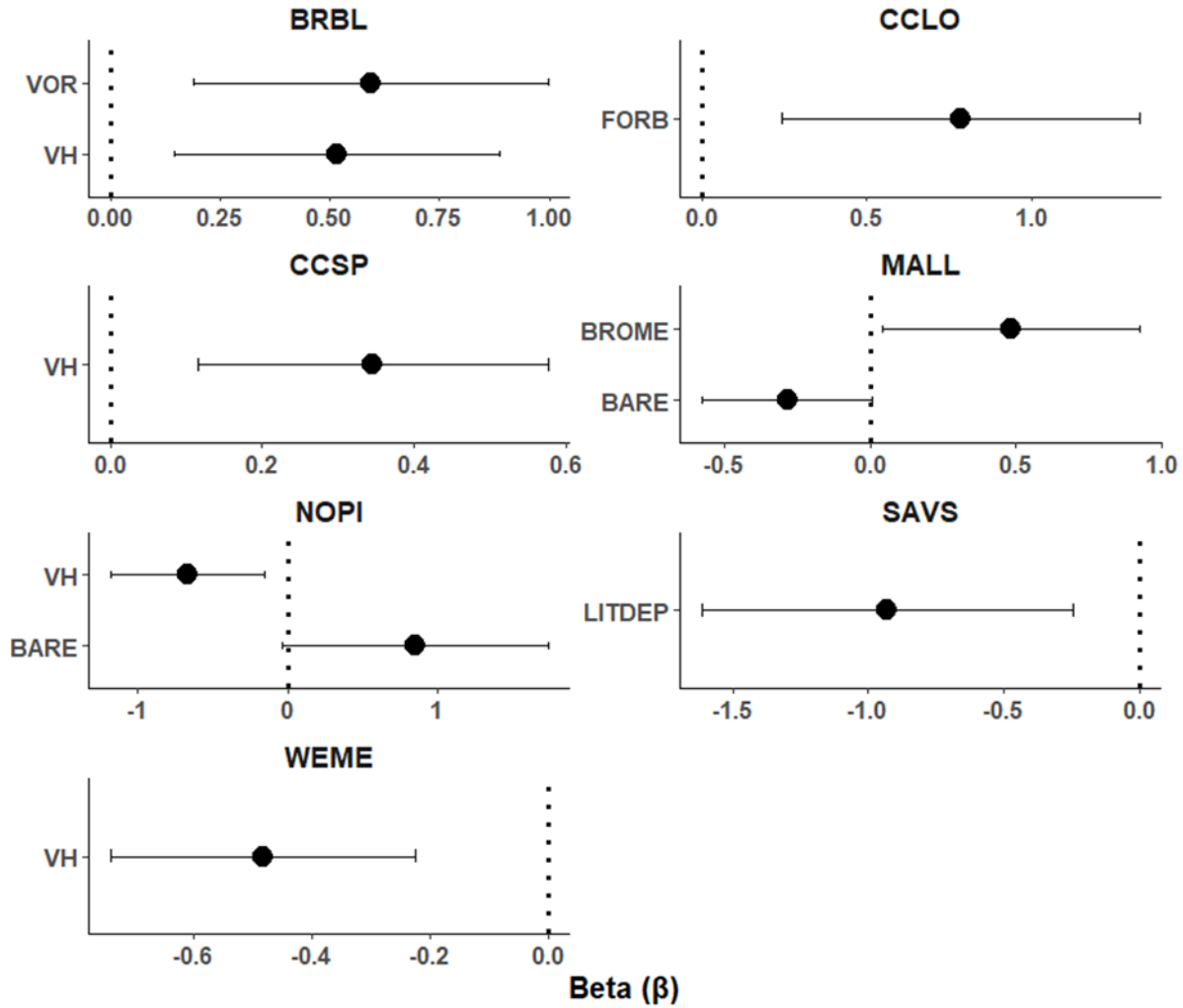


Figure 3.1. Compositional and structural parameters influencing nest survival in grassland birds from 2017-2020 at the Central Grasslands Research Extension Center near Streeter, North Dakota. Measurements were taken at nests. Values are standardized regression coefficients and lines represent 95% confidence intervals. Abbreviations for structure variables are as follows: VOR, Visual Obstruction Reading; VH, Vegetation Height; KBG, Kentucky bluegrass; LITDEP, Litter Depth. Species abbreviations are as follows: BRBL, Brewer’s Blackbird; BWTE, Blue-winged Teal; CCLO, Chestnut-collared Longspur; CCSP, Clay-colored Sparrow; Gadwall, Gadwall; GRSP, Grasshopper Sparrow; MALL, Mallard; NOPI, Northern Pintail; NSHO, Northern Shoveler; WEME, Western Meadowlark.

### Nest Density

Nest densities varied between grazing treatments ( $p \leq 0.05$ ) for Northern pintail, Brewer’s blackbird, and Chestnut-collared longspur, while densities for all other species did not vary ( $p > 0.05$ ) between treatments (Fig 3.2). Northern pintail densities were higher in the

dormant season only patch-burn treatments (PBG40) than either the dormant and growing season patch-burn (PBG20) and the season-long grazing pastures (SLG; Fig 3.2). Nest densities of Brewer's blackbirds and Chestnut-collared longspur were much higher in both patch-burn treatments compared to season-long grazing but did not differ from each other (Fig 3.2).

### **Vegetation Structure**

Despite the absence of a grazing treatment effect on nest survival, we found differences in key vegetation and structural components between grazing treatments. Patch-burn pastures had slightly shorter vegetation structure, more bare ground, over twice the forb cover, half the smooth brome cover, and shallower litter than SLG pastures (Fig 3.3). Litter cover did not vary between grazing treatments (Fig 3.3).



