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AVIAN COMMUNITY RESPONSES TO BISON GRAZING IN NORTH AMERICAN INTERMOUNTAIN GRASSLANDS

By

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ABSTRACT

Grassland and shrubland songbird species are a guild of conservation concern in North America. Many of these species have experienced severe population declines, due to habitat loss and land use change. This makes the conservation and management of remaining habitat of crucial importance for this guild. Grazing by large herbivores is an ecosystem process in grassland systems, and in North America, one of the major historic grazers was the Plains bison (*Bison bison*). Bison are considered ecosystem engineers, because they modify habitat to be more or less suitable for other species, such as grassland and shrubland songbirds. Bison grazing can affect avian habitat by altering the vegetation structure. In turn, birds respond to these changes in vegetation structure. Bison are becoming more common due to recent reintroductions. From 2009-2017, at least eight bison reintroductions have occurred in North America. Lands where bison exist are good candidates for songbird conservation because bison are typically present in protected areas with a large grass and shrub component. Despite this potential, there is limited research about the effects of bison grazing on grassland and shrubland songbirds. Further research on this subject will inform bison management for songbird conservation. I investigate the relationship between bison grazing and songbird responses in two intermountain grasslands: the National Bison Range and Yellowstone National Park. In Chapter 1, I explore two ecological processes that may maintain species richness of grassland and shrubland songbirds: habitat heterogeneity from bison grazing, and productivity, a measure of the resources available to individuals. I analyzed the relationship between these variables and the occupancy of 10 avian species. I conclude that bison grazing has a stronger influence on bird occupancy and species richness than site productivity. In Chapter 2, I test whether differences between the study sites influence the abundance responses of vesper sparrow (*Pooecetes gramineus*) and western meadowlark (*Sturnella neglecta*) to bison grazing intensity. The differences, such as scale of bison grazing, herd size and density, and vegetation type show minimal influence on these species’ responses to bison grazing, but may be worth considering in conservation applications.

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Chapter 1: The Relative Importance of Habitat Heterogeneity and Productivity to Intermountain Grassland Songbird Species Richness

Introduction

Ecologists have long observed that the number of different species in a community or region can vary substantially across environmental conditions (MacArthur & MacArthur 1961; Pianka 1966). Understanding patterns in species richness is a major goal of ecology, demonstrated by more than 120 hypotheses (e.g. habitat area hypothesis, intermediate disturbance hypothesis) that have been proposed (Palmer 1994). The multitude of potential explanations indicates there is little scientific consensus on the primary mechanisms that maintain species richness. Many correlates with species richness have been identified (Palmer 1994; Willig et al. 2003; Rahbek 2005), yet their relative importance remains debatable and is sensitive to the temporal and spatial scale of inquiry (Waide et al. 1999; Mittelbach et al. 2001; Whittaker 2010; Šímová et al. 2013). Thus, clarifying the mechanisms that maintain species richness remains an important goal to further the science of ecological relationships.

Understanding the maintenance of species richness is not only theoretically significant, it is critical to the identification of conservation priorities. Numerous constituencies value biodiversity, but with limited resources, decision-makers must often prioritize means to benefit the greatest number of species. A theoretical understanding of species richness provides key information by predicting which conditions support higher species richness. However, this information must be relevant to the scale at which conservation actions take place. Several studies suggest that species richness is more variable and less predictable at small spatial scales (Field et al. 2009; Mcbride et al. 2014). Thus, more research is needed at local management levels to inform conservation decisions.

Songbird species in intermountain grasslands are a guild that provides an opportunity to further our theoretical understanding of species richness and apply that understanding to conservation. Intermountain grassland refers to the non-forested valley lands of the Rocky Mountain region, composed of a blend of prairie grasslands and shrublands (Seastedt 2002). Grassland and shrubland avian species found in intermountain grasslands have shown long-term, nationwide, population declines (Paige & Ritter 1999; Knick et al. 2003; Brennan & Kuvlesky 2005). These declines are largely due to habitat loss from fragmentation and land use change (Knick & Rotenberry 1995; Askins et al. 2007) making the management and conservation of remaining habitat of critical importance. Ensuring that conservation efforts can support as many intermountain grassland songbird species as possible will be crucial to their persistence into the future. To inform management for these species, I use species richness to test two hypotheses that have practical applications for conservation: the habitat heterogeneity hypothesis and the species-energy hypothesis.

The habitat heterogeneity hypothesis predicts that species richness will be maximized in habitats that are the most heterogeneous because it provides the highest diversity of niches for species to utilize (MacArthur & MacArthur 1961). Grazing by large herbivores may affect the habitat heterogeneity of intermountain grasslands by altering the vegetation structure. Vegetation structure refers to the characteristics of density, height, and dispersion (Fisher & Davis 2010) of grasses and shrubs. As an ecosystem process, grazing manipulates vegetation structure by reducing vegetation height (Tastad 2013), increasing bare ground (Augustine et al. 2012), and altering the spatial heterogeneity of vegetation (Adler et al. 2001). Increases in the heterogeneity of vegetation structure due to grazing have been documented at a variety of spatial scales (Lwiwski et al. 2015; Bleho 2009). Grassland obligate species respond to differences in vegetation structure (Fisher & Davis 2010), and other grassland and shrubland species have been shown to respond to grazing (Saab et al. 1995). As birds seek the vegetation structure they prefer, areas with higher heterogeneity of vegetation structure may support more species (Hovick et al. 2014, 2015).

Historically, one of the major grazers of North America was the American bison (*Bison bison*). Bison were once widespread, ranging from as far west as Oregon and Washington, to eastern states such as Pennsylvania (Gates et al. 2010). These grazers played an important role in creating and maintaining heterogeneity in their habitat. Gates et al. (2010) defined bison as ecosystem engineers—a species that modifies habitat to be more or less suitable for other species—because they created and responded to heterogeneity through grazing, wallowing, and horning behaviors. The ecological effects of bison helped provide habitat conditions that supported a wide range of bird species (Askins et al. 2007).

The presence of bison is becoming more common through recent reintroduction efforts (Appendix 1, Table A1-2). Areas where bison are currently present, or will be reintroduced, are strong candidates for bird conservation efforts for several reasons. Bison primarily eat grasses and sedges (McCullough 1980; Singer and Norland 1994), thriving in areas with a large grass component, also providing habitat for grassland and shrubland species. Bison are often present and are likely to be reintroduced on lands that have protected status, such as national parks (e.g. Banff, Yellowstone, and Grand Teton National Parks), private lands managed by non-governmental organizations (e.g. The American Prairie Foundation and The Nature Conservancy), or state parks (e.g. Antelope Island State Park, UT). Areas with protected status are often created under the explicit goal of conservation, with funding and staff allocated to that goal. These attributes, combined with the ability of bison to create structural heterogeneity in vegetation, suggest lands with bison are valuable for bird conservation. Testing the habitat heterogeneity hypothesis as a mechanism of songbird species richness will inform current and future bison management to support songbird conservation.

I also tested the species-energy hypothesis as a mechanism for maintaining species richness. The species-energy hypothesis predicts that habitats have higher species richness in areas of higher productivity (Wright 1983). Productivity is defined as the rate at which energy, originating from solar radiation, is converted to resources and biomass to be utilized by individuals (Wright 1983). Higher productivity supports a greater number of individuals, thereby reducing local species extinction rates, and supporting a greater number of species (Srivastava & Lawton 1998). Understanding this relationship may be especially important for songbirds in grassland systems because of the extent to which their habitat has been fragmented and reduced (Knick & Rotenberry 1995; Askins et al. 2007). The most productive areas of North American grasslands (with higher available energy) have undergone extensive land use change and are overwhelmingly under heavy human use (Scott et al. 2001). If productivity is important for maintaining species richness, this makes identifying remaining areas of high species richness a priority for conservation. My research contributes to a theoretical understanding of the species richness-energy relationship at a scale that is applicable for conservation actions.

I investigated the effect of bison grazing and site productivity on avian species richness in two intermountain grasslands of the Rocky Mountain Region to test the habitat heterogeneity and species-richness hypotheses. I selected two study areas of differing primary productivity to test the species-energy hypothesis, and stratified by grazing intensity between sites to test the habitat heterogeneity hypothesis. I then sampled grassland and shrubland songbird occupancy and species richness across a spectrum of productivity and grazing intensity. I predict from the habitat heterogeneity hypothesis that grazing intensity will have a unimodal effect on species richness with species richness highest at intermediate levels of grazing (Figure 1-1). Because grazing increases structural heterogeneity, the low end of the grazing spectrum will have lower structural heterogeneity. As grazing increases, structural heterogeneity will increase, until biomass of vegetation becomes limiting at the high end of the grazing spectrum, at which point structural heterogeneity decreases (Ausden 2007). Secondly, I predict from the species-energy hypothesis that productivity will have a positive, linear effect on species richness as suggested by Cusens et al. (2012) (Figure 1-2). The relative importance of habitat heterogeneity and productivity to species richness will help guide conservation for intermountain grassland songbird species.

Study Areas

I conducted my research in two study sites. The first was the National Bison Range (NBR), in the Mission Valley near Moiese, MT. The NBR is federally managed by the U.S. Fish and Wildlife Service and was established in 1908 for the conservation of bison. There are approximately 350 bison on the NBR. In the past, bison management consisted of rotating bison among 8 pastures during summer months and leaving one pasture ungrazed for an entire year (A. Lisk, personal communication). Since 2015, bison movement has been unrestricted except to be contained within the boundary of the NBR (A. Lisk, personal communication). The NBR is approximately 76 km^2 and the vegetation is 75% intermountain grassland similar to Palouse prairie. The remaining area consists of conifer forest and riparian habitat. The grasslands are characterized by bunchgrasses such as Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Agropyron spicatum*), and prairie junegrass (*Koeleria macrantha*). Intermixed in the grasslands are forbs such as arrowleaf balsamroot (*Balsamorrhiza sagittata*), and low shrubs such as Wood’s rose (*Rosa woodsia*) and snowberry (*Symphoricarpus occidentalis*).

My second study site was the Northern Range of Yellowstone National Park (YNP). YNP is federally managed by the National Park Service. There are approximately 5,000 bison in YNP, 3,500 of which use the Northern Range (Geremia et al. 2014). The Northern Range of YNP constitutes a large part of the herd’s summer range and encompasses about 890 km^2. Bison movements are minimally managed within YNP, but boundaries are enforced to contain bison within YNP. I conducted surveys in the Lamar Valley. The area is composed of shrub steppe, dominated by mountain big sagebrush (*Artemisia tridentata*), and grass species such as Idaho fescue, bluebunch wheatgrass, and prairie junegrass.

Methods

Field Methods:

To measure avian species richness, I established sampling plots in areas I predicted would represent the spectrum of low to high bison grazing intensity. I then measured avian species occupancy, bison grazing intensity, and productivity at each plot.

Plot Size:

I defined sampling plots at 250 x 250 m (62,500 m^2) for three reasons. First, by walking a transect through the middle of the plot, observers were able to survey for birds up to 125 meters to either side. Beyond 125 meters, human detection of birds declines dramatically (Ralph et al. 1995). Secondly, this area is approximately twice the size of the breeding territory western meadowlarks (*Sturnella neglecta*), the species of interest expected to have the largest territory size (Lanyon 1956; Aweida 1995). Lastly, the study sites have varying topography with steep slopes and drainages. To maximize visibility, I chose a plot size that reduced the probability of visual obstructions within the plot.

Sampling Frame:

I stratified my plot selection across three levels of bison grazing intensity. I developed these bison grazing strata using a habitat suitability index (HSI) (Steenweg et al. 2016, Wiggins 2016), using slope (U.S. Geological Survey 2015), distance to water (U.S. Geological Survey 2013), and vegetation type (Landfire 2012). HSI models use a species' known affinities for habitat characteristics to predict suitability of a habitat for a given species. I binned the continuous HSI values from both study sites into three strata of bison grazing intensity, using the Natural Jenks tool in ArcGIS: Low (0.169-0.459), Medium (0.460-0.611), and High (0.612-0.795). HSI values range from 0 to 1, with 0 representing the least suitable habitat, and 1 representing the most suitable habitat for bison.

I randomly selected plots in each stratum, and sampled plots by the following criteria: 1.) the plot contained ≥ 75% grassland or shrub steppe vegetation, and 2.) the plot contained a continuous segment of habitat ≥ 75% of the plot (Wiggins 2016). At the NBR site, I sampled 10 plots in the Low stratum, 30 plots in the Medium stratum, and 30 plots in the High stratum each year. Compared to Medium and High stratum (43% and 32% of NBR, respectively), there was less Low stratum available in the NBR (approximately 11% of NBR), because much of this area was also forested. This resulted in sampling fewer Low stratum plots in this study site. To compensate, I sampled a larger number of Low stratum plots at the YNP site. In YNP, I sampled 30 plots in the Low stratum, 13 plots in the Medium stratum, and 12 in the High stratum in 2016. In 2017, I sampled 25 plots in the Low stratum, 8 in the Medium stratum, and 11 in the High stratum (Appendix 1, Table A1-1). I selected plots in YNP from an area similar in size to the NBR (YNP = 69 km^2, NBR = 76 km^2).

Avian Occupancy Surveys:

A line transect of 250 meters was walked through the middle of each plot in which observers recorded all songbird species seen within the plot. Visual confirmation of the bird within plot boundaries was required, thus detections in which the bird was heard but not seen were not recorded. Observers used rangefinders to confirm each bird was within plot boundaries. Observers walked slowly and stopped occasionally, such that each bird survey took approximately 20-30 minutes per plot. All surveys were conducted in the early morning hours, from dawn until 1000 MDT in order to target the hours when birds are most active and easily detectable. Surveys were not conducted in rain or winds higher than 24 km/hr because these conditions result in reduced detectability of birds. In NBR, bird surveys were conducted from May 20 to July 7 in 2016 and from May 19 to June 30 in 2017. In YNP, bird surveys were conducted from June 1 to July 1 in 2016 and from May 31 to July 9 in 2017. All plots were sampled twice within a field season.

Covariate Data:

Bison Grazing Intensity:

I measured bison grazing intensity by counting bison patties in each plot. Density of patties estimates bison grazing intensity at patch-level spatial scales and has been shown to reflect vegetation responses to grazing intensity (Tastad 2013). Following Sliwinski (2011), patties were either individual, well-formed piles, or several closely associated piles. Observers counted all patties, regardless of age, representing bison use over recent years. Observers walked four bison grazing transects within each plot. Two transects were sampled each time immediately following a bird survey in each plot. These transects were located to both sides of the bird transect and were midway between the bird transect and the edge of the plot (see Appendix 1, Figure A1-1). Observers walked two transects in an East-West direction, and two transects in a North-South direction. Observers walked slowly, counting all patties within 1 m to the left and right of the line transect.

Productivity data:

I measured productivity using the mean of the cumulative Normalized Difference Vegetation Index (NDVI) at each plot from April 1 to June 30 of each year. I chose this timeframe to capture the beginning of the growing season for vegetation and the end of the bird breeding season. NDVI is a remotely sensed measurement of photosynthetic pigments in vegetation and is considered a proxy for primary production of vegetation (Tucker & Sellers 1986; Paruelo et al. 1997). Primary production, and its conversion to higher trophic levels, creates resources and biomass that are utilized by individuals and support species. NDVI values range from -1 to 1, with -1 indicating the lowest measurement of vegetative productivity and 1 indicating the highest measurement of vegetative productivity. I used an established NDVI product (Robinson et al. 2017) that uses gap-filling and smoothing techniques, and has a resolution of 30 m. I obtained NDVI data online at http://ndvi.ntsg.umt.edu.

Analytical Methods:

Correlation between covariates:

I investigated relationships between patty counts and NDVI value using pairwise plot matrices, linear regressions, and variance inflation factor. Because bison grazing could be influenced by NDVI, I used these methods to determine whether patty counts and NDVI were collinear.

Multi-species Occupancy Model:

To analyze species richness across bison grazing intensity and productivity, I used a Bayesian multi-species occupancy model (MSOM) developed by Zipkin et al. (2010). This hierarchical model uses parameters estimated from the observation process to describe parameters in the ecological process of interest (occupancy). The observation process is almost always imperfect, but failure to detect a species can be distinguished from true absence of a species through repeated sampling of a plot. The field data is thus corrected for detection, and then used to model the ecological relationship. This allows us to estimate true occupancy, which is unobservable. The use of community-level hyper-parameters adds another level to the hierarchy because species-level parameters are assumed to be drawn from a common distribution (Zipkin et al. 2010). Thus, hyper-parameters represent a mean response of all species. Incorporating hyper-parameters enables better estimates of species-specific estimates, and allows estimation for species that are rare or even unobserved in the data set. I augmented species data to estimate unobserved species following Zipkin (2010).

