ASSOCIATIONS OF BROAD SCALE VEGETATION CHARACTERISTICS AND ABUNDANCES, NEST DENSITIES, AND NEST SURVIVAL OF MIXED-GRASS PRAIRIE SONGBIRDS IN NORTHERN MONTANA

by

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ABSTRACT

Grassland bird populations are declining faster than any other avian guild. In northern Montana, four species are experiencing severe population declines: Baird's sparrow (*Centronyx bairdii*), chestnut-collared longspur (*Calcarius ornatus*), McCown's longspur (*Rynchophanes mccownii*), and Sprague's pipit (*Anthus spragueii*). In 2017 and 2018, I evaluated abundance, nest density and nest survival of these species in relation to local vegetative conditions with the goal of identifying important breeding season vegetation conditions to inform management. I conducted fixed-radius point-counts at 100 sites to estimate local abundance, rope drag surveys to estimate nest density, nest monitoring to estimate nest survival, and vegetation surveys to estimate vegetation structure and composition across grassland habitats in Phillips County, MT. Point-counts and rope drag surveys were carried out with replicated visits to allow estimation of species-specific detection probabilities. Vegetation conditions were measured at the plot level (9-ha) to provide information at scales relevant for land managers. The abundance of Baird's sparrows was positively associated with residual grass cover and litter cover. Chestnut-collared longspur abundance was negatively associated with residual grass, exotic grass, and shrub cover and had a quadratic relationship with biomass. Plot-level abundance of McCown's longspurs was negatively associated with both shrub cover and biomass. Sprague's pipit abundance declined with exotic grass cover and exhibited a quadratic relationship with biomass. Limited sample size only allowed inference of nest density and nest survival for chestnut-collared longspurs. Nest density was negatively associated with plot scale exotic grass cover, biomass, and slope. I did not find support for any vegetation covariates on nest survival for chestnut-collared longspurs. These results provide some guidance for landscape managers interested in improving habitat for these species. The contrasting results among species, however, emphasize the need for heterogeneity in vegetation structure and composition. The disconnect between relevant covariates for nest density and nest survival suggest possible maladaptation for chestnut-collared longspurs. This result suggests that an index of productivity for this species that does not include both nest density and nest survival may produce erroneous results.

CHAPTER ONE

LITERATURE REVIEW

Grassland Birds in the Northern Great Plains

Grassland birds, especially those endemic to the Great Plains, have become a focus of conservation due to widespread populations declines over the past 40 years (Knopf 1994, Sauer et al. 2015; Fig 1) associated with loss, degradation, and fragmentation of grassland habitat (Hoekstra et al. 2005). Across North America, historic losses of grasslands total approximately 70% (Samson et al. 2004). In the northern Great Plains, native grassland is being converted to agricultural fields five times faster than it can be protected (Doherty et al. 2013).

It has been argued that maintaining or improving heterogeneity with respect to vegetation structure is essential to maintain diverse avifauna communities in North American grassland systems (Knopf 1996, Fuhlendorf et al. 2006, Hovick et al. 2014). Heterogenous landscapes allow for more unique ecological niches allowing specialist species to cohabitate with little or no competition (Tews et al. 2004). Historic patterns of temporally and spatially variable disturbance in the Great Plains have allowed for structural specialization of native fauna (Knopf 1996).

Prior to European settlement in the region, native herbivores, most notably bison, ranged over vast areas of grassland. Where bison herds grazed, native vegetation, especially non-woody plants, were heavily impacted by both consumption and trampling. After the herd finished grazing a specific area it would move on, leaving behind an extreme reduction in vegetation (Knopf 1996). Bison herds may not return to the same spot to graze for many years, giving it time to recover. The interaction of fire and grazing by large herbivores created a shifting mosaic of vegetation conditions across the landscape, with vegetation structures and compositions varying across both time and space (Fuhlendorf and Engle 2001). Some species coevolving in such a landscape may specialize in certain vegetation structures (e.g. areas of high disturbance with sparse vegetation) as well as develop nomadic behavior, ranging across wide areas to find the new location of their specialized niche. Migratory songbirds provide a good example of these adaptations. These species hold relatively small territories compared to larger fauna allowing them to potentially only use an area with one specific vegetation structure. Furthermore, many species are nomadic and inhabit different areas each year. The specialization for different vegetation conditions by grassland songbirds supports the shifting mosaic theory (Knopf 1996; Fig 2). In areas where native prairie remains, vegetation composition and structure seem to influence abundance and breeding success for grassland songbirds (Winter et al. 2005, Kerns et al. 2010, Davis et al. 2016).