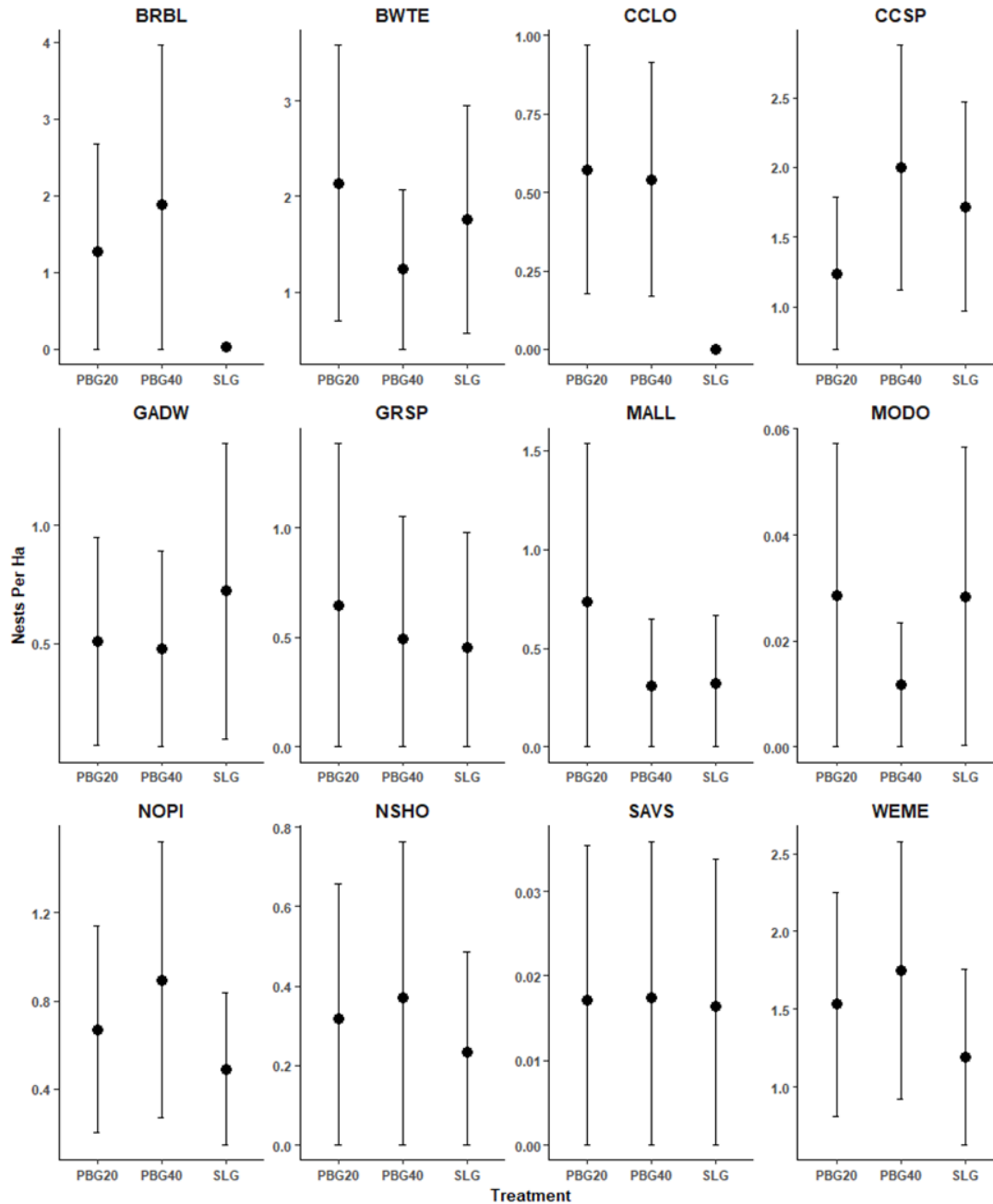


Figure 3.2. Grassland bird nest density by grazing treatment in 2017-2020 at the Central Grasslands Research Extension Center near Streeter, North Dakota. Lines represent 95% confidence intervals. Abbreviations for structure variables are as follows: VOR, Visual Obstruction Reading; VH, Vegetation Height; KBG, Kentucky bluegrass; LITDEP, Litter Depth. Species abbreviations are as follows: BRBL, Brewer’s Blackbird; BWTE, Blue-winged Teal; CCLO, Chestnut-collared Longspur; CCSP, Clay-colored Sparrow; Gadwall, Gadwall; GRSP, Grasshopper Sparrow; MALL, Mallard; NOPI, Northern Pintail; NSHO, Northern Shoveler; WEME, Western Meadowlark. Treatment abbreviations are as follows: PBG20, Patch-burn grazing with dormant and growing season fires; PBG40, Patch-burn grazing with dormant season only fires; SLG, Season-long grazing.