In the MSOM, the binary state of occurrence for each species i, at site j, in year l, is assumed to arise from a Bernoulli random variable such that:

$$\mathrm{z}\ (i, j, l) \sim Bern\ (\Psi_{i,j,l})$$

and $\Psi_{i,j,l}$ represents the probability that species i occurs at point j in year l. $\Psi_{i,j,l}$ is imperfectly observed, but from the data (x), one can estimate the probability of detection ($p_{i,j,k}$) for each species i, at point j, replicate k, and year l, such that:

$$x(i, j, k, l) \sim Bern(p_{i,j,k,l}) * z(i, j, l))$$

Thus, the likelihood is represented as follows:

$$L[x_{i,j,l} | \Psi_{i,j,l}, p_{i,j,l}]$$

$$= I_{\left\{\sum_{k=1}^{K_{j,l}} x_{i,j,k,l} > 0\right\}} \left(\Psi_{i,j,l} \prod_{k=1}^{K_{j,l}} p_{i,j,k,l}^{x_{i,j,k,l}} \left(1 - p_{i,j,k,l}\right)^{1-x_{i,j,k,l}} \right)$$

$$+ \left(1 - I_{\left\{\sum_{k=1}^{K_j} x_{i,j,k,l} > 0\right\}}\right) \left(\left(1 - \Psi_{i,j,l}\right) + \Psi_{i,j,l} \prod_{k=1}^{K_j} p_{i,j,k,l} \right)$$

My data met the assumptions of the MSOM, which are that sites are closed to extinction and colonization across repeated surveys, species are identified correctly, and the probability of occupancy and detection at a plot are independent of those probabilities at another plot. The first assumption was met by surveying plots during the breeding season. Birds have higher site fidelity during the breeding season as they establish a territory, build a nest, and raise young. This reduces the likelihood that individuals left or colonized sites between surveys. The second assumption was met by training observers to identify species by sight and sound. Observers were supervised in their observations until they could reliably identify species in order to assure data quality. The third assumption was met by consecutively surveying plots with a shared border to avoid the possibility of counting an individual in both plots.

I modeled occupancy as a function of study site (NBR or YNP), bison grazing intensity (patties), productivity (NDVI), and an interaction between bison grazing intensity and productivity, using the logit-link function:

$$logit\left(\Psi_{i,j,l}\right) = \; uNBR_i + uYNP_i + \; \alpha1_i * patties_{j,l} + \alpha2_i * \; {patties^2}_{j,l} + \; \alpha3_i * NDVI_{j,l}$$

$$+ \; \alpha4_i * NDVI_{j,l} * patties_{j,l} + \; \alpha5_i * Year$$

I augmented the number of species in the community as described by Royle et al. (2007), to estimate the total number of species in the community, including ones not detected during field surveys. I ran the model with three chains, for 60,000 iterations each, and an adaptation period of 30,000 iterations. Model convergence was assessed using the Gelman-Rubin statistic (Gelman & Rubin 1992) and visual inspection of trace plots, autocorrelation, estimate density, and the running mean. I assessed goodness of fit using a Bayesian p-value by comparing the estimated deviance values and predicted deviance values for each MCMC sample of each observation, following Broms et al. (2016).

Results

National Bison Range:

At NBR, field teams completed two surveys on 70 plots each year. For analysis, I included all grassland and shrubland species, with the exception of brown-headed cowbirds (*Molothrus ater*). I excluded this species because it feeds in association with grazers and is a brood-parasite (Robinson et al. 1995), thus its habitat is unlikely to be associated with vegetation structure. The species used in analysis included clay-colored sparrow (*Spizella pallida*), grasshopper sparrow (*Ammodramus savannarum*), lark sparrow (*Chondestes grammacus*), vesper sparrow (*Pooecetes gramineus*), and western meadowlark (*Sturnella neglecta*). In 2016, mean patty count per plot ranged from 2-85.5 patties (median = 23.5 patties, IQR = 26.9 patties) and in 2017 from 1.8-66.8 patties (median = 20.25 patties, IQR = 21.6 patties). In 2016, mean cumulative NDVI per plot ranged from 31.96 – 52.19 (median = 40.63, IQR = 5.97) and in 2017 from 35.95 – 58.26 (median = 47.19, IQR = 6.25). Patty counts and NDVI were not correlated in NBR. The R^2 value for patty counts and NDVI was 0.00 in 2016 (p = 0.87), and 0.00 in 2017 (p = 0.72). Patty counts and NDVI had very low variance inflation factors (2016 = 1.0004, 2017 = 1.002), indicating little concern for collinearity between these covariates.

The effect of patty counts (α_1) on species-specific occupancy probabilities was the strongest species-level covariate (Table 1-1). The 95% credible intervals for grasshopper sparrow, vesper sparrow, and western meadowlark did not cross zero. All coefficients for parameters in the MSOM are presented on the logit-link scale. Species responses ranged from -0.68 (95% CRI = -4.79, 3.08) for lark sparrows, to 2.11 (95% CRI = 0.77, 4.83) for grasshopper sparrows. The majority of species responses to patty counts were positive, with the exception of lark sparrows (mean = -0.68, 95% CRI = -4.79, 3.08). Most species showed negative quadratic responses to patty counts (α_2), with the most negative being -0.76 (95% CRI = -2.00, 0.11) for clay-colored sparrows. Additional species-specific responses are presented in Figure 1-5.

Species-specific responses to NDVI (α_3) were weaker than for patty counts and all credible intervals crossed zero (Table 1-1). Species responses ranged from -0.13 (95% CRI = -1.11, 0.78) for western meadowlarks to 0.30 (95% CRI = -0.39, 1.08) for clay-colored sparrows. Except for western meadowlarks, all species' linear responses to NDVI were positive (Figure 1-7). For all species, there was a negative response to the interaction between NDVI and patty counts. Responses ranged from -0.67 (95% CRI = -2.21, 0.18) for clay-colored sparrows to -0.14 (95% CRI = -1.46, 1.17) for lark sparrows.

The fixed effect of year (α_5) was weakly positive for most species, indicating species had higher occupancy rates in 2017 than in 2016. All credible intervals for the effect of year crossed zero. Only vesper sparrows had lower occupancy in 2017, with a response to year of -0.39 (95% CRI = -1.33, 0.80). Positive responses ranged from 0.04 (95% CRI = -2.64, 3.31) for lark sparrows, to 0.60 (95% CRI = -0.68, 2.15) for grasshopper sparrows.

Yellowstone National Park

At YNP, field teams completed two surveys on 53 plots in 2016 and on 42 plots in 2017. I included all grassland and shrubland species, with the exception of brown-headed cowbird. The species used in analysis included: Brewer's sparrow (*Spizella breweri*), green-tailed towhee (*Pipilo chlorurus*), horned lark (*Eremophila alpestris*) sage thrasher (*Oreoscoptes montanus*), savannah sparrow (*Passerculus sandwichensis*), vesper sparrow, and western meadowlark. In 2016, mean patty count ranged from 4.0 – 84.0 patties (median = 36.0 patties, IQR = 24.3 patties), and in 2017 from 12.8 – 110.8 patties (median = 41.3 patties, IQR = 31 patties). In 2016, mean cumulative NDVI per plot ranged from 29.04 – 44.64 (median = 35.20, IQR = 4.44), and in 2017 from 35.91 – 51.17 (median = 44.79, IQR = 5.99). Patty counts and NDVI were not correlated in YNP. The R^2 value for patty counts and NDVI was 0.00 in 2016 ($p = 0.92$), and 0.00 in 2017 ($p = 0.74$). Similar to NBR, patty counts and NDVI had very low variance inflation factors (2016 = 1.002, 2017 = 1.0002), indicating little concern for collinearity between these covariates.

The effect of patty counts (α_1) on species-specific occupancy probabilities was also the strongest species-level covariate in YNP (Table 1-1). Credible intervals for Brewer's sparrow, sage thrasher, savannah sparrow, vesper sparrow, and western meadowlark did not cross zero. Species responses ranged from -1.09 (95% CRI = -4.76, 2.00) for horned larks to 2.66 (95% CRI = 0.68, 5.90) for sage thrashers. The majority of species responses to patty counts were positive, with the exception of horned larks (mean = -1.09, 95% CRI = -4.76, 2.00), and green-tailed towhees (mean = -0.53, 95% CRI = -1.55, 0.32). Most species showed negative quadratic responses to patty counts (α_2), with the most negative being -0.43 (95% CRI = -1.69, 0.99) for sage thrashers. The only positive quadratic response to patty counts was for Brewer's sparrows (0.38, 95% CRI = -0.35, 1.63). See Table 1-1 and Figure 1-6 for more species-specific details.

Species-specific responses to NDVI (α_3) were also less than for patty counts in YNP and credible intervals for all species crossed zero (Table 1-1). Most linear responses to NDVI were negative, with the exception of savannah sparrows. Coefficients ranged from -0.47 (95% CRI = -1.18, 0.14) for green-tailed towhees to 0.23 (95% CRI = -0.75, 1.52) for savannah sparrows. Responses to the interaction between NDVI and patty counts were mixed, with four species responding positively and three species responding negatively. Negative responses ranged from -0.57 (95% CRI = -1.36, 0.07) for vesper sparrows to -0.30 (95% CRI = -1.28, 0.59) for Brewer's sparrows. Positive responses ranged from 0.10 (95% CRI = -0.43, 1.03) for horned larks to 0.28 (-0.38, 1.05) for green-tailed towhees. See Table 1-1 and Figure 1-8 for more species-specific details.

The fixed effect of year (α_5) was weakly negative for most species, indicating species had higher occupancy rates in 2016 than in 2017. All credible intervals for the effect of year crossed zero, except for Brewer's sparrow. Negative responses to year ranged from -1.73 (95% CRI = -3.30, -0.47) for Brewer's sparrows to -0.39 (95% CRI = -1.33, 0.80) to -0.39 (95% CRI = -1.33, 0.80) for vesper sparrows. Only western meadowlarks had a positive effect of year (mean = 0.07, 95% CRI = -2.47, 3.76).

Community-level responses:

The Bayesian p-value for the goodness-of-fit test of the MSOM was p = 0.12. P-values less than 0.05 or higher than 0.95 are considered to have poor model fit (Broms et al. 2016), thus the model has an adequate fit to the data. The community parameters, representing the mean response of all species, showed little effect of the covariates on community occupancy. All credible intervals for community parameters overlapped zero (Table 1-3). Patty counts had a positive effect on community occupancy ($\mu\alpha_1$mean = 0.97, 95% CRI = -0.49, 2.58), with a slightly negative quadratic effect ($\mu\alpha_2$ mean = -0.21 95% CRI = -0.82, 0.53). NDVI had a slightly negative linear effect on the probability of community occupancy ($\mu\alpha_3$ mean = -0.11, 95% CRI = -0.67, 0.45). The effect of the interaction between NDVI and patty counts also had a negative effect on the probability of community occupancy ($\mu\alpha_4$ mean = -0.22, 95% CRI = -0.94, 0.39). Overall, the probability of community occupancy was lower in 2017 than in 2016, as the effect of year was negative ($\mu\alpha_5$ mean = -0.54, 95% CRI = -1.79, 0.63).

Detection Parameters:

Detection was essentially unaffected by date across the breeding season (Table 1-4). At the community level, the effect of date on detection of any species ($\mu\beta_1$) was 0.00 (95% CRI = -0.22, 0.22), with a quadratic effect ($\mu\beta_2$) of 0.01 (95% CRI = -0.14, 0.18). The effect of date on species-specific detection (β_1) was more variable ranging from -0.21 (95% CRI = -0.73, 0.19) for savannah sparrows to 0.26 for horned larks (95% CRI = -0.20, 0.86). The 95% credible intervals for all species crossed zero, with the exception of Brewer's sparrows (mean = 0.19, 95% CRI = 0.03, 0.37) (Table 1-2). The quadratic effect of date (β_2) was small for all species, ranging from -0.13 for lark sparrows (95% CRI = -0.48, 0.14) to 0.15 (95% CRI = -0.14, 0.63) for savannah sparrows.

The estimated number of species in the community (N) was 11.77 (95% CRI = 10.00 16.00). This indicates that between the two study sites, 1 to 2 additional species were present, but not detected in the grassland and shrubland bird community.

Discussion

My results suggest weak support for the habitat heterogeneity hypothesis and my prediction that bison grazing intensity would have a unimodal effect on species richness. Across all species and both study locations, species richness increased with higher bison grazing intensity, as measured by patty counts. This effect became less positive with continued increases in bison grazing intensity, indicating that intermediate bison grazing intensities supported the highest species richness (Figure 1-3). Though the credible intervals for the community parameters associated with bison grazing intensity all crossed zero (Table 1-3), the linear effect of patty counts had the strongest effects on occupancy probability for individual species (Figure 1-5 and 1-6). Patty counts had a significant and positive effect for six of ten avian species (Table 1-1). This supports an increase in species richness because those six species are more likely to be present under conditions of higher bison grazing.

The distribution of grazing intensity in my study sites was skewed towards lower grazing intensity, and I sampled relatively few plots with very high grazing intensity, especially at the NBR site. More data at the high end of the grazing spectrum would be especially informative to determine the shape of the relationship between bison grazing intensity and avian species richness. More data may provide stronger support for the observed relationship, but it is also possible that avian species richness could level off and remain at similar levels to intermediate grazing.

The relationship between bison grazing intensity and avian species richness is entirely correlational, as I did not measure the effect of bison grazing intensity on heterogeneity of vegetation structure in avian habitat. Thus, alternative explanations are possible. For example, bison grazing has been shown to increase arthropod and grasshopper species diversity and abundance (Joern 2005, Moran 2014). These invertebrates are prey items for many grassland and shrubland songbird species. Instead of affecting habitat heterogeneity, bison grazing intensity could increase avian species richness by creating greater food (and thus energy) resources. If this is the case, then species richness increases until intermediate grazing, at which point species richness declines, perhaps due to increased interspecific competition. Further studies should explore the causative relationship between bison grazing intensity, the heterogeneity of multiple characteristics of vegetation structure, and avian species richness to establish a comprehensive understanding of how habitat heterogeneity influences avian species richness.

My results do not support the species-energy hypothesis. I predicted productivity would have a positive, linear effect on species richness (Figure 1-2). Instead, species richness decreased slightly with increased NDVI (Figure 1-4). The effect of productivity was very small for both species richness and the probability of individual species occupancy, with all credible intervals overlapping zero (Table 1-1 and 1-3). Though the observed result is unexpected, it is not unprecedented. In their meta-analysis, Milchunas et al. (2001) found that negative relationships with productivity are common for studies of animals at several ecological scales. An alternative prediction of the species-energy hypothesis is that richness increases in a unimodal relationship with productivity. This is explained by a decline in richness at higher productivities due to increased interspecific competition. If this were the case, my results may have only captured the negative part of the unimodal relationship, due to sampling a limited range of productivity values.

For most species, there was a small negative interaction between NDVI and patty counts (Table 1-1 and 1-3). While this was not a strong effect, it suggests that as productivity and grazing intensity both increase, fewer species are present. The effect of productivity was negative at the community level, and in combination with higher intensities of grazing, the effect becomes more negative. This interaction may warrant further investigation. While there was no correlation present between NDVI and patty counts in my study, others have found that grazing may influence plant primary productivity (Manier & Hobbs 2007). Such interaction may in turn influence how grassland and shrubland songbirds respond to these conditions in their habitat.

Habitat heterogeneity from bison grazing had a relatively stronger effect on species richness than productivity. This may be partly due to the scale at which I measured these relationships. My results apply to the local management scale where habitat heterogeneity may be more variable, but productivity is less variable. This could result in a stronger influence of habitat heterogeneity than productivity. Field et al. (2009) concluded that productivity strongly influenced species richness at large scales, but the effect was less evident at small scales because of the limited range of productivity at that scale. Bohning-Gaese (1997) notes that habitat heterogeneity is often important at small scale investigations of avian species richness, while energy-related variables are more important at large spatial scales. This suggests that habitat heterogeneity may be a more important consideration for conservation at a local management level than productivity.

In the context of intermountain grassland songbird conservation, the correlation between bison grazing intensity and plot-level species richness suggests that bison grazing may support occupancy for multiple species in the avian community. This relationship should be considered by conservation constituents and decision-makers in areas where bison are already present and in bison-reintroduction scenarios. However, the results should not be interpreted to recommend a particular grazing intensity. The effects of grazing on vegetation can vary substantially based on moisture availability (Milchunas & Lauenroth 1988), herding behavior (McNaughton 1984), pre-existing vegetation patterns (Adler et al. 2001), and spatial scale (Adler et al. 2001). In particular, grazing effects can vary based on the length of evolutionary history of grazing (Milchunas & Lauenroth 1988), as this influences the development of grazing-related adaptations in plants

(Mack & Thompson 1982). The intermountain grasslands where I conducted my research are considered to have a short evolutionary history of grazing (Milchunas & Lauenroth 1988), where bison were less abundant than in the Great Plains (Mack & Thompson 1982). Thus, a given intensity of bison grazing could have very different effects on vegetation structure and avian species richness across locations, and results from my study may not transfer to other locations. To successfully incorporate bison grazing management into avian conservation plans, decision-makers must first understand how grazing interacts with the management area.

From the perspective of local-scale avian conservation, my results suggest productivity is a less important factor for decision-makers to consider. Within my study sites, plot-level species richness was not strongly correlated with productivity. At a similar scale in other management areas, the variability in productivity may not be sufficient to strongly impact species richness. If this is the case, decision-makers can focus their efforts on other factors, such as habitat heterogeneity, that have a stronger influence on species richness at this scale.

My study informs conservation priorities for intermountain grassland avian communities and indicates a stronger relative influence of habitat heterogeneity over productivity in supporting species richness. These results can be considered for conservation scenarios in which bison grazing may provide habitat heterogeneity for avian species, and should be considered at a similar scale as this study. Lastly, the results inform a theoretical understanding of species richness and lend modest support for the habitat heterogeneity hypothesis.