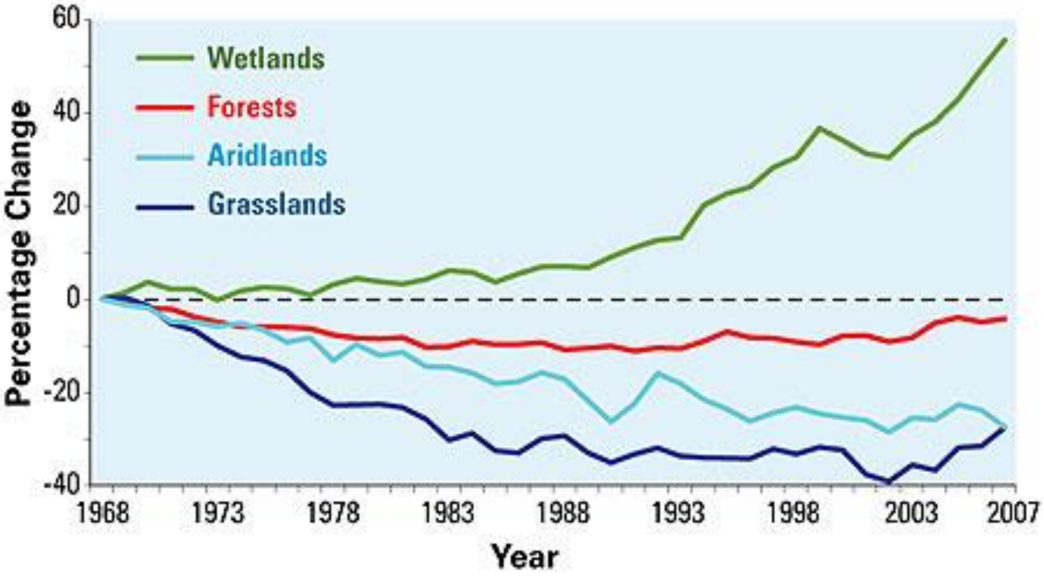

Figure 1: Changes in relative bird abundances in the U.S.A. Species organized by common habitat (North American Bird Conservation Initiative 2009).

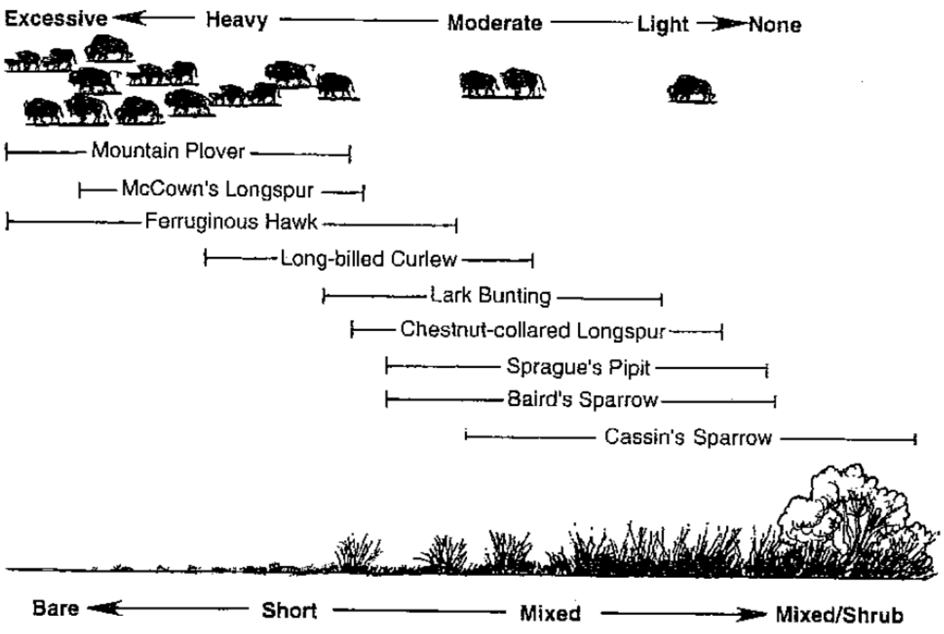

Figure 2: Distribution of endemic birds of prairie uplands relative to historical grazing pressure across the western landscapes of the Great Plains (Knopf 1996)