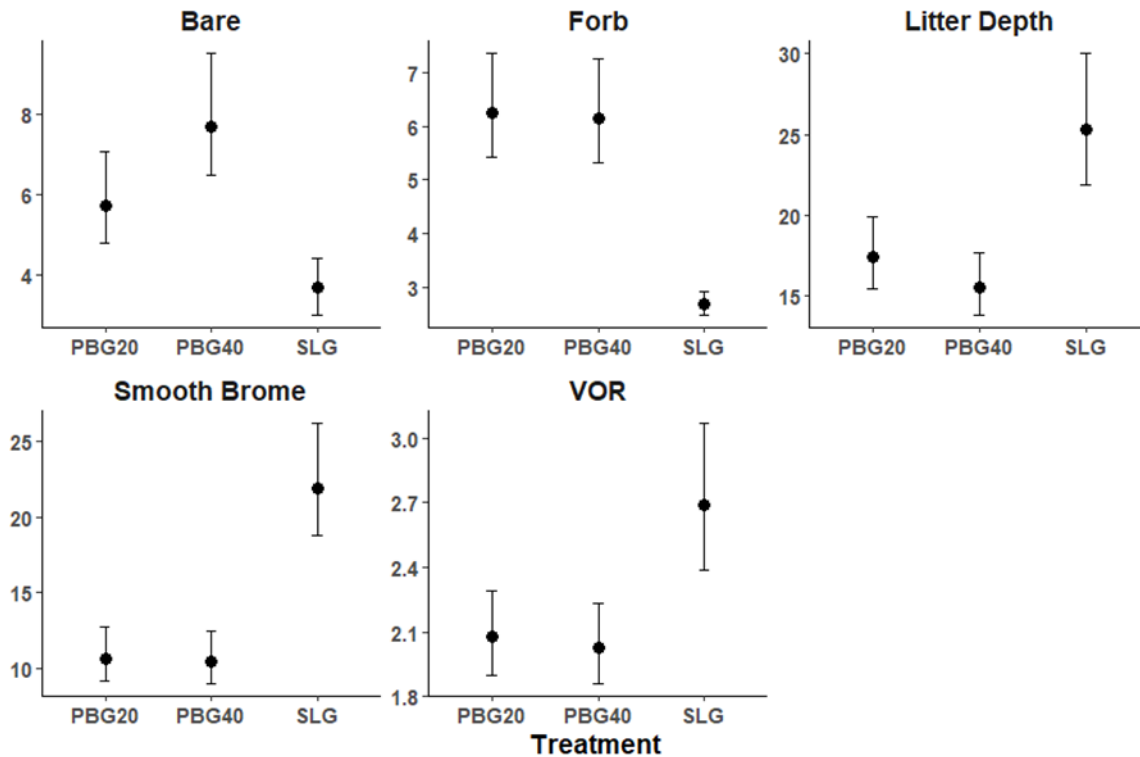


Figure 3.3. Patch-level vegetation compositional and structural components influencing grassland bird nest survival from 2017-2020 at the Central Grasslands Research Extension Center near Streeter, North Dakota. Lines represent 95% confidence intervals. Units are in percentages except for Litter Depth and visual obstruction reading (VOR), which are in mm and dm, respectively. Treatment abbreviations are as follows: PBG20, Patch-burn grazing with dormant and growing season fires; PBG40, Patch-burn grazing with dormant season fires; SLG, Season-long grazing.

### Discussion

Nesting decisions made by grassland birds occur at multiple scales, and flexibility within a species can mediate pasture-level changes in vegetation structure (Carroll et al. 2017). Our research shows that although grazing systems create differences in vegetation structure that are key determinants of nest survival, grassland birds appear to be able to moderate survival through selection at finer scales. Even though we did not see differences in nest density between grazing treatments for most species, patch-burn grazing may create valuable nesting cover for species that rely on sparse nesting cover, including species of local concern such as Northern pintail and Chestnut-collared longspur (Davis et al. 1999, Beauchamp et al. 1996). Though fully-stocked

grazing management appears to provide suitable nesting habitat for many species of grassland birds in northern mixed-grass prairie regardless of specific management strategy, the heterogeneity-generating interaction of grassland fire and grazing maximizes the number of species able to nest successfully in grazed landscapes.

Our study complements other work showing that grazing management has an effect on vegetation variables that influence grassland bird nest survival, even if treatment effects do not influence survival directly (Hovick et al. 2012, Skagen et al. 2017, Shew et al. 2019). In addition, inherent landscape heterogeneity that is already present can be a driver of both vegetation diversity (Fuhlendorf and Smeins 1998) and the diversity of higher taxa such as birds and butterflies (Myers et al. 2015). It is likely that a full-use stocking rate combined with topographic variability across all study pastures provided sufficient nesting habitat for most species. The Prairie Pothole Region as a whole is a topographically complex, and variation in vegetation structure across ecological sites likely creates a wide gradient from which a diverse bird community may nest. However, differences in nesting density between treatments for three short vegetation specialists indicate that short-statured vegetation is limiting in season-long grazing treatments in spite of vegetation heterogeneity. Without fire to direct grazing behavior, cattle do not seem to be applying enough grazing pressure to create large areas of short-statured vegetation.