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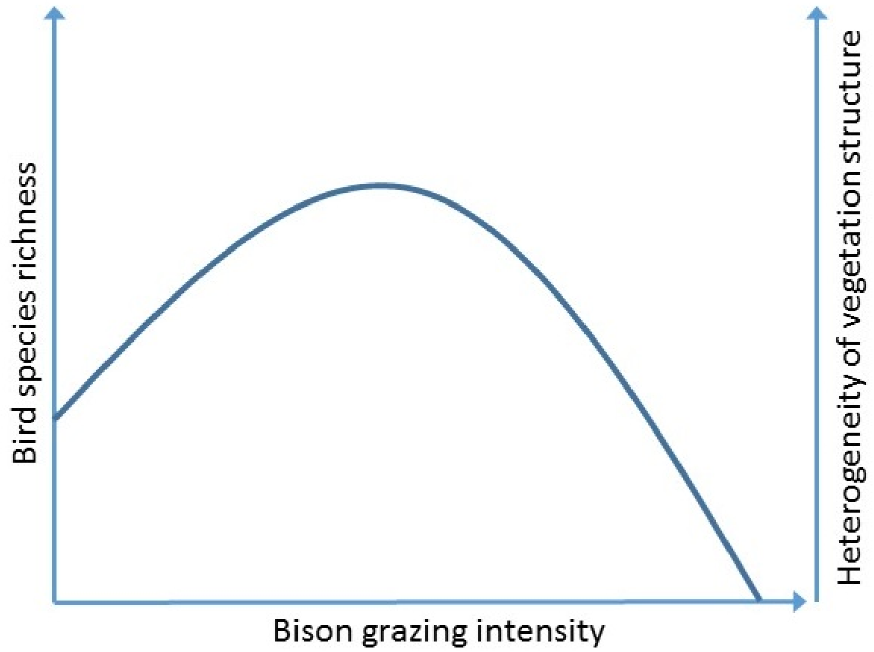
Figures and Tables



<u>Figure 1-1:</u> Predicted response of bird species richness as bison grazing intensity increases. Bison grazing intensity increases heterogeneity of vegetation in a unimodal pattern. Bird species richness increases in response to the heterogeneity of vegetation, and thus also responds to bison grazing intensity in a unimodal pattern.

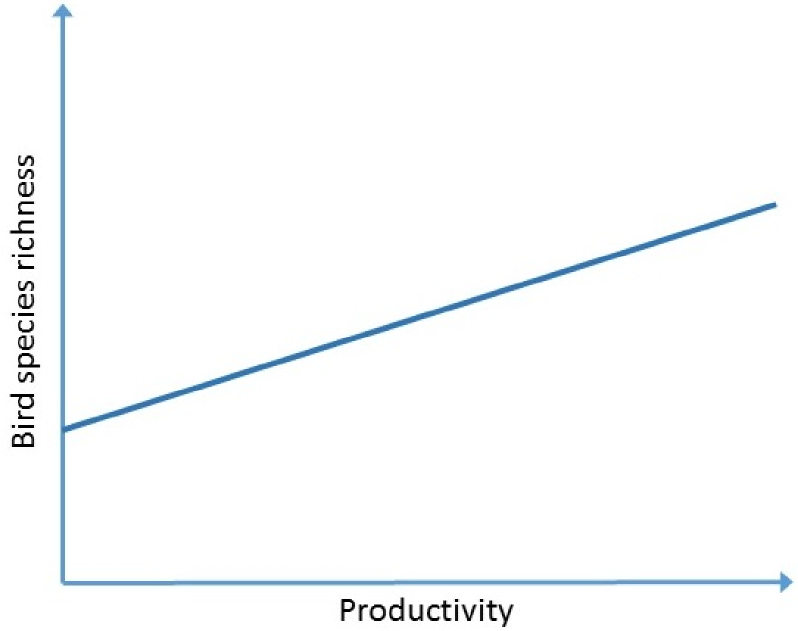


Figure 1-2: Predicted response of bird species richness to productivity. Increases in productivity result in more individuals, thus reducing local extinction rates and supporting a greater number of species.

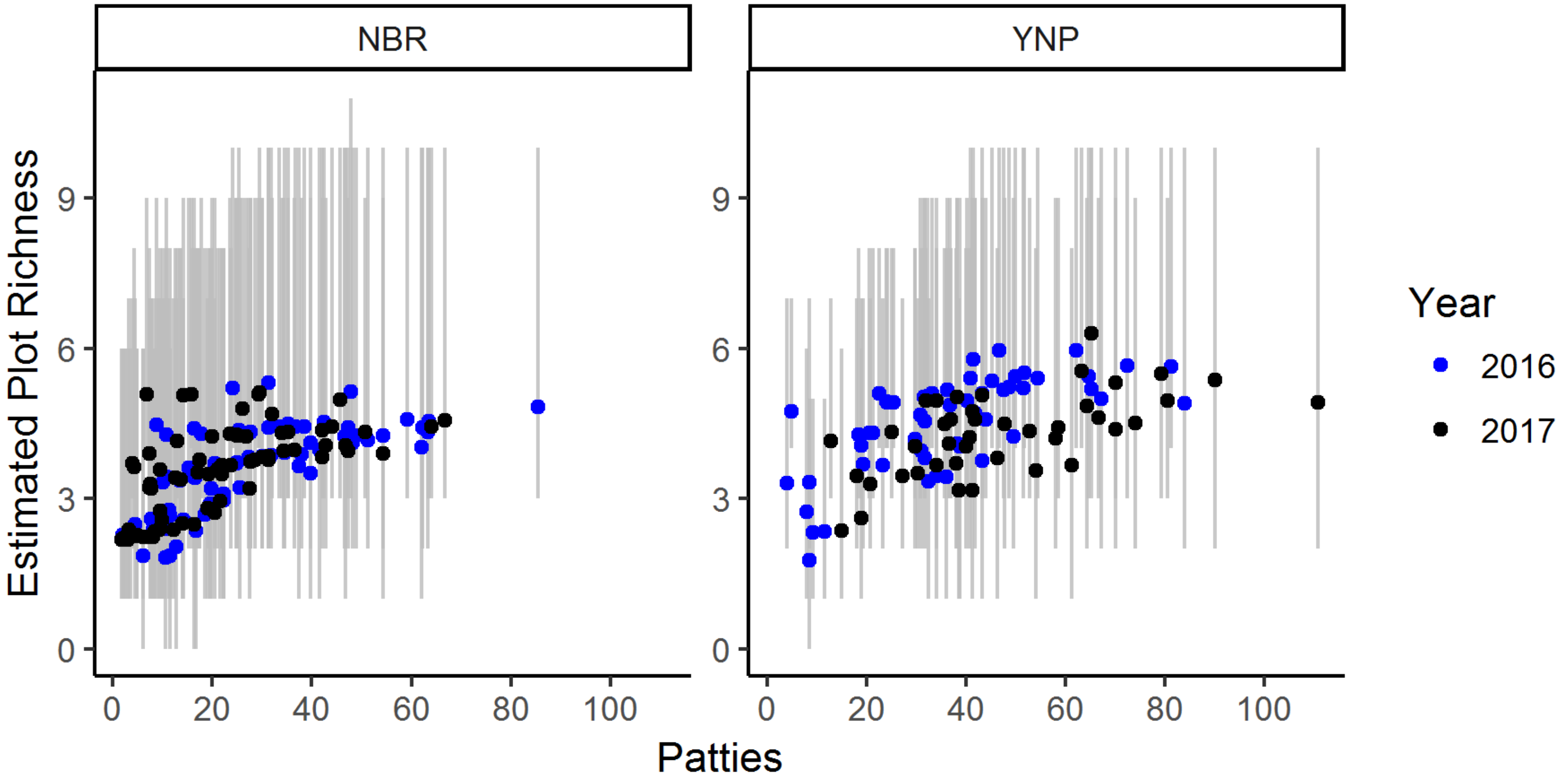


Figure 1-3: The relationship between patty counts and plot species richness at the National Bison Range (NBR) and Yellowstone National Park (YNP) study sites in 2016 and 2017. Data points show the mean plot richness estimate and lines through the point show 95% credible intervals.

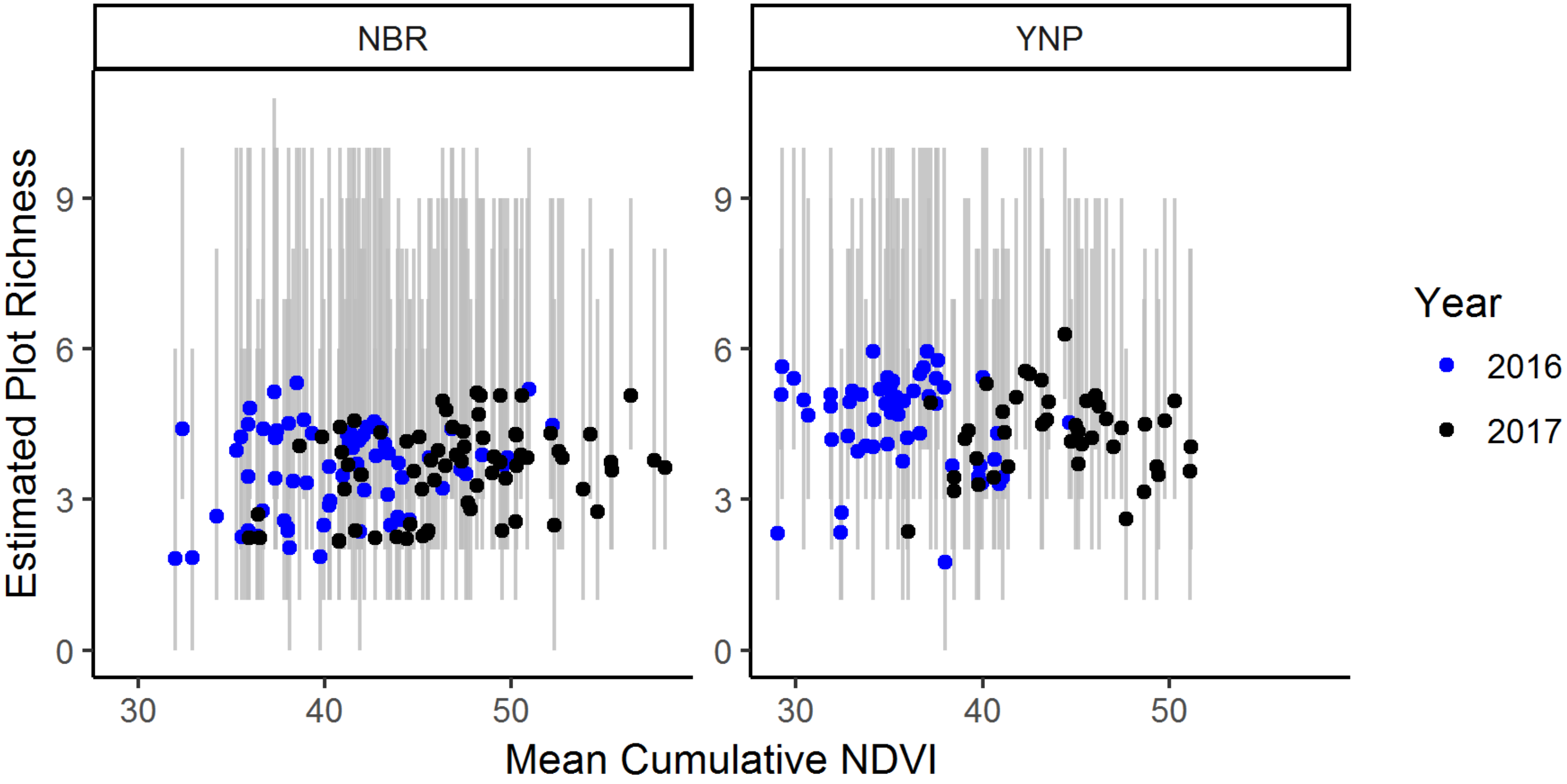
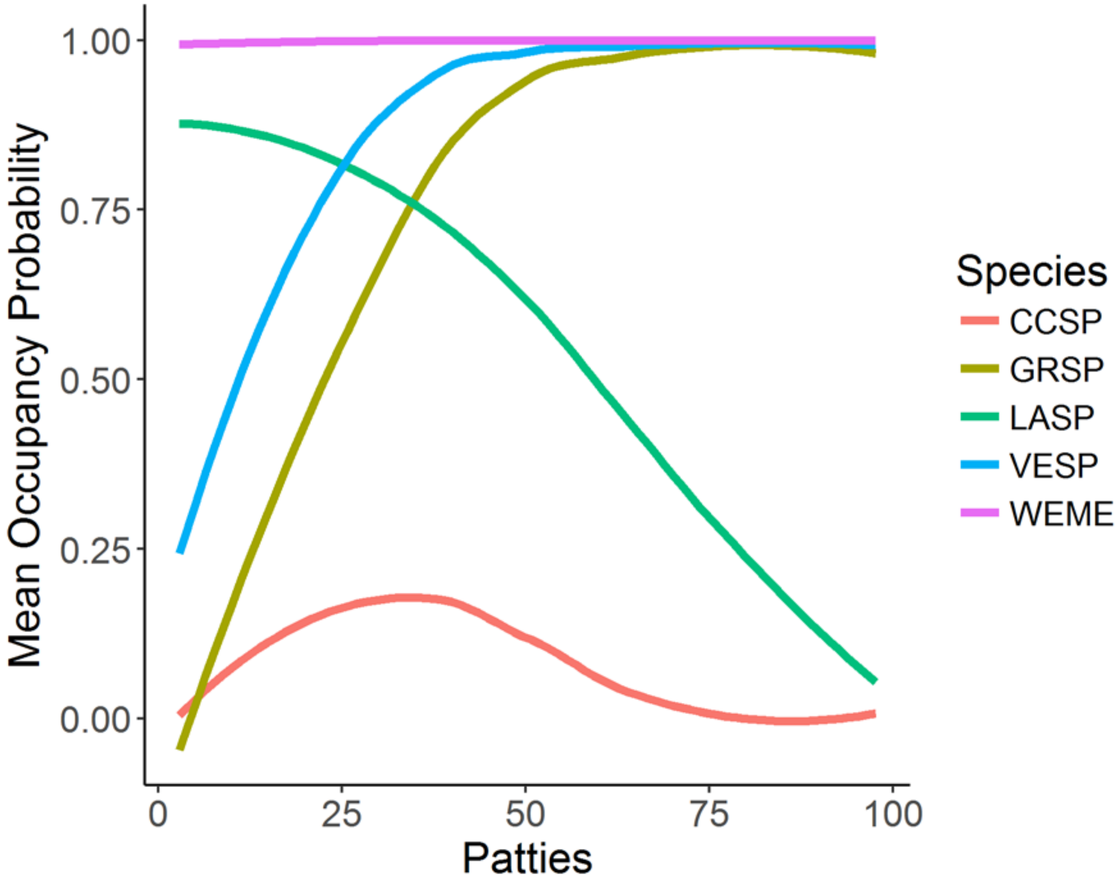


Figure 1-4: The relationship between mean cumulative NDVI and plot species richness at the National Bison Range (NBR) and Yellowstone National Park (YNP) study sites in 2016 and 2017. Data points show the mean plot richness estimate and lines through the point show 95% credible intervals.



<u>Figure 1-5:</u> The relationship between mean species occupancy probability and patty counts at the National Bison Range. Species identity is indicated by the four letter code for the common name: clay-colored sparrow (CCSP), grasshopper sparrow (GRSP), lark sparrow (LASP), vesper sparrow (VESP), and western meadowlark (WEME).