In the northern mixed-grass prairie, four species of prairie specialist have become species of interest due to their ongoing and severe declines (Sauer et al. 2015, Somershoe 2018). Baird’s sparrow (*Centronyx bairdii*), chestnut-collared longspur (*Calcarius ornatus*), McCown’s longspur (*Rhynchophanes mccownii*), and Sprague’s pipit (*Anthus spragueii*) rely on large sections of intact native mixed-grass prairie (Lipsey 2015, Davis et al. 2016). The North American Breeding Bird Survey (BBS) estimates the annual population decline to be 2.9% for Baird’s sparrows, 4.4% for chestnut-collared longspurs, 6.2% for McCown’s longspurs, and 3.5% for Sprague’s pipit (Sauer et al. 2015). The BBS routes are exclusively along roads which some studies suggest that these species will avoid (Keller and Scallan 1999, Sutter et al. 2000, Davis 2004, Thompson et al. 2015), possibly biasing estimates of population size downward (Keller and Scallan 1999, Sutter et al. 2000).

Slowing or stopping the declines of these species will require management strategies that optimize habitat that supports large populations with high reproductive success. A conservation strategy for these species recently published by the U.S. Fish and Wildlife Service and the Prairie Potholes Joint Venture identified the need for a better understanding of how grassland structure and composition affect demographic success for these species at a pasture scale (Somershoe 2018). Previous research on vegetation associations of grassland songbirds typically used point counts to evaluate adult abundance and nest searching to evaluate nest-site selection then related these to the local vegetation conditions. However vegetation surveys in previous studies typically evaluated vegetation at each point count and nest-site, sometimes pairing this information with nearby random survey points or with a transect of survey points in a random direction (Sutter 1997, Winter 1999, Madden et al. 2000, Davis 2005, Davis et al. 2016). This fine spatial scale may be relevant to songbirds that hold relatively small territories, but evaluating landscape at this fine scale is of limited use to managers. Management strategies cannot reasonably be implemented on patches of land the size of an individual bird's territory. To assist managers, there is a need for an evaluation of associations between bird metrics and vegetation conditions at scales large enough for reasonable implementation of management. Grassland bird biologists need to start thinking at the pasture scale.

Baird's Sparrow Breeding Behavior

The breeding range of Baird's sparrows covers southeastern Alberta, southern Saskatchewan, southwestern Manitoba, eastern Montana, western North Dakota, and northwestern South Dakota (Green et al. 2002). Baird's sparrow arrive on the breeding grounds as early as the last week of April in Montana and the first two weeks of May in Manitoba (Cartwright et al. 1937, Davis and Sealy 1998). Nests are built into the base of a clump of grass in a depression dug out by the female or a natural depression from a hoof print or other source (Green et al. 2002). Nests may have overhanging grass, shrub, or other vegetation to conceal the nest from above, or may have no overhead concealment at all (Davis and Sealy 1998). In Manitoba clutch initiation begins as early as May 25th and peaks (majority of breeding females initiating a clutch) between May 29th and June 4th (Davis and Sealy 1998). Clutch size ranges from two to six but four or five is most typical (Green et al. 2002). Incubation lasts 11 – 12 days and hatching is synchronous suggesting that incubation does not begin until the final egg is laid, juveniles fledge 8 – 11 days after hatching (Davis and Sealy 1998). Even after fledging juveniles remain reliant on parental care until about 19 days after hatching when they typically leave their parents' territory (Cartwright et al. 1937). Double brooding is common for this species and time between the completion of one nest and the beginning of another can be as brief as one day (Cartwright et al. 1937) with others observing a delay of five to eight days (Davis and Sealy 1998).