The need to create areas of sparse cover for nesting species may be more important now than ever in the Northern Great Plains. In recent decades, rapid and widespread proliferation of Kentucky bluegrass, a non-native, thatch-forming C3 species, has caused significant changes to grassland vegetation structure (Palit et al. 2021). The success of Kentucky bluegrass invasion is partly due to conservation practices designed to increase dense nesting cover for waterfowl in the

1960s (Dixon et al. 2019). However, our work shows that currently the opposite end of the vegetation structure spectrum may be at a premium. Grassland bird population management must balance the need to preserve biodiversity with the provision of specific habitats for species of concern (Duchardt et al. 2018). By creating a mosaic of vegetation structure on the landscape, patch burn grazing will ensure a consistent proportion of diverse vegetation structures creating the availability and temporal constancy of nesting cover.

As the body of work on grazing management and avian nesting has grown, it has become clear that the benefits of patch-burn management vary based on the system in which it is practiced. For example, in semi-arid rangeland, patch-burning grazing successfully created breeding habitat for mountain plovers, but reduced the densities of most species considered (Augustine and Derner 2015). This is likely because tall, dense vegetation was limiting, and they did not find that patch-burning increased vegetation density in unburned patches relative to controls (Augustine and Derner 2015). As a result, the authors advocate for patch-burning combined with other grazing strategies that generate dense vegetation. In our study system, higher primary productivity and thatch-forming invasive grasses mean that effective strategies to remove litter and promote shorter vegetation are needed to benefit the full suite of grassland birds.

Nest survival and nest density are only two parameters governing grassland bird reproduction, and they may not always accurately reflect population trends (Knutson et al. 2006). Future work should consider survival of passerine fledglings and waterfowl, grouse, and shorebird young. Mortality during the post-nest life stages is a significant and understudied aspect of grassland bird reproduction that has been shown to be responsive to habitat management (Cox et al. 2014). Thus far, research on fire, grazing, and fledgling survival is

limited, and early results are mixed. Grasshopper sparrow survival was not influenced by patch-burn grazing (Hovick et al. 2011), while Henslow's sparrow survival decreased in recently burned patches (Young et al. 2019). As grassland birds appear to display extreme flexibility in nesting decisions, the simultaneous study of nest selection, survival, and brood/nestling survival is likely necessary to fully understand the impact of grazing management on grassland bird reproduction.

### **Conclusion**

In the Northern Great Plains, patch-burn grazing should be viewed as a tool for creating suitable nesting structure for short vegetation specialists while avoiding rangeland degradation from overgrazing. It enhances rangeland heterogeneity by creating areas of sparse vegetation when they would otherwise be limiting. As grassland bird species are variable in their nesting preferences, we did not expect to see a net positive or negative result when looking at species individually. However, even with this expectation, we found no negative impacts to nest survival or density for species relying on vegetation of medium and high density. In addition, patch-burn grazing improves cattle forage, decreases livestock pest burden, and creates a grass bank in times of drought (Scasta et al. 2012, Polito et al. 2013, McGranahan et al. 2014, Spiess et al. 2020). Therefore, this management strategy is an important tool for advancing livestock production and conservation goals simultaneously. Management strategies for grassland bird diversity may require a multiplicity of approaches to encourage heterogeneity and maximize nest survival and nest numbers for the greatest number of species possible.