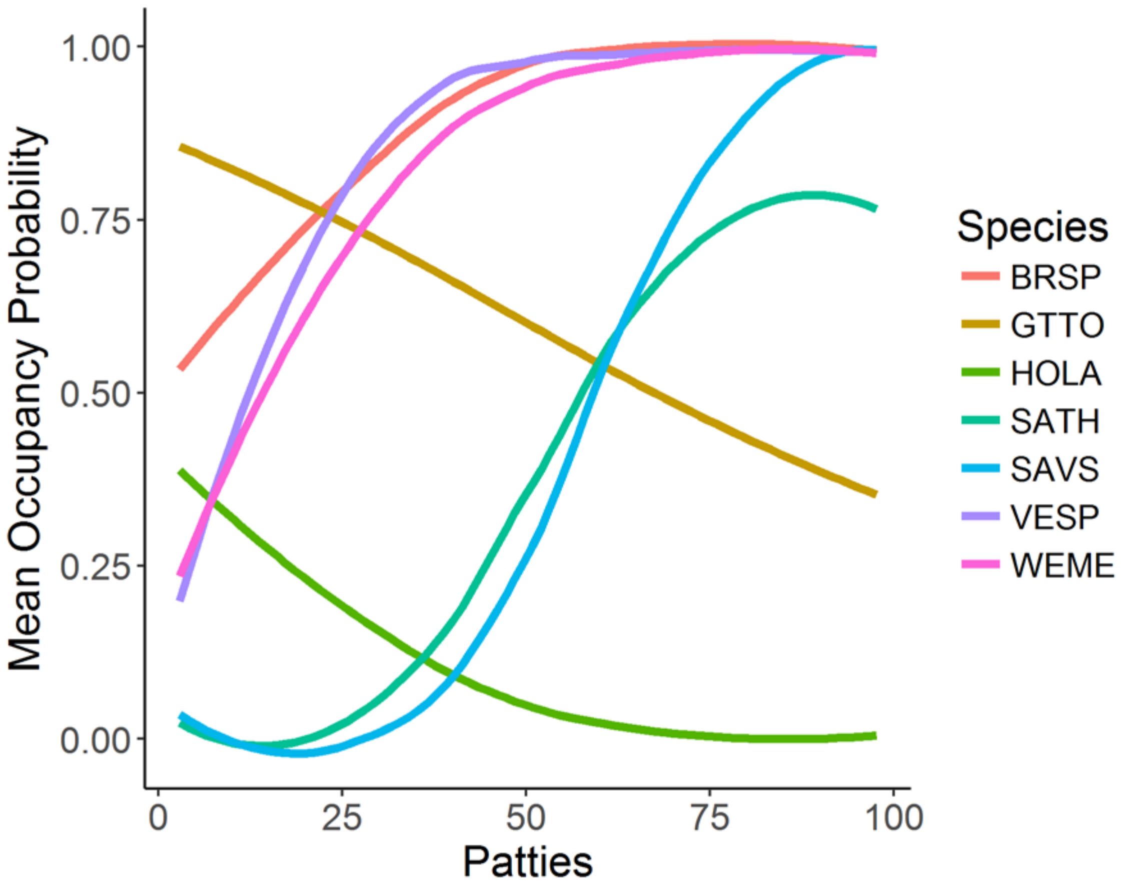
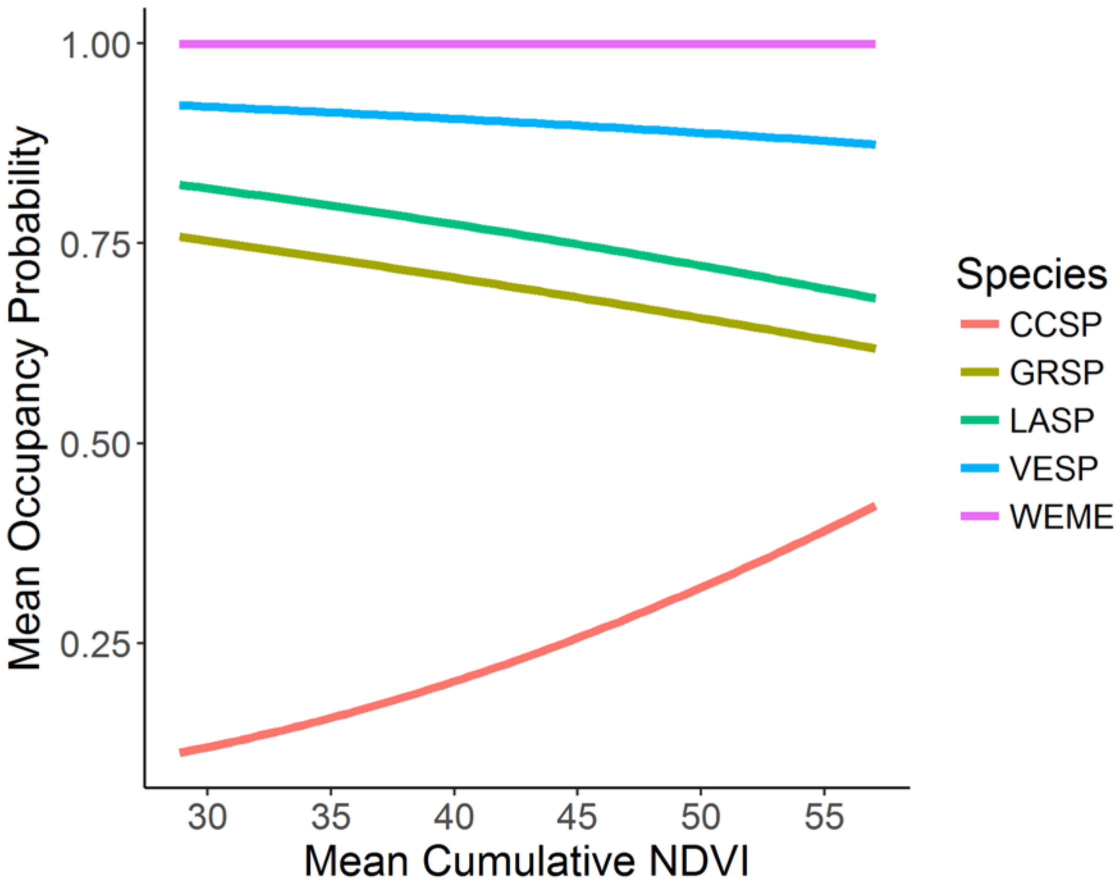


Figure 1-6: The relationship between mean species occupancy probability and patty counts in Yellowstone National Park. Species identity is indicated by the four letter code for the common name: Brewer's sparrow (BRSP), green-tailed towhee (GTTO), horned lark (HOLA), sage thrasher (SATH), savannah sparrow (SAVS), vesper sparrow (VESP), and western meadowlark (WEME)



<u>Figure 1-7:</u> The relationship between mean species occupancy probability and mean cumulative NDVI at the National Bison Range. Species identity is indicated by the four letter code for the common name: clay-colored sparrow (CCSP), grasshopper sparrow (GRSP), lark sparrow (LASP), vesper sparrow (VESP), and western meadowlark (WEME).

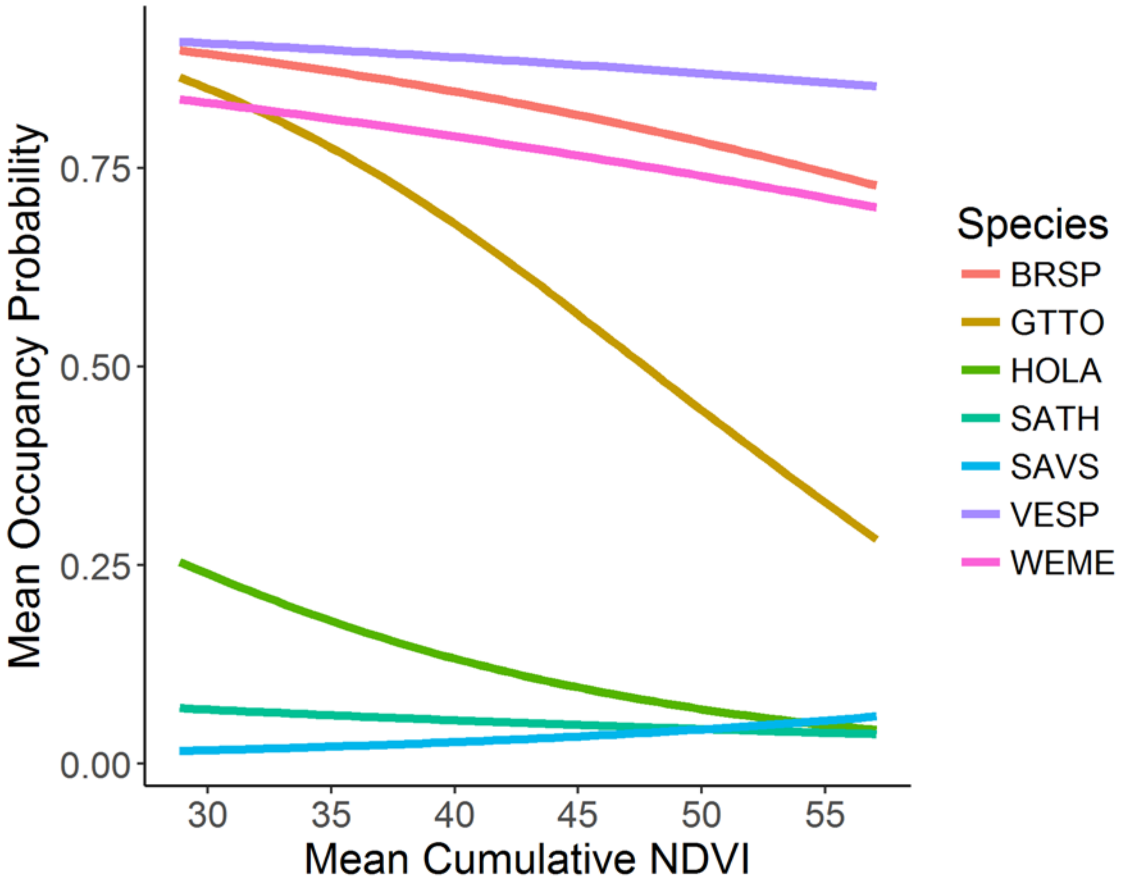


Figure 1-8: The relationship between mean species occupancy probability and mean cumulative NDVI at Yellowstone National Park. Species identity is indicated by the four letter code for the common name: Brewer's sparrow (BRSP), green-tailed towhee (GTTO), horned lark (HOLA), sage thrasher (SATH), savannah sparrow (SAVS), vesper sparrow (VESP), and western meadowlark (WEME).

Table 1-1: Coefficient values that affect the probability of species occupancy for grassland and shrubland songbird species present in the National Bison Range and Yellowstone National Park in 2016 and 2017. Values are presented on the logit-link scale as mean (95% credible interval; CRIs). Bolded values show estimates with 95% CRIs that do not cross zero.

Species	Intercept (α_0)	Patties: linear (α_1)	Patties: non-linear (α_2)	NDVI: linear (α_3)	NDVI*Patties: interaction (α_4)	Year: fixed effect (α_5)
National Bison Range						
Clay-colored sparrow	-1.47 (-2.93, 1.70)	0.21 (-0.90, 1.51)	-0.76 (-2.0, 0.11)	0.30 (-0.39, 1.08)	-0.67 (-2.21, 0.18)	0.37 (-0.91, 1.70)
Grasshopper sparrow	0.92 (-0.74, 3.64)	**2.11 (0.77, 4.83)**	-0.31 (-1.08, 0.69)	-0.11 (-0.86, 0.62)	-0.43 (-1.43, 0.33)	0.60 (-0.68, 2.15)
Lark Sparrow	1.27 (-8.09, 23.94)	-0.68 (-4.79, 3.08)	-0.12 (-1.46, 1.36)	-0.13 (-1.29, 1.01)	-0.14 (-1.46, 1.17)	0.04 (-2.64, 3.31)
Vesper sparrow	**2.29 (1.14, 4.03)**	**1.86 (0.88, 3.98)**	-0.29 (-0.82, 0.44)	-0.09 (-0.75, 0.70)	-0.57 (-1.36, 0.07)	-0.39 (-1.33, 0.80)
Western meadowlark	**7.39 (2.25, 28.68)**	**1.50 (0.21, 3.73)**	-0.07 (-1.02, 1.52)	-0.13 (-1.11, 0.78)	-0.31 (-1.56, 0.73)	0.07 (-2.47, 3.76)
Yellowstone National Park						
Brewer's Sparrow	**1.77 (0.67, 3.30)**	**1.59 (0.54, 2.91)**	0.38 (-0.35, 1.63)	-0.20 (-0.89, 0.45)	-0.30 (-1.28, 0.59)	**-1.73 (-3.39, -0.47)**
Green-tailed towhee	**0.91 (0.10, 1.90)**	-0.53 (-1.55, 0.32)	-0.03 (-0.41, 0.54)	-0.47 (-1.18, 0.14)	0.28 (-0.38, 1.05)	-0.60 (-1.57, 0.32)
Horned lark	-1.77 (-6.23, 7.08)	-1.09 (-4.76, 2.00)	-0.16 (-1.39, 1.16)	-0.35 (-1.70, 0.68)	0.10 (-0.43, 1.03)	-1.00 (-4.29, 1.58)
Sage thrasher	**-2.81 (-5.04, -0.73)**	**2.66 (0.68, 5.90)**	-0.43 (-1.69, 0.99)	-0.11 (-1.16, 0.90)	-0.34 (-1.21, 1.76)	-1.49 (-4.11, 0.35)
Savannah sparrow	**-3.64 (-6.54, -0.87)**	**2.58 (0.55, 6.16)**	-0.08 (-1.02, 1.24)	0.23 (-0.75, 1.52)	0.13 (-2.00, 0.77)	-0.95 (-3.19, 0.90)
Vesper sparrow	**2.12 (0.13, 6.29)**	**1.86 (0.88, 3.98)**	-0.29 (-0.82, 0.44)	-0.09 (-0.75, 0.70)	-0.57 (-1.36, 0.07)	-0.39 (-1.33, 0.80)
Western meadowlark	1.37 (-1.09, 7.41)	**1.50 (0.21, 3.73)**	-0.07 (-1.02, 1.52)	-0.13 (-1.11, 0.78)	-0.31 (-1.56, 0.73)	0.07 (-2.47, 3.76)

Table 1-2: Coefficient values that affect the probability of detection for grassland and shrubland songbird species present in the National Bison Range and Yellowstone National Park in 2016 and 2017. Values are presented on the logit-link scale as mean (95% credible intervals; CRIs). Bolded values show estimates with 95% CRIs that do not cross zero.

Species	**Intercept (β_0)**	**Date: linear (β_1)**	**Date: non-linear (β_2)**
National Bison Range			
Clay-colored sparrow	-0.69 (-2.10, 0.46)	-0.04 (-0.39, 0.25)	0.10 (-0.08, 0.34)
Grasshopper sparrow	-0.41 (-1.08, 0.35)	0.07 (-0.10, 0.26)	-0.02 (-0.09, 0.05)
Lark sparrow	-2.85 (-6.17, 1.22)	-0.03 (-0.54, 0.45)	-0.13 (-0.48, 0.14)
Vesper sparrow	**0.49 (0.06, 0.95)**	0.05 (-0.05, 0.15)	0.00 (-0.04, 0.04)
Western meadowlark	**1.70 (1.26, 2.18)**	-0.10 (-0.22, 0.01)	-0.02 (-0.07, 0.04)
Yellowstone National Park			
Brewer's sparrow	**1.36 (0.82, 1.94)**	**0.19 (0.03, 0.37)**	-0.04 (-0.11, 0.02)
Green-tailed towhee	**0.75 (0.12, 1.39)**	-0.01 (-0.18, 0.15)	-0.01 (-0.08, 0.07)
Horned lark	-3.03 (-7.26, 0.66)	0.26 (-0.20, 0.86)	0.10 (-0.13, 0.41)
Sage thrasher	-1.33 (-3.21, 0.63)	-0.17 (-0.60, 0.19)	0.11 (-0.06, 0.34)
Savannah sparrow	-1.35 (-3.18, 0.47)	-0.21 (-0.73, 0.19)	0.15 (-0.14, 0.63)
Vesper sparrow	0.14 (-0.44, 0.79)	0.05 (-0.05, 0.15)	0.00 (-0.04, 0.04)
Western meadowlark	-1.09 (-1.94, 0.84)	-0.10 (-0.22, 0.01)	-0.02 (-0.07, 0.04)

Table 1-3: Coefficient values that affect the probability of community occupancy for grassland and shrubland songbirds in the National Bison Range and Yellowstone National Park in 2016 and 2017. Values are presented on the logit-link scale as mean (95% credible intervals; CRIs). All 95% CRIs for the parameters crossed zero.

Parameter	**Mean (95% CRI)**
NBR Community Intercept ($\mu\alpha_0$)	-1.97 (-4.91, 3.48)
YNP Community Intercept ($\mu\alpha_0$)	-1.91 (-4.80, 1.67)
Patties: linear ($\mu\alpha_1$)	0.97 (-0.49, 2.58)
Patties: non-linear ($\mu\alpha_2$)	-0.21 (-0.82, 0.53)
NDVI: linear ($\mu\alpha_3$)	-0.11 (-0.67, 0.45)
NDVI*Patties: interaction ($\mu\alpha_4$)	-0.22 (-0.94, 0.39)
Year: fixed effect ($\mu\alpha_5$)	-0.54 (-1.79, 0.63)

Table 1-4: Coefficient values that affect the probability of community detection for grassland and shrubland songbirds in the National Bison Range and Yellowstone National Park in 2016 and 2017. Values are presented on the logit-link scale as mean (95% credible intervals; CRIs). All 95% CRIs for the parameters crossed zero.

Parameter	**Mean (95% CRI)**
NBR community intercept ($\mu\boldsymbol{\beta_0}$)	-1.54 (-4.81, 1.32)
YNP community intercept ($\mu\boldsymbol{\beta_0}$)	-1.21 (-4.63, 0.61)
Date: linear ($\mu\boldsymbol{\beta_1}$)	0.00 (-0.22, 0.22)
Date: non-linear ($\mu\boldsymbol{\beta_2}$)	0.01 (-0.14, 0.18)

Chapter 2: Variation in Avian Abundance Response to Bison Grazing Intensity

Introduction

Plains bison (*Bison bison*) have been an important component of North American ecosystems for millennia. Estimates of their historic population range from 30-60 million (Flores 1991; Knopf & Samson 1997). Currently, in the United States, Canada, and Mexico, there are approximately 21,000 bison in 62 conservation herds (Gates et al. 2010). The number of bison herds continues to increase as interest grows in reintroducing bison to their former native range. From 2009-2017, at least eight reintroductions have occurred in North America (Appendix 1, Table A1-2). These reintroductions were undertaken by the U.S. Department of the Interior, Native American Tribes, non-governmental organizations, and international efforts in Canada and Mexico. Reintroduction is expected to continue, given the strong institutional support for increasing bison numbers. The U.S. Department of the Interior's Bison Conservation Initiative seeks to "restore [bison herds] to their ecological and cultural role on appropriate landscapes" (U.S. Department of the Interior 2008), and ten nations and tribes signed the Northern Tribes Buffalo Treaty with the goal of restoring bison on tribal lands (American Bison Society 2017).

As bison become more common and have increasing impacts on the landscape, their ecological effects are important to integrate into conservation planning. Bison are ecosystem engineers—a species that modifies habitat to be more or less favorable for other species (Gates et al. 2010). Bison both generate, and react to, spatial and temporal heterogeneity of various resources that are important to other species of the ecological community. For example, through their grazing, they can affect plant species composition (Coppock et al. 1983a, 1983b; Anderson 2006), and their movements promote seed dispersal (Rosas et al. 2008). When bison take dust baths, they create wallows, which then retain precipitation and augment water availability (Butler

2006). Such changes to the distribution of resources in turn influence the ecology of species that rely on them. Developing a predictive understanding of how bison affect other species of the ecological community will help inform conservation goals, including the role of bison as conduits of habitat modification.