Chestnut-collared Longspur Breeding Behavior

The breeding range of the chestnut-collared longspur extends from southern Alberta, Saskatchewan, and Manitoba down into Montana, North and South Dakota and extreme northern Wyoming with populations in southern Wyoming, western Nebraska and northern Colorado. Males arrive on the breeding grounds in Montana in early–mid April with females arriving one to two weeks later (Lloyd and Martin 2005). First nests are initiated in Montana as early as April 30th (Jones et al. 2010). Nests are built into a depression in the ground dug out by the female. Nests are open cups typically made from woven dried grass with the upper lip of the nest slightly above the ground surface (Bleho et al. 2015). Clutch size is typically four eggs with three or five eggs also common, and rarely two or six (Bleho et al. 2015). Incubation ranges from 7 – 15 days, with an average of 10.9 days (Jones et al. 2010). Juveniles fledge from the nest after another 7 – 15 days with an average of 11.1 days (Jones et al. 2010). Juveniles are cared for by parents after fledging until about 24 days after hatching when they become independent (Harris 1944). Double brooding is common with females initiating a second clutch in as little as six days after the completion of the previous nest (range of 6 – 18 days, mean 9.7 days; Bleho et al. 2015).

McCown's Longspur Breeding Behavior

McCown's longspur's breeding range covers southeast Alberta, southern Saskatchewan, eastern Montana, western North Dakota, central Wyoming, extreme western Nebraska, and extreme northern Colorado. Individuals arrive on the breeding grounds in mid- to late April (Saunders and Bailey 1917). Nests are built in shallow depressions in the ground dug out by the female with an open cup of woven dried grass within, such that the nest edge is flush with the ground (Mickey 1943, With 2010). Egg laying for the first brood begins in early May, and incubation typically begins once the clutch is complete and lasts 12 days (Mickey 1943). Nestlings can fledge from 8 – 11 days old with 10 days old being the most common (Mickey 1943). Fledglings remain reliant on parental feeding for three weeks after fledging after which females will typically initiate a second brood (With 2010).

Sprague's Pipit Breeding Behavior

The breeding range of the Sprague's pipit extends from southeastern Alberta, southern Saskatchewan, and southwestern Manitoba, down into parts of Montana east of the Rockies, throughout North Dakota except some eastern counties, as well as a small part of northwestern South Dakota (Davis et al. 2014). Individuals arrive on the breeding grounds from late April through mid-May (Maher 1973). Nest cups are woven from dried grass frequently with a dome (Sutter 1997). Nests can range from fully exposed cup to highly concealed with a dome, but domed nests are more common than open cup nests (Sutter 1997, Davis 2005, Davis et al. 2014). In Montana females can initiate clutches from the first week of May to the end of July (median date = 25 May; Jones et al. 2010). Clutch sizes range from three to six eggs, with four of five being the most common (Maher 1973). Incubation takes from 12 – 15 days (mean = 13.4 ± 0.3 SE; Davis 2009). Juveniles fledge from 11 – 14 days in Saskatchewan (12.1 ± 0.2; Davis 2009) and 9 – 17 days in Montana (mean = 12.9; Jones et al. 2010). The age at which juveniles are independent of their parents in unknown but one known age juvenile was observed feeding without any assistance of adults at 18 days old (Davis et al. 2014). Re-nesting attempts occur 6 – 17 days after first nest failure. Due to long incubation and brooding periods and high predation rates, second breeding attempts after a successful first attempt may be uncommon (Davis 2009).

Habitat Preferences

Collectively, these four species represent a range of habitat preferences. Chestnut-collared and McCown’s longspurs are believed to prefer short sparse grass with abundant bare areas, the sort that would have been consistent with areas grazed heavily by a roaming bison herd (Knopf 1996, Davis 2005). Baird’s sparrows and Sprague’s pipits by contrast, prefer taller more dense herbaceous vegetation, typically with visual obstruction readings (VOR) around 1 dm, more consistent with areas moderately or lightly grazed or otherwise in ecological sites that support vegetation with this stature without disturbance (Madden et al. 2000). However, there is an upper limit to this preference. Use appears to decline as VOR increases above 1 dm with Sprague's pipit and Baird's sparrow absent when average VOR exceeds 3 and 5 dm, respectively (Madden et al. 2000, Davis 2005). The absence of these species from areas with such tall and dense vegetation suggests that a lack of disturbance to the prairie, either in the form of grazing or burning, or ecological sites that favor tall vegetation, can reduce abundance of these species (Hobbs and Huenneke 1992, Kerns et al. 2010). All four species also seem to avoid tall or dense shrubs (With 1994, Davis 2005). The effects of relative cover of forbs, club moss, bare ground, and litter within an area are less well understood with studies often finding no significant effect or only weak effects (Davis et al. 1999, Madden et al. 2000, Davis 2004, Davis et al. 2016).