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APPENDIX. SPECIES ABBREVIATIONS USED IN MODELING FLORAL RESOURCE

ABUNDANCE.

| <b>Abbreviation</b> | <b>Full Name</b>                   | <b>Common Name</b>          |
|---------------------|------------------------------------|-----------------------------|
| <i>ACHMIL</i>       | <i>Achillea millefolium</i>        | Common Yarrow               |
| <i>ALLSTE</i>       | <i>Allium stellatum</i>            | Prairie Onion               |
| <i>AMOCAN</i>       | <i>Amorpha canescens</i>           | Leadplant                   |
| <i>ANECAN</i>       | <i>Anemone canadensis</i>          | Canada Anemone              |
| <i>ANECYL</i>       | <i>Anemone cylindrica</i>          | Thimbleweed                 |
| <i>ASCOVA</i>       | <i>Asclepias ovalifolia</i>        | Oval-leaf Milkweed          |
| <i>ASTAGR</i>       | <i>Astragalus agrestis</i>         | Purple Milkvetch            |
| <i>ASTFLE</i>       | <i>Astragalus flexuosus</i>        | Flexile Milkvetch           |
| <i>CAMROT</i>       | <i>Campanula rotundifolia</i>      | Bluebell Bellflower         |
| <i>CIRARV</i>       | <i>Cirsium arvense</i>             | Canada Thistle              |
| <i>CIRFLO</i>       | <i>Cirsium flodmanii</i>           | Flodman's Thistle           |
| <i>DALPUR</i>       | <i>Dalea purpurea</i>              | Purple Prairie Clover       |
| <i>ECHANG</i>       | <i>Echinacea angustifolia</i>      | Blacksamson Echinacea       |
| <i>ERISTR</i>       | <i>Erigeron strigosus</i>          | Prairie Fleabane            |
| <i>ERYINC</i>       | <i>Erysimum inconspicuum</i>       | Shy Wallflower              |
| <i>EUPESU</i>       | <i>Euphorbia esula</i>             | Leafy Spurge                |
| <i>GALBOR</i>       | <i>Galium boreale</i>              | Northern Bedstraw           |
| <i>GLYLEP</i>       | <i>Glycyrrhiza lepidota</i>        | American Licorice           |
| <i>HELMAX</i>       | <i>Helianthus maximiliani</i>      | Maximillian Sunflower       |
| <i>HELPAU</i>       | <i>Helianthus pauciflorus</i>      | Stiff Sunflower             |
| <i>LACTAT</i>       | <i>Lactuca tatarica</i>            | Blue Lettuce                |
| <i>MEDLUP</i>       | <i>Medicago lupulina</i>           | Black Medic                 |
| <i>MEDSAT</i>       | <i>Medicago sativa</i>             | Alfalfa                     |
| <i>MELALB</i>       | <i>Melilotus albus</i>             | White Sweetclover           |
| <i>MELOFF</i>       | <i>Melilotus officinalis</i>       | Yellow Sweetclover          |
| <i>ONOMOL</i>       | <i>Onosmodium molle</i>            | False Gromwell              |
| <i>OXYLAM</i>       | <i>Oxytropis lambertii</i>         | Purple Locoweed             |
| <i>PEDARG</i>       | <i>Pediomelum argophyllum</i>      | Silverleaf Indian Breadroot |
| <i>PENGRA</i>       | <i>Penstemon gracilis</i>          | Lilac Penstemon             |
| <i>POLALB</i>       | <i>Polygala alba</i>               | White Milkwort              |
| <i>POLVER</i>       | <i>Polygala verticillata</i>       | Whorled Milkwort            |
| <i>RATCOL</i>       | <i>Ratibida columnifera</i>        | Upright Prairie Coneflower  |
| <i>RUDHIR</i>       | <i>Rudbeckia hirta</i>             | Blackeyed Susan             |
| <i>SOLMIS</i>       | <i>Solidago missouriensis</i>      | Missouri Goldenrod          |
| <i>SYMOCC</i>       | <i>Symphoricarpos occidentalis</i> | Western Snowberry           |
| <i>VICAME</i>       | <i>Vicia americana</i>             | American Vetch              |