Historically, bison helped create habitat conditions that supported a wide variety of grassland bird species (Askins et al. 2007; Knopf 1996). Research in grassland systems of North America has shown that bison grazing can induce differences in vegetation structure (Tastad 2013; Sliwinski 2011; Towne et al. 2005). As an ecosystem process, grazing by large ungulates can alter the vegetation structure in songbird habitat by reducing vegetation height (Tastad 2013), increasing bare ground (Augustine et al. 2012; Lwiwski et al. 2015), and affecting the spatial heterogeneity of vegetation (Adler et al. 2001). Changes to vegetation structure are the primary known mechanism for songbird responses to grazing (Knopf 1996; Derner et al. 2009). Under different intensities of grazing, these effects create distinct habitat conditions to which bird species respond. Grassland obligate songbirds, which rely entirely on grassland habitat (Vickery et al. 1999), show responses to these differences in vegetation structure (Fisher & Davis 2010).

One way to evaluate the grassland songbird species' responses to the effects of bison grazing is to measure adult songbird density. Higher animal density is often indicative of higher quality habitat (Fretwell & Lucas 1969; Rosenzweig 1981), informing researchers about the resource requirements of a given species. Past research on the relationship between bison grazing and grassland songbird density is limited, making it difficult to predict species' responses (Griebel et al. 1998; Leuders et al. 2006; Powell 2006; Sliwinski 2011; Williams & Boyle 2018). However, a body of literature exists on the relationship between cattle grazing and grassland songbird density, showing notably variable songbird responses (Saab et al. 1995). For example, western meadowlarks (*Sturnella neglecta*) generally prefer light to moderate grazing and avoid heavy grazing (Giezentanner 1970; Kantrud & Kologiski 1982, Bock et al. 1993; Dechant et al. 2002), yet there are exceptions. Several studies have found that western meadowlarks have no response to various intensities of grazing (Renken 1983; Messmer 1990; Dale & McKeating 1996; Prescott & Wagner 1996). Other studies have found no difference in western meadowlark abundance between grazed and ungrazed habitat (Dale 1984; Saab et al. 1995,) and alternatively, that they are three times more abundant in ungrazed versus grazed habitat (Maher 1973, 1974). Site-specific responses of western meadowlarks and other grassland songbird species to grazing appear to vary considerably, resulting in few meaningful generalizations for management (Lipsey & Naugle 2017).

One explanation for the lack of a robust response pattern is that grassland songbirds show plasticity in their habitat selection behavior. Habitat selection, the process by which an organism chooses habitat components to use (Johnson 1980), is a hierarchical, scale-dependent, behavioral decision by the organism (Jaenike & Holt 1991). Many factors influence habitat selection for an organism in a particular ecological context, such as landscape structure, population size, and historical processes (Fuller 2012). This may result in different patterns of species density, based on known habitat relationships in other contexts. Thus, the resources and conditions that make up habitat for a given species should not be considered fixed across a species' range (Fuller 2012).

The inconsistency in grassland songbird response to grazing suggests their responses may be sensitive to other factors. The conditions under which bison are managed across North America vary widely in scale, vegetation type, and herd size. Such differences could be important for predicting species' responses and managing grassland songbird populations successfully. Therefore, to understand the effects of bison grazing on grassland songbirds, it must be determined whether grassland songbird responses to bison grazing vary by ecological context.

I examined the density of vesper sparrows (*Pooecetes gramineus*) and western meadowlarks in relation to bison grazing in two ecological contexts. These contexts are defined by differences in bison herd size, bison density, spatial scale of bison grazing, and vegetation type. I hypothesized that the ecological context would influence how both species responded to bison grazing. I predicted that western meadowlarks would show a larger difference in their response to grazing, based on their more limited preference for grazing intensity (Bock et al. 1993). This indicates they would be more sensitive to habitat differences produced by each ecological context. I predicted vesper sparrows would show a smaller difference in their response to grazing between the ecological contexts, because they are considered a grassland generalist (Jones & Cornelly 2002; Lusk & Koper 2013), and are less responsive to changes in grazing intensity (Bock et al. 1993).

Study Areas

To examine the importance of the ecological context of bison grazing, I conducted my research in two study sites. The first is the National Bison Range (NBR), in the Mission Valley near Moiese, MT. The NBR is federally managed by the U.S. Fish and Wildlife Service and was established in 1908 for the conservation of bison. Currently, there are approximately 350 bison in the NBR. In the past, bison management consisted of rotating bison among eight pastures during summer months and leaving one pasture ungrazed for an entire year (A. Lisk, personal communication). Since 2015, bison movement has been unrestricted except to be contained within the boundary of the NBR (A. Lisk, personal communication). The NBR is approximately 76 km^2, and the vegetation is 75% intermountain grassland similar to Palouse prairie. The remaining area consists of conifer forest and riparian habitat. The grasslands are characterized by bunchgrasses such as Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Agropyron spicatum*), and prairie junegrass (*Koeleria macrantha*). Intermixed in the grasslands are forbs such as arrowleaf balsamroot (*Balsamorrhiza sagittata*), and low shrubs such as Wood's rose (*Rosa woodsia*) and snowberry (*Symphoricarpus occidentalis*).

My second study site is the Northern Range of Yellowstone National Park (YNP). YNP is federally managed by the National Park Service. There are approximately 5,000 bison in YNP, 3,500 of which use the Northern Range (Geremia et al. 2014). The Northern Range of YNP constitutes a large part of the herd's summer range and encompasses about 890 km^2. Bison movements are minimally managed, but boundaries are enforced to contain bison within YNP. I conducted surveys in the Lamar Valley. The area is composed of shrub steppe, dominated by mountain big sagebrush (*Artemisia tridentata*), and grass species such as Idaho fescue, bluebunch wheatgrass, and prairie junegrass.

Methods

Field Methods:

To measure avian density in each ecological context, I established sampling plots in areas I predicted would represent the spectrum of low to high bison grazing intensity. I measured vesper sparrow and western meadowlark density and bison grazing intensity at each plot and related these variables using a multi-species abundance model.

<u>Plot Size:</u>

I defined sampling plots at 250 x 250 m (62,500 m^2) for three reasons. First, by walking a transect through the middle of the plot, we were able to survey for birds up to 125 meters to either side. Beyond 125 meters, human detection of birds declines dramatically, so this helps ensure that birds detected are within the plot (Ralph et al. 1995). Secondly, this area is approximately twice the size of the breeding territory of western meadowlarks, the study species with the largest territory size (Lanyon 1956, Aweida 1995). Lastly, the study sites have varying topography with steep slopes and drainages. To maximize visibility, I chose a plot size that reduced the probability of visual obstructions within the plot.

<u>Sampling Frame:</u>

I stratified my plot selection across three levels of bison grazing intensity. I developed these bison grazing strata using a habitat suitability index (HSI) (Steenweg et al. 2016, Wiggins 2016), using slope (U.S. Geological Survey 2013), distance to water (U.S. Geological Survey 2013), and vegetation type (Landfire 2012). HSI models use a species' known affinities for habitat characteristics to predict suitability of a habitat for a given species. I binned the continuous HSI values from both study sites into three strata of bison grazing intensity, using the Natural Jenks tool in ArcGIS: Low (0.169-0.459), Medium (0.460-0.611), and High (0.612-0.795). HSI values range from 0 to 1, with 0 representing the least suitable habitat, and 1 representing the most suitable habitat for bison.

I randomly selected plots in each stratum, and sampled plots by the following criteria: 1.) the plot contained ≥ 75% grassland or shrub steppe vegetation, and 2.) the plot contained a continuous segment of habitat ≥ 75% of the plot (Wiggins 2016). At the NBR site, I sampled 10 plots in the Low stratum, 30 plots in the Medium stratum, and 30 plots in the High stratum each year. Compared to Medium and High stratum (43% and 32% of NBR, respectively), there was less Low stratum available in NBR (approximately 11% of NBR), because much of this area was also forested. This resulted in sampling fewer Low stratum plots in this study site. To compensate, I sampled a larger number of Low stratum plots at the YNP site. In YNP, I sampled 30 plots in the Low stratum, 13 plots in the Medium stratum, and 12 in the High stratum in 2016. In 2017, I sampled 25 plots in the Low stratum, 8 in the Medium stratum, and 11 in the High stratum (Appendix 1, Table A1-1). I selected plots in YNP from an area similar in size to the NBR (YNP = 69 km^2, NBR = 76 km^2).

Avian Density Surveys:

To measure grassland songbird density, I used a dependent double observer method as described by Nichols et al. (2000) and Tipton et al. (2008), and recently implemented by Golding and Dreitz (2017). Because it requires two observers, this method produces a detection rate for each species by each observer, and allows me to create corrected density estimates based on imperfect detection.

To execute the dependent double observer method, two observers walk transects through the middle of a plot. The primary observer walk first and communicates all adult birds they see within the plot to the secondary observer. The secondary observer walks 3-5 meters behind the primary observer on the transect, records the birds the primary observer detects, and records any additional birds the primary observer fails to detect. Visual confirmation of the bird within plot boundaries is required, thus detections in which the bird was heard but not seen were not recorded. Observers use rangefinders and binoculars to confirm each bird was within plot boundaries. Observers walk slowly, and stop occasionally along the transect to look and listen for birds. They switch roles between consecutive surveys.

All surveys were conducted in the early morning hours, from dawn until 1000 MDT in order to target the hours when birds are most active and easily detectable. Surveys were not conducted in rain or winds higher than 24 km/hr due to reduced detectability of birds. In NBR, bird surveys were conducted from May 20 to July 7 in 2016 and from May 19 to June 30 in 2017. In YNP, bird surveys were conducted from June 1 to July 1 in 2016 and from May 31 to July 9 in 2017. All plots were sampled twice within a field season.

Bison Grazing Intensity:

I measured bison grazing intensity by counting bison patties in each plot. Density of patties estimates bison grazing intensity at the patch-level spatial scale and has been shown to reflect vegetation responses to grazing intensity (Tastad 2013). Following Sliwinski (2011), patties were either individual, well-formed piles, or several closely associated piles. Observers counted all patties, regardless of age, representing bison use over recent years. Observers walked four bison grazing transects within each plot. Two transects were sampled each time immediately following a bird survey in each plot. These transects were located to both sides of the bird transect and were midway between the bird transect and the edge of the plot (see Appendix 1, Figure A1-1). Observers walked two transects in an East-West direction, and two transects in a North-South direction. Observers walked slowly, counting all patties within 1 meter to the left and right of the line transect.

Analytical Methods:

Correlation Between Covariates:

I investigated relationships between patty counts and HSI value using pairwise plot matrices, summary statistics and linear regressions. I used these methods to explore the relationship between predicted bison grazing and measured bison grazing and to inform my conclusions.

Abundance Model:

To examine bird response to bison grazing intensity, I used an extension of the multispecies dependent double-observer abundance model (MDAM) developed by Golding et al. (2017). This model uses a Bayesian framework and incorporates the survey process of the dependent double observer method into the likelihood statement, accounting for imperfect detection and creating detection-adjusted density estimates.

The MDAM models the biological and observation processes in a hierarchical way to produce coefficient and density estimates. The biological process uses a model in which mean species abundance of each species i, plot j, and year k ($\Lambda_{i,j,k}$) is estimated from the linear model. Abundance (N) of each species i at plot j in year k is then derived from a Poisson distribution with mean species abundance as the shape parameter such that:

$$N_{i,j,k} \sim \text{Poisson}\ (\Lambda_{i,j,k})$$

The observation process informs the biological process by modeling observed abundance (y) for species i at plot j in year k and survey l from a multinomial random variable. This variable is a function of $N_{i,j,k}$ and the cell probabilities of the three observation outcomes ($\pi_{i,j,k}$) of the dependent double observer method (see Golding et al. 2017 for details on cell probabilities). These observation outcomes are: 1) the primary observer detects an individual, 2) the secondary observer detects an individual that the primary observer fails to detect, and 3) both the primary and secondary observers fail to detect and individual.

$$y_{i,j,k,l} \sim \mathit{Multinomial}\ (N_{i,j,l}, \pi_{i,j,k,l})$$

Thus, the likelihood for the observation of a single species is represented by the probability that at least one observer detects an individual ($pcap$), the probability of detection by the primary observer (p_1) and the probability of detection by the secondary observer (p_2) given the counts of birds by the primary observer during observation i (y_{1i}), the total number of individuals detected by either the primary or secondary observer during observation i (C_i), and the total number of individuals available for detection (N). The likelihood function is as follows:

$$L(pcap, p_1, p_2 | y_{1i}, C_i, N) = \prod_{i=1}^{obs} \left[\binom{N}{C_i} (pcap)^{C_i} (1 - pcap)^{N-C_i} \binom{C_i}{y_{1i}} (p_1)^{y_i} \big((1 - p_1)p_2\big)^{C_i - y_{1i}} \right]$$

My data met the three assumptions of the MDAM: 1) the population is closed to emigration, immigration, births, and deaths during the sampling period; 2) the detectability of both species and individuals does not change between repeating sampling; and 3) the chosen distribution suitably describes the biological and observation data. The first assumption was met by surveying plots during the breeding season. Birds have higher site fidelity during the breeding season as they establish a territory, build a nest, and raise young. This reduces the likelihood that individuals immigrated or emigrated from the population. Only adult birds were included in the data, as young of the year can readily be distinguished from adults by appearance and behavior. Lastly, the data was partitioned by breeding season year, such that deaths between years did not violate the first assumption. The second assumption was met by restricting the sampling period. Surveys were conducted in the early morning hours, during the breeding season, and in favorable weather conditions to assure detection of species and individuals did not vary. The third assumption was met by incorporating covariates into the biological and observation models. The Poisson distribution assumes animals are distributed randomly on the landscape (Royle 2004), and the multinomial distribution is based on the cell probabilities of the dependent double observer method (Golding et al. 2017). The added covariates account for deviation of the data from these distributions.

I developed a model to represent my study design and hypothesis as follows:

$$\begin{aligned}\log(\Lambda_{i,j,k}) = {} & \beta_{0i} + \beta_{1i} * patties_{j,k} + \beta_{2i} * {patties^2}_{j,k} + \beta_{3i} * year + \beta_{4i} * location \\ & + \beta_{5i} * year * location + \beta_{6i} * location * patties_{j,k} + \beta_{7i} * location \\ & * {patties^2}_{j,k}\end{aligned}$$

I allowed detection (p) to vary by observer and species. I used uninformative priors for parameters β_0 –β_7, using a normal distribution of N(0, 1000). I ran the model with 3 chains, for 35,000 iterations each, and a burn-in period of 15,000 iterations. Model convergence was assessed using the Gelman-Rubin statistic (Gelman & Rubin 1992) and visual inspection of trace plots, autocorrelation, estimate density, and the running mean. I assessed goodness of fit using a Bayesian p-value by comparing the estimated deviance values and predicted deviance values for each MCMC sample of each observation, following Broms et al. (2016).

Results

At NBR, field teams completed two surveys of 70 plots in 2016 and 2017. In 2016, field teams made 104 observations of vesper sparrows, and 226 observations of western meadowlarks. In 2017, field teams made 149 observations of vesper sparrows, and 321 observations of western meadowlarks. In 2016, mean patty count per plot ranged from 2 – 85.5 patties (median = 23.5, IQR = 26.9), and in 2017 from 1.8-66.8 patties (median = 20.25, IQR = 21.6). See Appendix 1, Table A1-1 for more details. Linear regression showed a weak but significant relationship between mean patties (averaged between 2016 and 2017) and mean HSI value ($R^2 = 0.07$, $p = 0.02$).

At YNP, field teams completed 106 surveys of 53 plots in 2016, and 88 surveys of 42 plots in 2017. In 2016, they recorded 221 observations of vesper sparrows and 38 observations of western meadowlarks. In 2017, they recorded 58 observations of vesper sparrows, and 17 observations of western meadowlarks. In 2016, mean patty count ranged from 4.0 – 84.0 patties (median = 36.0, IQR = 24.3), and in 2017 from 12.8 – 110.8 patties (median = 41.3, IQR = 31). See Appendix 1, Table A1-1 for more details. Linear regression showed a moderately strong relationship between mean patties (averaged between 2016 and 2017) and mean HSI value ($R^2 = 0.39$, $p < 0.001$).

The MDAM model converged, with R-hat values less than 1.1 for all parameters. The p-value for the goodness-of-fit test of the MDAM model was $p = 0.34$. P-values less than 0.05 or greater than 0.95 do not fit the data well (Broms et al. 2016), thus the model has an adequate fit to the data. Posterior distributions for parameters from the model indicated that bird densities have a positive association with bison patties for both species (Table 2-1). All posterior distributions for coefficients are presented on the log-link scale. For vesper sparrows, the mean effect of bison patties on density (β_1) is 0.37 (95% CRI = 0.20, 0.54) and for western meadowlarks is 0.13 (95% CRI = 0.00, 0.25). Both species showed a negative quadratic response to bison patties, although the 95% credible interval for vesper sparrows crossed zero (β_2 mean = -0.14, 95% CRI = -0.30, 0.02) and did not for western meadowlarks (β_2 mean = -0.12, 95% CRI = -0.24, 0.00). The effect for the interaction between location and bison patties was weakly negative for vesper sparrows (β_6 mean = -0.10, 95% CRI = -0.41, 0.2) and positive for western meadowlarks (β_6 mean = 0.54, 95% CRI = -0.05, 1.18). Although the credible interval for this effect crossed zero for both species, there was a 0.96 probability that the effect was positive for western meadowlarks. The effect for the interaction between location and the quadratic effect of patties was weakly positive for vesper sparrows (β_7 mean = 0.13, 95% CRI = -0.06, 0.32) and weakly negative for western meadowlarks (β_7 mean = -0.17, 95% CRI = -0.51, 0.13).