The underlying biological processes that drive vegetation associations of many grassland birds are not fully understood, but assumptions based on life-history theory are often made. The most common hypothesis is that breeding grassland birds select sites with vegetation characteristics that provide concealment from nest predators and nest parasites, i.e., Brown-headed Cowbird (*Molothrus ater*) (Davis 2005). There is some support for this hypothesis as predation is the most common cause of nest failure and observed rates of nest predation for these species often exceed 60%, with parasitism rates typically 15–29% (Davis and Sealy 1998, Davis 2003).

The nest concealment theory is often invoked to explain observed avoidance of landscape edges by these species (Sutter et al. 2000, Winter et al. 2000, Davis 2004, Sliwinski and Koper 2012, Lipsey 2015). Where prairie meets another landscape type, either natural or man-made, there will be changes to landscape features that either reduce vegetative concealment of nests or increase the local number of potential nest predators or parasites. Wooded areas provide trees and roads that are typically bordered by fences, both of which can provide potential perch points for avian nest predators or parasites (Winter et al. 2000). Roads are often bounded by drainage ditches, creating a buffer of greater moisture availability and denser vegetation which may be unusable for some grassland birds, and may be more attractive to potential mammalian nest predators (Barker et al. 1990, Kirby and Grosz 1995, Gilbert et al. 1996, Fondell and Ball 2004, Warren et al. 2008). The negative effects of these landscape features suggest that many grassland species benefit from or even require large contiguous expanses of prairie (Davis 2004).

In addition to vegetation structure, there is also some evidence that breeding site selection is influenced by encroachment of exotic grasses. Davis et al. (2016) found that Sprague’s pipits, Baird’s sparrows, and chestnut-collared longspurs in southern Saskatchewan were all more abundant in native prairie than in pasture comprised of introduced vegetation. Furthermore, Sprague’s pipits and Baird’s sparrows in introduced vegetation experienced higher predation rates, lower renesting rates, and lower reproductive success overall. In contrast, reproductive success of chestnut-collared longspurs did not differ between native and non-native pastures (Davis et al. 2016). A study in eastern Montana found that while chestnut-collared longspurs were equally abundant in non-native crested wheatgrass (*Agropyron* cristatum) fields and native prairie, they experienced lower nest survival and fledged fewer young per nest in the nonnative fields compared with the native prairie (Lloyd and Martin 2005).

An understanding of how these habitat characteristics influence these avian species is needed to address bird population declines. Previous studies of these relationships did not assess vegetation characteristics at a useful scale for management. Specifically, while there have been previous studies into nest-site selection and nest survival, they typically related those responses to vegetation conditions at or near the nest-site and which is of limited utility to managers. Results of previous work also suggest that species abundance may not always be correlated with reproductive success and functional relationships between these two parameters are still poorly understood (Madden et al. 2000, Bock and Jones 2004).

Information needed for practical implementation of habitat enhancement includes whether and how vegetation structure and composition are linked to reproductive success of these species, under what habitat conditions abundance is associated with reproductive success, and if or how vegetation structure and composition at the nest site scale are related to structure and composition at broad scales.

This thesis evaluates the relationships among broad scale vegetation structure and composition and abundance, reproductive effort, and reproductive success for Baird’s sparrow, chestnut-collared longspur, McCown’s longspur, and Sprague’s pipit. In Chapter 2, I assess the relationship between adult abundances of each species and broad scale vegetation conditions. In Chapter 3, I evaluate the relationships between vegetation conditions at broad scale and nest density and survival. Finally, in Chapter 4 I summarize important results, conclusions, and recommendations from the previous chapters.

CHAPTER TWO

EFFECTS OF VEGETATION CONDITIONS ON ABUNDANCE OF NORTHERN MIXED-GRASS PRAIRIE SONGBIRDS

Introduction

Temperate grasslands are among the most imperiled ecosystems in the world and the birds that live there are experiencing population declines (Knopf 1994, Hoekstra et al. 2005, Azpiroz and Blake 2009). In North America grassland birds have declined more severely than any other guild of wildlife over the past 40 years (North American Bird Conservation Initiative 2014, Sauer et al. 2015). The decline is largely attributed to the loss, degradation, and fragmentation of grassland habitats due to the conversion to row crop agriculture and encroachment of exotic plants (Samson et al. 2004, Hoekstra et al. 2005). Currently the majority of native prairies are being managed for livestock grazing (Knopf 1996). Slowing or stopping grassland songbird population declines requires land and livestock grazing management strategies for North American grasslands that maximize habitat for at risk species.

Grassland bird species in the Great Plains evolved with climatic conditions that varied widely in productivity and experienced landscape-level disturbances from fire and wild ungulates. Consequently, these grasslands are naturally heterogeneous with respect to plant structure and composition (Fuhlendorf and Engle 2001). Over evolutionary time, such historic variability in disturbance led to specialization of different bird species for certain plant structural forms or species compositions (Knopf 1996, Fuhlendorf et al.

2006). Characteristics commonly influential to bird abundance include cover and densities of different plant growth forms (e.g., grass, forbs, shrubs, etc.), as well as cover of litter and bare ground (Fisher and Davis 2010). Grass is used as a nest substrate and, along with forbs and shrubs, can conceal birds and nests from predators or serve as perches for singing males. The value of plant litter to bird habitat is less well understood but some have argued that large amounts of litter may be an index of improved nutrient cycling, soil retention, and better rangeland health overall (Pyke et al. 2002). Bare ground is thought to increase ease of foraging as well as improve birds ability to detect approaching predators (Fisher and Davis 2010).

In the mixed grass prairies of the northern United States (U.S.) and southern Canada, four endemic grassland songbird species are of particular interest given their severe rates of population decline. Baird's sparrows (*Centronyx bairdii*) are experiencing an estimated annual population decline of 2.9%, chestnut-collared longspurs (*Calcarius ornatus*) are declining an estimated 4.4%, McCown's longspurs (*Rynchophanes mccownii*) 6.2%, and Sprague's pipits (*Anthus spragueii*) 3.5% (Sauer et al. 2015). An understanding of the local vegetation conditions associated with occurrence of grassland songbirds can provide insight into their population declines and identify useful habitat characteristics (Davis et al. 1999, Vickery and Herkert 2001, Fisher and Davis 2010).

Previous research on vegetation associations of grassland songbirds typically used point counts to evaluate adult abundance and evaluated vegetation conditions only at the count points or with the addition of a few nearby random points or transects (Sutter 1997, Madden et al. 2000). Evaluating landscape at this fine scale, while perhaps biologically meaningful, is of limited use to landscape managers. Management strategies aimed at improving habitat for at risk species cannot reasonably be implemented on patches of land the size of a single bird's territory. To assist managers, there is a need for an evaluation of associations between bird abundances and vegetation conditions at scales large enough for reasonable implementation of management.

To address this question, I conducted point counts to evaluate the abundance of each species and vegetation surveys to assess conditions within 9-ha study plots. My objectives were to: 1) evaluate associations between local abundance and plot-level vegetation characteristics, 2) compare the magnitude and direction of habitat associations among species, and 3) provide management recommendations regarding grassland bird vegetation associations. Previous research has suggested that herbaceous biomass (typically indexed using visual obstruction readings) and the amount of vertical and horizontal cover largely determine grassland bird abundance (With 1994, Sutter et al. 1995, Sutter 1997, Davis et al. 1999, Madden et al. 2000, Davis 2003; 2005, Winter et al. 2005, Fisher and Davis 2010). In addition, local densities of obligate grassland birds may be altered by exotic grasses, but results of previous studies have been inconsistent (Sutter et al. 1995, Davis et al. 1999, Lloyd and Martin 2005, Lipsey 2015, Davis et al. 2016).