For the fixed effects in the model, there was a strong effect of location for western meadowlarks (β_4 mean = -1.81, 95% CRI = -2.27, -1.38), no or minimal effect of year (β_3 mean = -0.02, 95% CRI = -0.25, 0.29), and the interaction between year and location was weakly negative (β_5 mean = -0.32, 95% CRI = -1.04, 0.38). For vesper sparrows, there were no strong fixed effects. See Table 2-1 for a full list of coefficient values.

I modeled detection to vary by species and observer. Of 15 observers, detection for vesper sparrows ranged from 0.14 (95% CRI = 0.07, 0.24) to 0.80 (95% CRI = 0.45, 0.99). For western meadowlarks, observer detection ranged from 0.20 (95% CRI = 0.07, 0.40) to 0.82 (95% CRI = 0.58, 0.97). On average, detection for meadowlarks was slightly higher than for vesper sparrows, with a mean detection of 0.45 (95% CRI= 0.08, 0.88), compared to a mean detection of 0.38 (95% CRI= 0.08, 0.87) for vesper sparrows.

Predicted mean plot density for vesper sparrows is higher in YNP, ranging from 1.21 – 5.05 birds per plot, compared to 1.03 – 3.03 birds per plot in NBR. The optimal grazing intensity for vesper sparrows, which is the intensity where they are predicted to reach a maximum density, is 60.2 patties per plot in NBR where they reach a density of 3.02 birds per plot (95% CRI = 2.06, 4.15) (Figure 2-2). The optimal grazing intensity for vesper sparrows in YNP is 110 patties per plot, where they reach a density of 5.03 birds per plot (95% CRI = 1.76, 10.70). In NBR, mean vesper sparrow density is 1.41 times higher at 60.2 patties per plot (their optimal grazing intensity in NBR) than at 110 patties per plot (their optimal grazing intensity in YNP). In YNP, mean vesper sparrow density is 1.99 times higher at 110 patties per plot than at 60.2 patties per plot. Predicted mean plot density for western meadowlarks is higher in NBR, ranging from 1.65

– 4.27 birds per plot, compared to 0.15 – 0.86 birds per plot in YNP. The optimal grazing intensity for western meadowlarks is 42.7 patties per plot in NBR and 54.6 patties per plot in YNP. In NBR, western meadowlark density is 1.04 times higher at 42.7 patties per plot than at 54.6 patties per plot. In YNP, western meadowlark density is 1.1 times higher at 54.6 patties per plot than at 42.7 patties per plot (Figure 2-2).

Discussion

Vesper sparrow density showed a positive association with bison grazing intensity, which is consistent with results from Sliwinski (2011). The shape of vesper sparrow response to bison grazing was different between NBR and YNP (Figure 2-1), and vesper sparrows showed more variability in predicted density based on location-specific responses than western meadowlarks (Figure 2-2). However, their positive association with bison grazing intensity (β_1), was the only important covariate for understanding vesper sparrow density (Table 2-1). Vesper sparrows are described as grassland generalists (Jones & Cornely 2002; Lusk & Koper 2013) because they are able to utilize a wide range of grassland habitat. This flexibility may explain why neither the effect of study location, nor the interaction between study location and patties influenced vesper sparrow density.

Western meadowlark density showed a positive association with bison grazing intensity, and a negative quadratic response to bison grazing intensity, such that the effect of bison grazing intensity becomes less positive at higher levels of grazing (Figure 2-1). This is consistent with the general trend that western meadowlarks prefer light to moderate grazing (Giezentanner 1970; Kantrud & Kologiski 1982, Bock et al. 1993). I observed far fewer western meadowlarks in YNP than NBR, and this was reflected in the strong negative effect of location. NBR may be inherently more suitable habitat than YNP due to the higher grass component, resulting in higher densities at that location. In NBR, the grass component is 54.5% and the shrub component is 29.1% of the study area (Landfire 2012). In YNP, the grass component is 24.8% and the shrub component is 48.7% of the study area (Landfire 2012). Both McAdoo et al. (1989) and Knick and Rotenberry (1995) found western meadowlarks to be associated with a low density of shrubs. The high proportion of sagebrush cover in YNP may reduce the availability of suitable conditions for western meadowlarks.

In addition to differences between locations, there is some weak evidence that western meadowlarks respond more positively to the same level of bison grazing intensity in YNP than they do in NBR. This provides partial support for my prediction that vesper sparrows and western meadowlarks would both show location-specific responses, and that the magnitude of the effect would be larger for western meadowlarks. The credible interval for the interaction between location and patties (β_6) crossed zero, and the difference in predicted densities based on site-specific optimal grazing intensities was small (Table 2-1 and Figure 2-2). However, there is a 0.96 probability that the effect was positive, suggesting the effect may be worth considering in management and conservation applications. The differences inherent to each location, such as vegetation type, bison herd size and density, and the scale over which bison grazing occurs may influence the habitat selection process for western meadowlarks. Other factors such as soil productivity and precipitation may also contribute, as they can determine the magnitude of grassland songbird response to grazing (Lipsey & Naugle 2017). Though I cannot discern which differences may be important from this study, it nonetheless demonstrates that species' responses to bison grazing may differ based on the ecological context.

Understanding site-specific responses may be especially important for grassland songbirds with more specific habitat requirements and less so for generalists. This could pose a challenge when managing a species with more specialized needs for vegetation structure or with more vulnerable populations than the western meadowlark. This challenge could be mitigated by encouraging a broad range of grazing intensities to create a broad range of vegetation structure. Doing so will provide the vegetation structure birds need, regardless of location-specific fluctuations in response. This will reduce the need to understand species' site-specific associations with bison grazing intensity.

An important limitation to this study is the possibility that the patty counts at each study site are not equivalent measures of bison grazing intensity. While many studies have successfully used dung counts as a measure of herbivore use (Barnes 2001; Hendricks et al. 2005; Manthey & Peper 2010), Brodie (2006) notes that fecal decay rates can vary spatially and temporally, decoupling the relationship between dung counts and herbivore use. If this is true between NBR and YNP, comparable bison patty counts in each location could actually mean different intensities of bison grazing. This would mean that differences in avian species' responses to bison grazing by location are actually responses to different intensities of bison grazing. Researchers who want to use this method to compare grazing intensity across study sites should consider measuring a patty persistence rate to correct for variation in decay rates (Brodie 2006, Marquez et al. 2001).

My study focused on a single parameter (density) that contributes to avian populations. However, other demographic parameters may be important for understanding the effect of bison grazing on avian populations. Demographic rates such as nest success and reproductive output are important indicators of habitat quality, and higher density does not always correlate with higher reproductive rates (Van Horne 1983; Vickery et al. 1992). Van Horne (1983) suggests this is more likely to be true for species that are habitat generalists because they often have high reproductive capacities, yet also use many habitat types. Therefore, further research that assesses the effects of bison grazing in different ecological contexts on grassland songbirds should also include reproductive rates and grassland specialist species to attain a more comprehensive understanding of the relationship.

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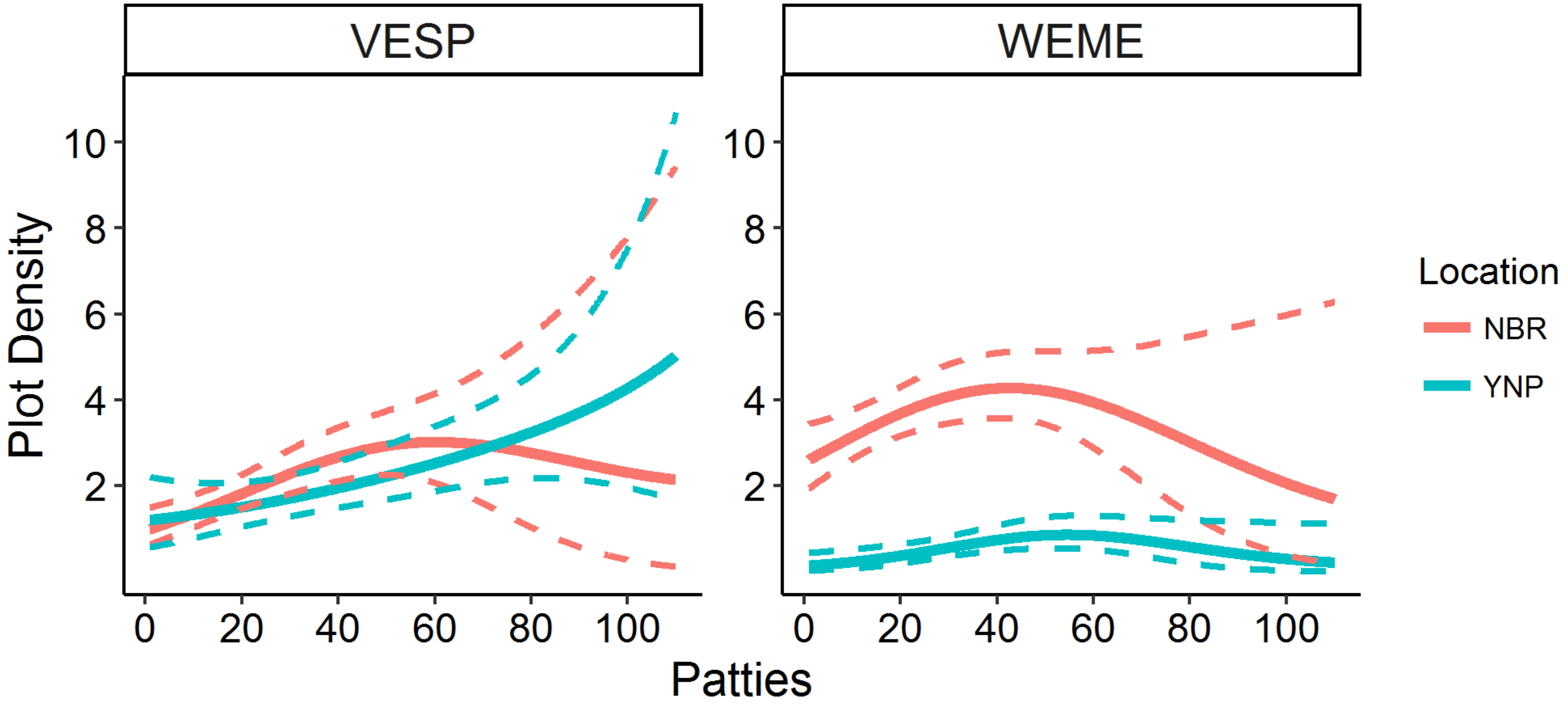
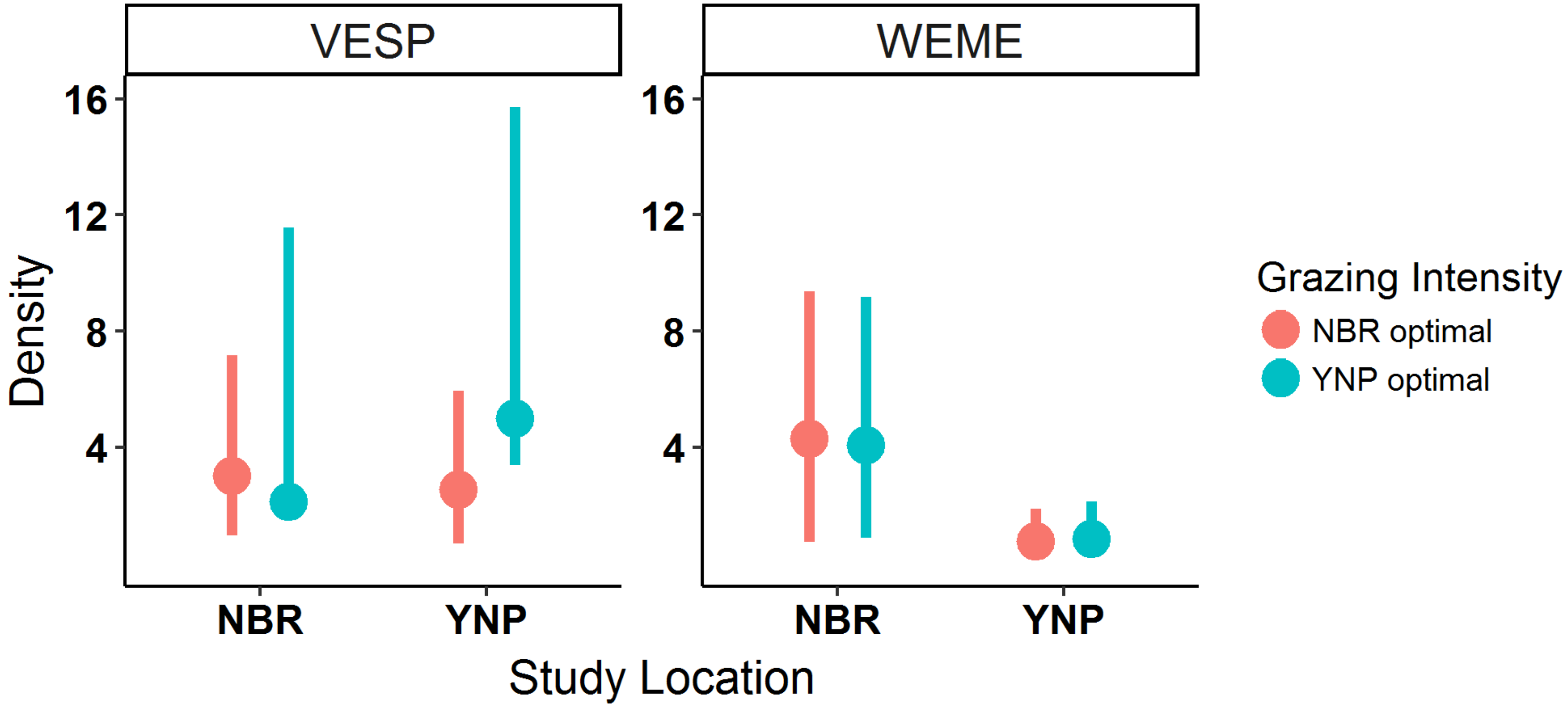
Figures and Tables



<u>Figure 2-1:</u> Predicted mean plot density for vesper sparrows (VESP) and western meadowlarks (WEME) across the spectrum of bison grazing intensity measured by patty counts in the National Bison Range (NBR) and Yellowstone National Park (YNP) in 2016 and 2017. Solid lines represent the mean response, and dashed lines represent 95% credible intervals.



<u>Figure 2-2:</u> Predicted vesper sparrow (VESP) density and western meadowlark (WEME) density by optimal grazing rate. Optimal grazing rate is the grazing rate that maximized bird density in the National Bison Range (NBR) and Yellowstone National Park (YNP) in 2016 and 2017. The figure demonstrates the predicted bird density at each study site, showing the effect of site-specific responses to grazing. Circles represent the mean prediction, and lines represent 95% credible intervals.

Table 2-1: Coefficient values that affect density of vesper sparrows and western meadowlarks. The location parameter and interactions with location indicate the effect of differences between the National Bison Range and Yellowstone National Park in 2016 and 2017. Values are presented on the log-link scale as mean (95% credible interval; CRI). Bold values show estimates with 95% CRI that do not cross zero.

Parameter	**Vesper sparrow**	**Western meadowlark**
Intercept ($\boldsymbol{\beta_0}$)	**0.77, (0.45, 1.11)**	**1.42, (1.17, 1.69)**
Patties: linear ($\boldsymbol{\beta_1}$)	**0.37, (0.20, 0.54)**	**0.13, (0.00, 0.25)**
Patties: non-linear ($\boldsymbol{\beta_2}$)	-0.14, (-0.30, 0.02)	**-0.12, (-0.24, 0.00)**
Year:($\boldsymbol{\beta_3}$)	0.15, (-0.24, 0.51)	-0.02, (-0.25, 0.29)
Location: ($\boldsymbol{\beta_4}$)	-0.13, (-0.49, 0.30)	**-1.81, (-2.31, -1.38)**
Year*location: ($\boldsymbol{\beta_5}$)	-0.34, (-0.89, 0.27)	-0.32, (-1.12, 0.34)
Location*patties: linear ($\boldsymbol{\beta_6}$)	-0.10, (-0.41, 0.22)	0.54, (-0.05, 1.18)
Location*patties: non-linear ($\boldsymbol{\beta_7}$)	0.13, (-0.06, 0.32)	-0.17 (-0.51, 0.13)

Table 2-2: Detection probabilities for vesper sparrow and western meadowlarks at the National Bison Range and Yellowstone National Park in 2016 and 2017, listed by observer. Values are presented as mean (95% credible interval; CRI). No 95% CRIs crossed zero, because detection probabilities range from zero to one.

Observer ID	Vesper sparrow	Western meadowlark
1	0.34 (0.23, 0.47)	0.31 (0.22, 0.42)
2	0.45 (0.32, 0.58)	0.63 (0.54, 0.71)
3	0.20 (0.11, 0.32)	0.40 (0.28, 0.54)
4	0.28 (0.12, 0.51)	0.51 (0.37, 0.64)
5	0.25 (0.16, 0.35)	0.24 (0.16, 0.33)
6	0.52 (0.28, 0.77)	0.59 (0.33, 0.82)
7	0.21 (0.04, 0.49)	0.82 (0.58, 0.97)
8	0.40 (0.26, 0.56)	0.55 (0.33, 0.77)
9	0.52 (0.38, 0.65)	0.62 (0.52, 0.71)
10	0.29 (0.17, 0.44)	0.51 (0.34, 0.69)
11	0.14 (0.07, 0.24)	0.20 (0.07, 0.40)
12	0.79 (0.45, 0.99)	0.36 (0.01, 0.93)
13	0.48 (0.22, 0.77)	0.36 (0.05, 0.78)
14	0.17 (0.02, 0.45)	0.29 (0.04, 0.69)
15	0.59 (0.36, 0.82)	0.40 (0.12, 0.74)

Appendix 1: Supporting Information

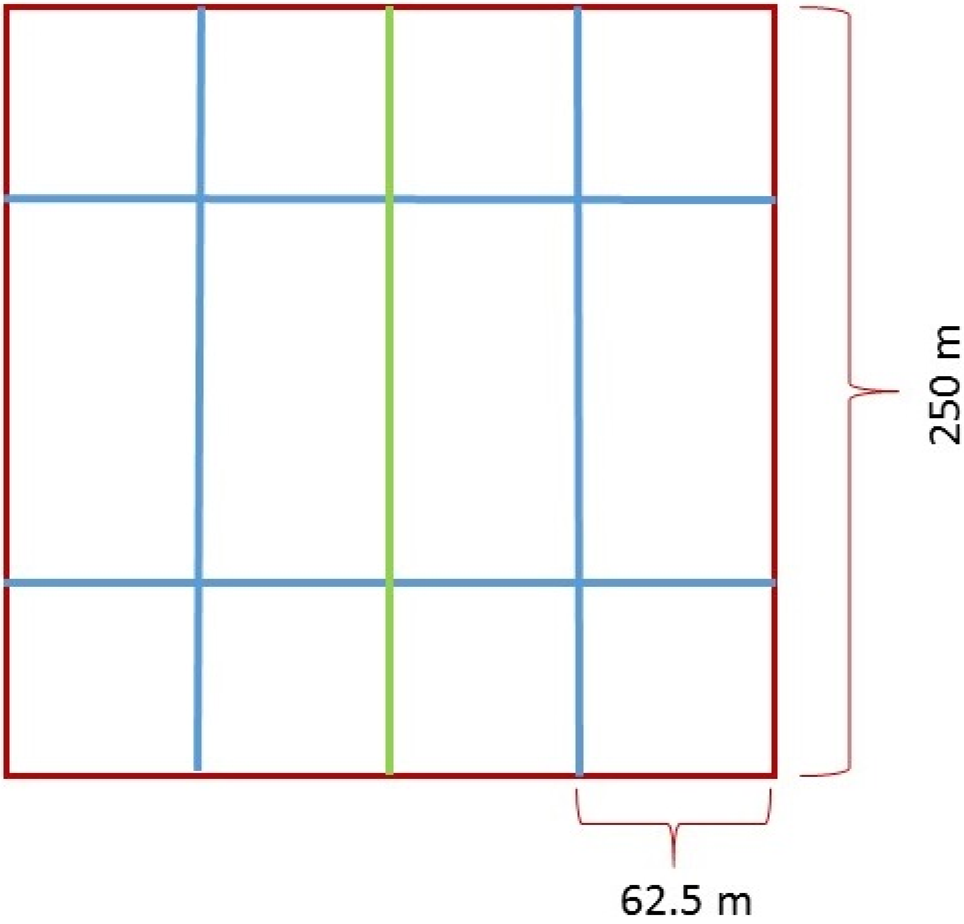


Figure A1-1: The schematic shows the placement of the bird survey transect and bison grazing transects in each plot sampled on the National Bison Range and Yellowstone National Park in 2016 and 2017. The green line represents the bird transect line. Blue lines represent bison patty count transects.

Table A1-1: The number of plots sampled in each category of predicted bison grazing, and associated patty counts on the National Bison Range and Yellowstone National Park in 2016 and 2017. Patties are reported as median and IQR of mean plot-level measurements. Predicted grazing category was determined using a habitat suitability index for bison (Steenweg et al. 2016).

Predicted Grazing Category	**2016**			**2017**		
	Plots	**Patties**		**Plots**	**Patties**	
National Bison Range	N	Median	IQR	N	Median	IQR
Low	10	18.25	19.43	10	19.00	13.23
Medium	30	18.50	22.83	30	18.38	23.25
High	30	31.25	30.63	30	24.88	20.38
Total	70			70		
Yellowstone National Park	N	Median	IQR	N	Median	IQR
Low	30	32.13	14.56	25	37.75	17.50
Medium	13	20.50	29.00	8	38.13	5.56
High	12	50.75	19.38	11	70.00	18.00
Total	55			42		

Table A1-2: Bison reintroductions in North America from 2009-2017. The table includes all reintroductions to the author's knowledge, but may not be a comprehensive list.

Location	Managing Agency	Year	Source:
Janos Biosphere Reserve, Mexico	The Nature Conservancy	2009	https://www.nature.org/ourinitiatives/regions/latinamerica/mexico/explore/bison-homecoming.xml
Book Cliffs, UT	Utah Division of Wildlife	2009	https://www.nps.gov/articles/bison-bellows-6-30-16.htm
Fort Peck Indian Reservation, MT	Fort Peck Fish and Game Department	2012	http://www.nytimes.com/2012/04/27/us/bison-return-to-montana-prairie.html
Fort Belknap Reservation, MT	Fort Belknap Fish and Wildlife Department	2013	https://www.usatoday.com/story/news/nation/2013/08/23/wild-bison-released-on-prairie/2694415/
Larimer County, CO	Larimer County Natural Resources	2015	http://csu-cvmbs.colostate.edu/academics/bms/ARBL/Pages/bison.aspx
Blackfeet Indian Reservation, MT	Blackfeet Nation Fish and Wildlife Department	2016	http://flatheadbeacon.com/2016/04/13/a-native-homecoming/
Banff National Park, Canada	Parks Canada	2017	http://www.pc.gc.ca/en/pn-np/ab/banff/info/gestion-management/bison
Wind River Reservation, WY	Eastern Shoshone Tribe	2017	https://www.fws.gov/news/blog/index.cfm/2017/5/16/Bison-Return-to-Wind-River-Reservation

Appendix 2: Study Area Figures

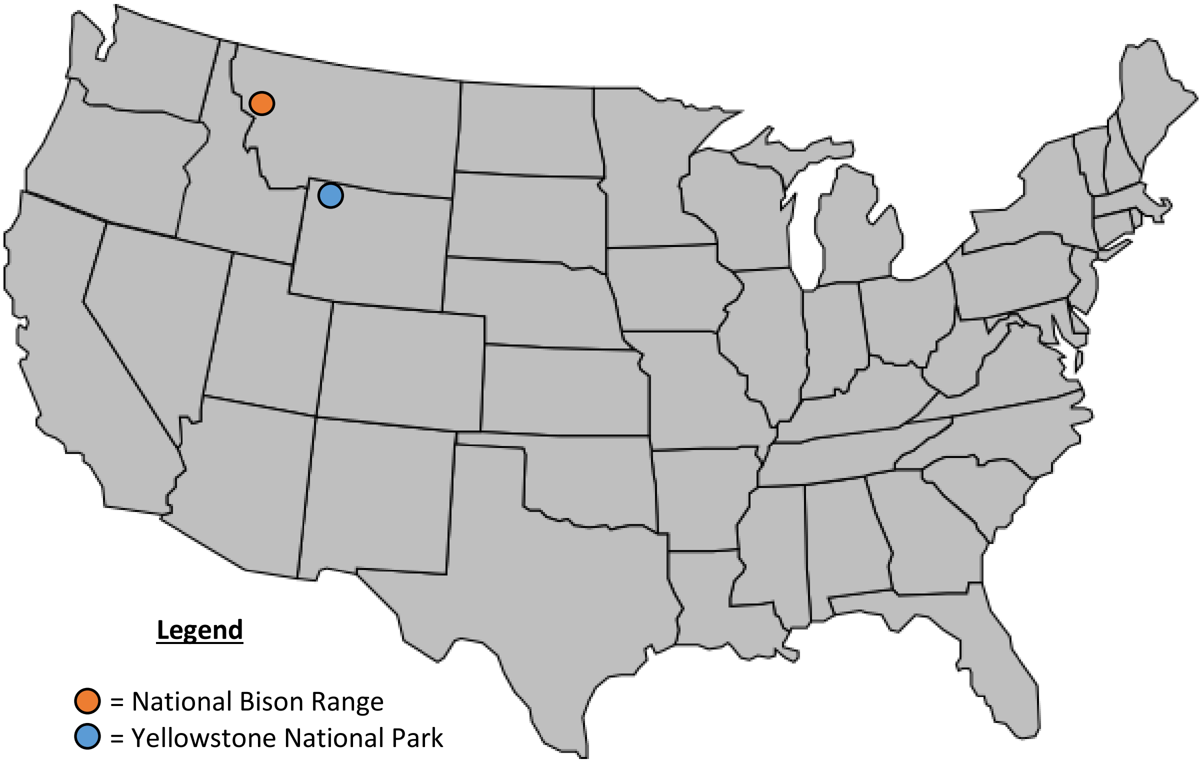
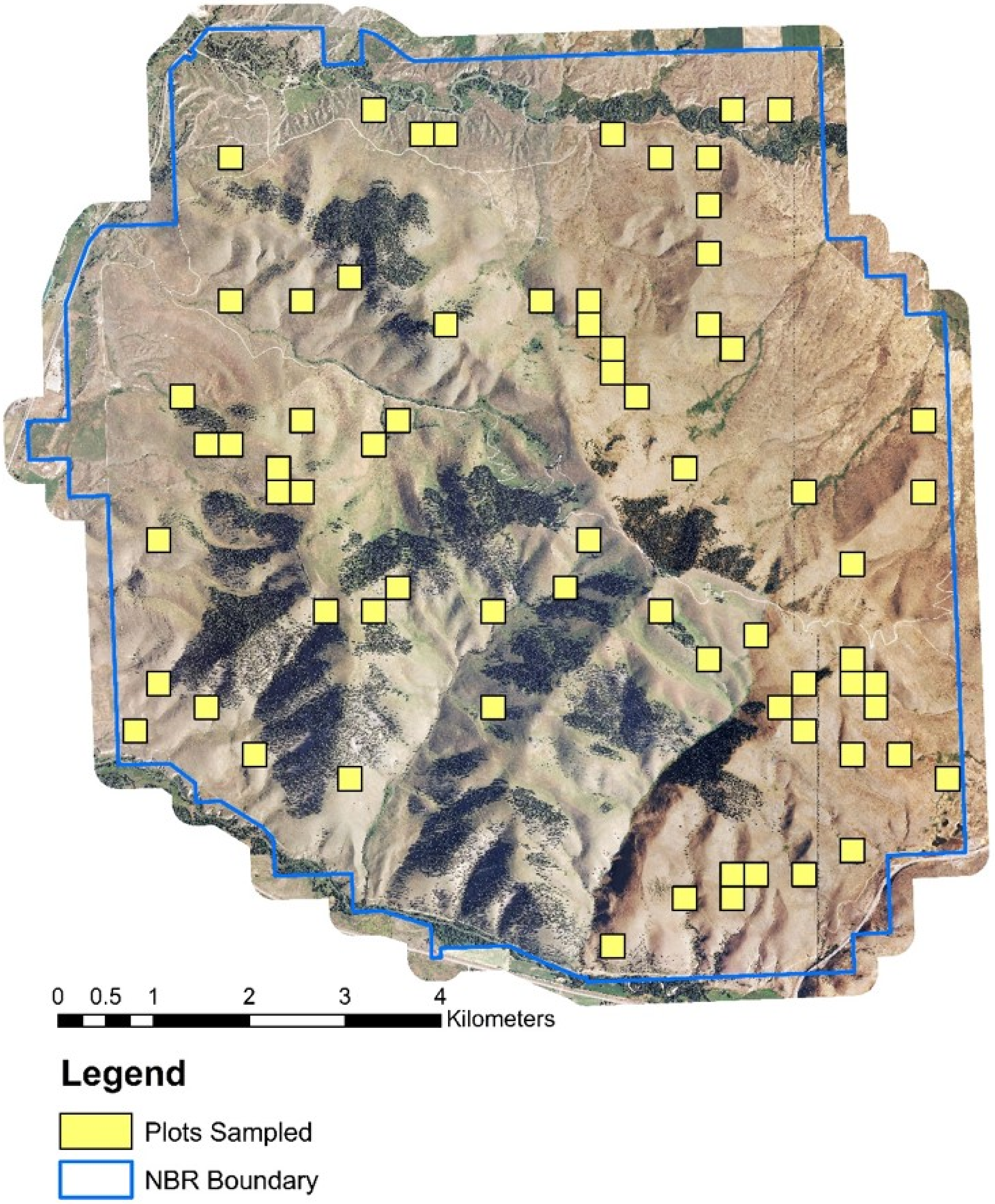


Figure A2-1: Map of the coterminous United States of America showing the location of the two study locations. The orange dot represents the National Bison Range study site and the blue dot represents the Yellowstone National Park study site. Map image credit: http://www.clker.com/clipart-gray-u-s-map.html.



<u>Figure A2-2:</u> Map of the National Bison Range study area and 70 plots surveyed for grassland and shrubland songbirds in 2016 and 2017.

Map by: Wiggins, Christine. Habitat Suitability Index for National Bison Range and Lamar Valley, Yellowstone National Park. April 2016. Using: ArcGIS Model Builder. Version 10.2. Redlands, CA: Environmental Systems Research Institute, Inc., 2013.
Imagery: USDA, 2015, National Agriculture Imagery Program. Accessed April 20, 2016 at https://gis.apfo.usda.gov/arcgis//rest/services

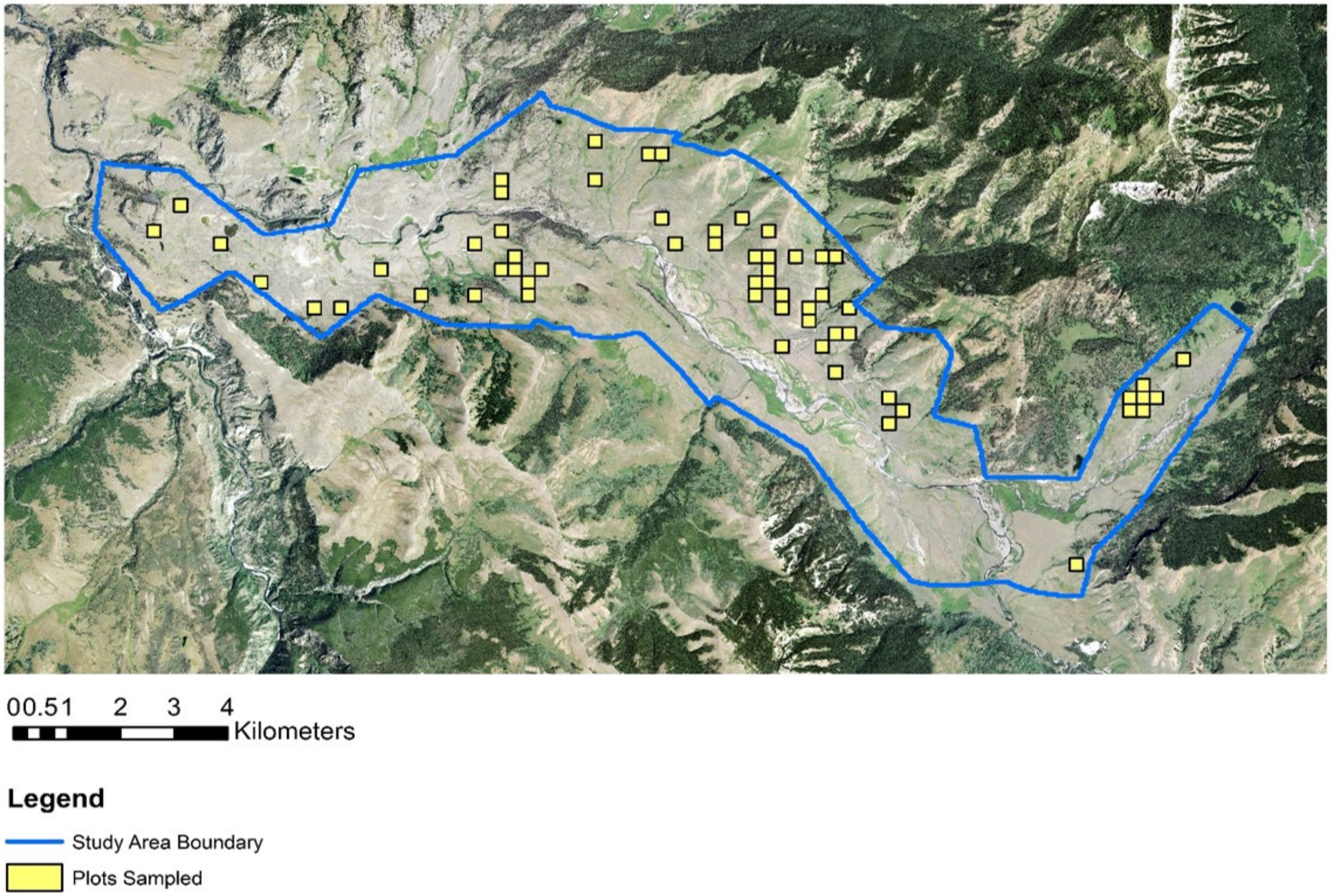


Figure A2-3: Map of the Yellowstone National Park study area and plots sampled for grassland and shrubland songbirds. All 53 plots were sampled in 2016, and 42 of the plots shown were sampled in 2017.

Map by: Wiggins, Christine. Habitat Suitability Index for National Bison Range and Lamar Valley, Yellowstone National Park. April 2016. Using: ArcGIS Model Builder. Version 10.2. Redlands, CA: Environmental Systems Research Institute, Inc., 2013.
Imagery: USDA, 2015, National Agriculture Imagery Program. Accessed April 20, 2016 at https://gis.apfo.usda.gov/arcgis//rest/services

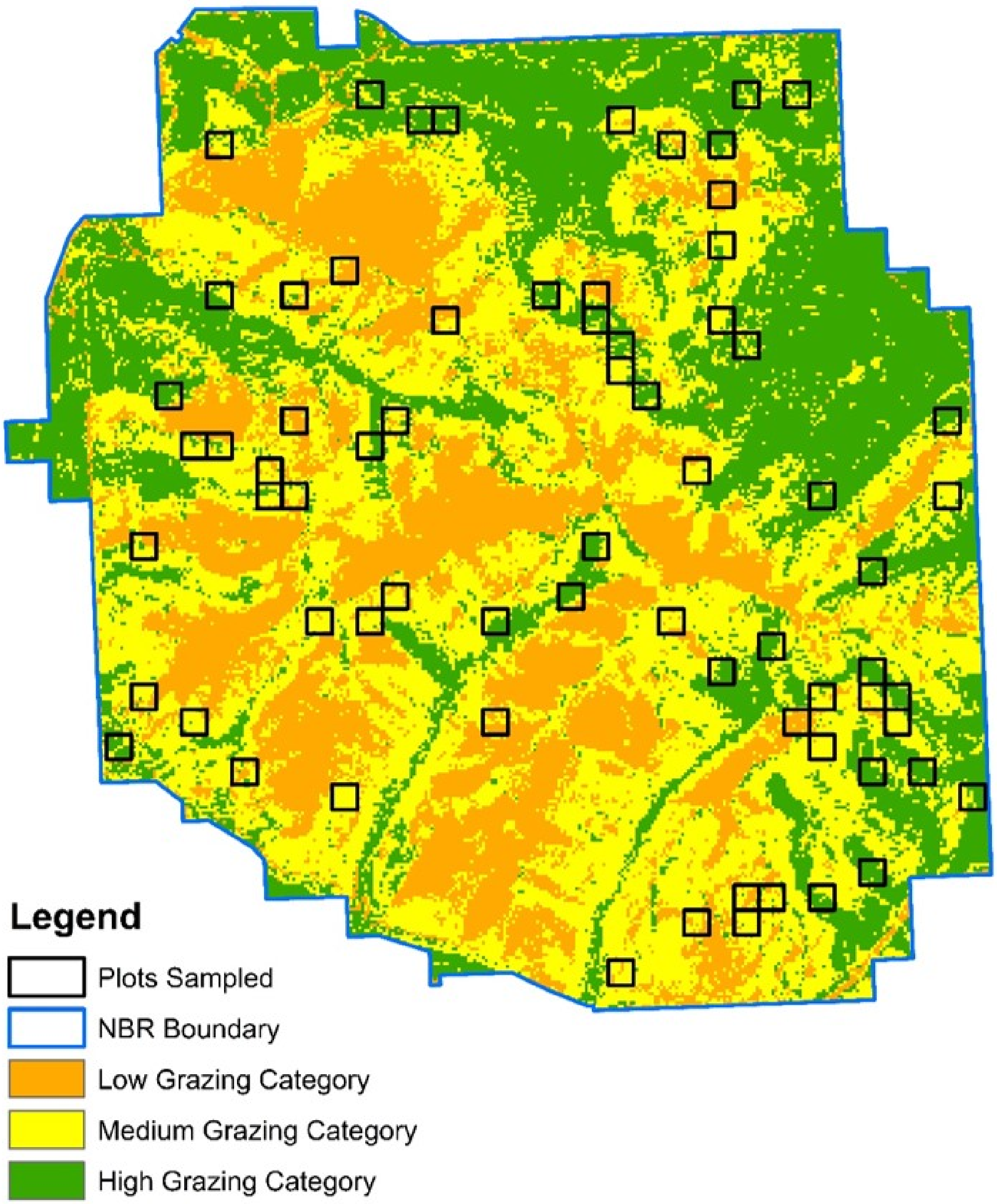


Figure A2-4: Map of the distribution of predicted bison grazing intensity based on the habitat suitability index values for the National Bison Range study area.

Map by: Wiggins, Christine. Habitat Suitability Index for National Bison Range and Lamar Valley, Yellowstone National Park. April 2016. Using: ArcGIS Model Builder. Version 10.2. Redlands, CA: Environmental Systems Research Institute, Inc., 2013.

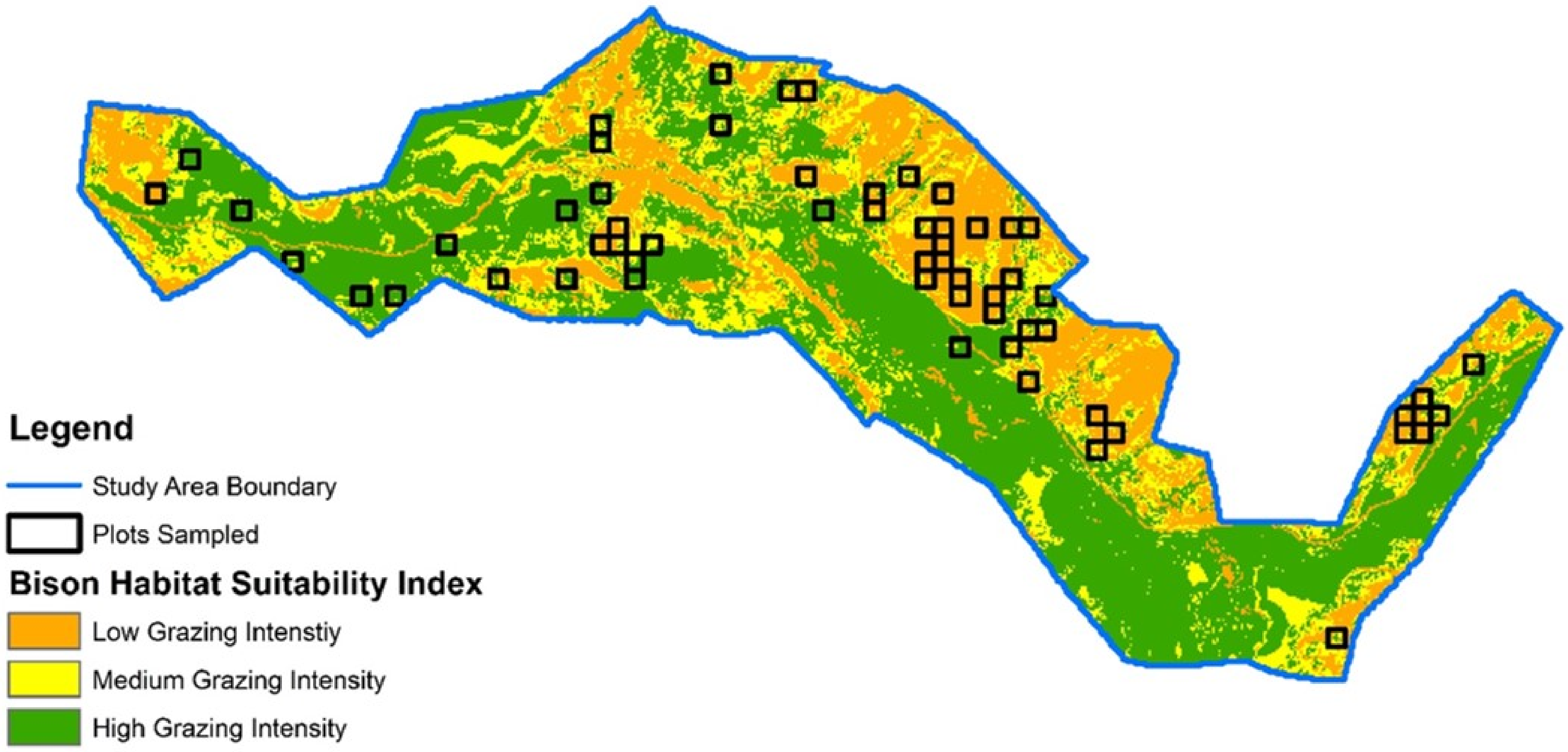


Figure A2-5: Map of the distribution of predicted bison grazing intensity based on the habitat suitability index values for the Yellowstone National Park study area. All 53 plots were sampled in 2016, and 42 of the plots shown were sampled in 2017.

Map by: Wiggins, Christine. Habitat Suitability Index for National Bison Range and Lamar Valley, Yellowstone National Park. April 2016. Using: ArcGIS Model Builder. Version 10.2. Redlands, CA: Environmental Systems Research Institute, Inc., 2013.

Appendix 3: Additional Field Data Collected

Methods

Canopy Height

I measured canopy height on the same transects where I counted bison patties. Observers took a canopy height measurement every 50 meters, for a total of 16 canopy height measurements per plot. Observers placed a 20x50 cm piece of cardboard on top of the canopy, then recorded canopy height to the nearest half centimeter (Tastad 2013). Observers also visually estimated the proportion of grass, forb, shrub, and bare ground/rock below the board.

Other Grazer Pellets

I counted pellets of other ungulates present in the study areas such as pronghorn antelope, elk, white-tail deer, and mule deer to control for the impact they may have on vegetation. Observers counted piles of pellets within 1 meter to the left and right of the same transects used for counting bison patties.

Relationships Among Variables

National Bison Range

In 2016, mean canopy height ranged from 10.41 – 26.78 cm (median = 18.3, IQR = 4.7), and in 2017 from 12.75 – 26.31 cm (median = 17.0, IQR = 4.32). In 2016, mean pellets per plot ranged from 0.3 – 69.5 piles (median = 5.5, IQR = 14.7), and in 2017 from 0.0 – 32.0 piles (median = 1.5, IQR = 5). Canopy height had a weakly negative log-linear relationship with pellet counts ($p < 0.001$, $R^2 = 0.20$), and HSI value ($p < 0.001$, $R^2 = 0.20$), and a non-significant relationship with patty counts ($p = 0.39$, $R^2 = 0.01$, square root transformation on canopy height and patty counts). Pellets had a weakly negative log-linear relationship with bison patties ($p < 0.001$, $R^2 = 0.17$). See Figure A3-1 for distributions and correlations among variables.

Yellowstone National Park

In 2016, mean canopy height ranged from 5.0 – 31.7 cm (median = 16.1, IQR = 8.1), and in 2017, from 6.4 – 29.0 cm (median = 18.5, IQR = 3.7). In 2016, pellets ranged from 0.0 – 34.5 piles (median = 1.3, IQR = 3.1), and in 2017, from 0.0 – 22.3 piles (median = 2.8, IQR = 3). Linear regression showed a non-significant relationship between canopy height and pellet counts ($p = 0.31$, $R^2 = 0.02$), a weak but significant negative relationship between canopy height and HSI ($p = 0.005$, $R^2 = 0.14$), and a stronger negative relationship between canopy height and patty counts ($p < 0.00002$, $R^2 = 0.30$). Pellets showed no significant relationship with patty counts ($p = 0.09$, $R^2 = 0.05$). See Figure A3-2 for distributions and correlations among variables.

Discussion

At both study sites, canopy height was negatively correlated with HSI value, indicating lower canopy height in areas that are more valuable for bison. However, canopy height was more related to pellet counts than patty counts in NBR, and was more related to patty counts than pellet counts in YNP. Additionally, pellet counts were negatively correlated with patty counts in NBR, but had no relationship in YNP. These results are consistent with the relationships between patty counts and HSI at each site. In NBR, patty counts and HSI had a weak relationship ($p = 0.02$, $R^2 = 0.07$), and there was a stronger relationship at YNP ($R^2 = 0.39$, $p < 0.001$), potentially explaining why the relationship between canopy height and patty counts is decoupled at NBR.

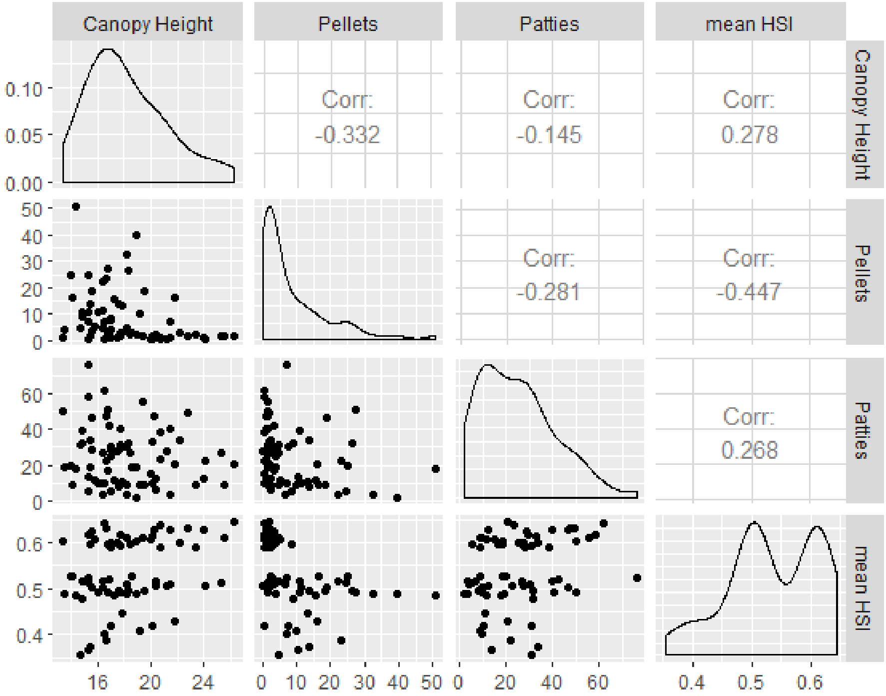
I decided not to incorporate these data types into my models of bird occupancy and abundance because of concerns about dependence and bias. Canopy height is only one of several ways in which bison grazing may affect vegetation structure, and therefore is not a comprehensive confirmation of the effect of bison grazing on vegetation structure. The two variables are theoretically related to one another, making the explanatory value of canopy height vague. I initially measured pellet counts to control for the effect of other ungulates on vegetation height. However, I did not identify pellets to species. Relationships between pellet distributions and use can vary by species (Neff 1968; Collins & Urness 1981), making this data of questionable explanatory value.

References:

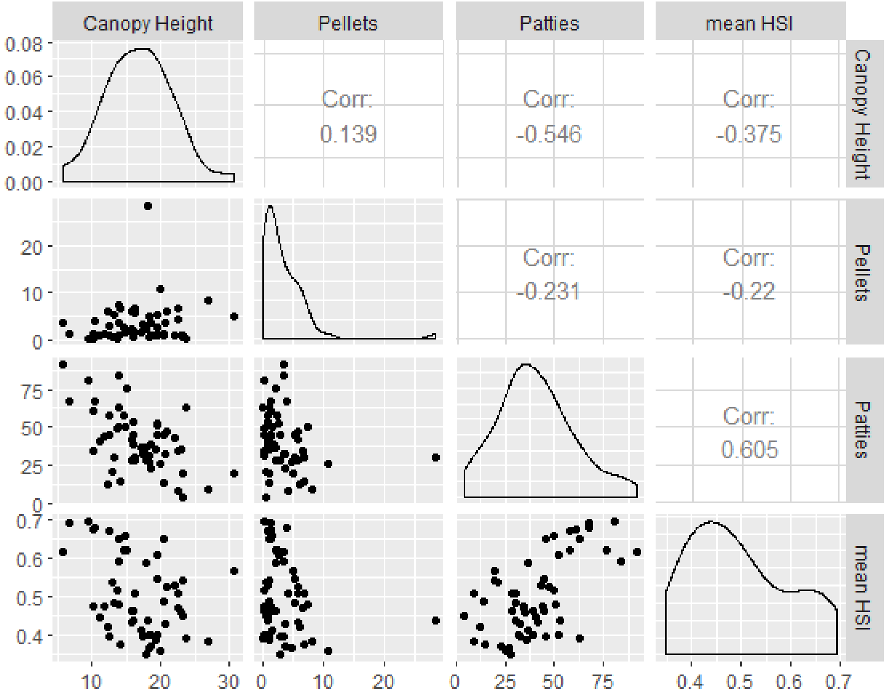
Collins WB, Urness PJ. 1981. Habitat preferences of mule deer as rated by pellet-group distributions. Journal of Wildlife Management. **45:**969-972.

Neff DJ. 1968. The pellet-group count technique for big game trend, census, and distribution: a review. Journal of Wildlife Management **32:**597–614.

Tastad AC. 2013. The relative effects of grazing by bison and cattle on plant community heterogeneity in northern mixed prairie [thesis]. University of Manitoba, Winnipeg, Manitoba.



<u>Figure A3-1:</u> Correlation plots between all untransformed field data collected at the National Bison Range study area in 2016 and 2017. Diagonal plots show the smoothed distribution of data, and scatter plots show relationships between each pair of data. Correlation values represent R.



<u>Figure A3-2:</u> Correlation plots between all untransformed field data collected at the Yellowstone National park study are in 2016 and 2017. Diagonal plots show the smoothed distribution of data, and scatter plots show relationships between each pair of data. Correlation values represent R.