I expect that the local abundances of chestnut-collared longspur and McCown's longspur will be greater in areas with sparse vegetation and will exhibit negative associations with biomass, grass cover, and litter cover, and positive associations with bare ground (Knopf 1996, Dechant 2002*a*; *b*, Davis 2005). I expect the abundances of Sprague's pipits and Baird's sparrows to exhibit a quadratic relationship with measures of herbaceous biomass, where local abundance is maximized at some intermediate level of biomass or vegetation structure (Madden et al. 2000). I anticipate all four species will be disassociated with shrub (With 1994, Davis et al. 1999, Davis 2004, Lipsey and Dreitz 2014) and exotic grass cover (Lipsey 2015, Davis et al. 2016).

Methods

Study Area

My study area was located in northern Phillips County, Montana, ranging from 24 km south of Malta, MT to eight km south of the Canadian border. This region contains one of the largest tracts of intact native mixed-grass prairie remaining in the U. S. (Cooper et al. 2001). A simulation of population distribution for my study species conducted by the U.S. Fish and Wildlife Service predicted that Phillips County contains some of the highest densities of my study species throughout their range (Lipsey 2015). The region is dominated by gently rolling grassy hills. The climate is semi-arid with short, hot summers and long, cold winters. Average annual precipitation typically comes as rain in May – July (Cooper et al. 2001). Total precipitation ranges from 193 – 493 mm per year (1981 – 2015; PRISM 2019). The dominant grasses are western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), green needlegrass (*Nassella viridula)*, and Sandberg bluegrass (*Poa secunda*) (Charboneau et al. 2013). Almost 75% of the region is managed for livestock grazing (Lipsey 2015). In areas where the native mixed-grass prairie is relatively intact, grassland bird populations are still relatively stable (Cooper et al. 2001).

Site Selection. I used a stratified random sampling approach to control for possible confounding factors that may influence the abundance and productivity of birds, including soil characteristics (soil type, productivity), expected annual precipitation, and distance to roads (Sutter et al. 2000, Lipsey and Naugle 2016). Soil survey data were downloaded from the Natural Resource Conservation Service (NRCS) web soil survey dataset (Soil Survey Staff) and used to identify and select areas in northern Phillips County identified as having silty ecological site types, with 250 – 330 mm of average precipitation and at least 1,120 kg ha^{-1} of vegetation productivity in a normal year. I constrained potential sites to these conditions because they are known to support all four of my focal species (M. Sather, U.S. Fish and Wildlife Service, personal communication). I further stratified sites by ownership, land use, and distance to roads. To ensure study sites represented the gradients of vegetative conditions and livestock use, I selected study sites occurring on private and public lands known to have diverse land and livestock management. I limited selection of study sites to lands managed by Bowdoin National Wildlife Refuge (NWR), the Bureau of Land Management (BLM), Montana state trust lands and private owners. For logistical reasons, I limited the selection of sites to those within 64 km of Bowdoin NWR. I used ArcMap 10.4.1 (ESRI 2016) to select broad areas that contained the selected soil conditions and land uses and were close enough together to allow for the access of multiple sites in a given field day. I then used ArcMap to randomly generate 300 × 300 m plots within these areas. Of the generated plots, I selected only plots that fit predefined soil conditions, were completely within one land ownership type (BLM, NWR, Montana state trust, or private), were not within 200 m of a road (Sutter et al. 2000), and did not overlap one another. In total, I generated 12 potential plots on school trust land, another 12 on NWR land, 97 on BLM, and 31 on private land. The disparity in the number of plots generated for each land use type is due to differences in the amount of acreage under each ownership type in the county. In Phillips county within 64 km of Bowdoin NWR, there are approximately 215,218 ha (72% of public land) of BLM land, 76,578 ha (26% of public land) of school trust land, and only 6,819 ha (2% of public land) of NWR land.

Beginning with an initial set of 121 plots on BLM, NWR, and state trust land, I ground-truthed all plots in 2017 prior to sampling. I examined plots for features that may negatively impact bird use of the area. These included features not identifiable from remote imagery (e.g., interior fences and roads). When possible, I moved plots ≥ 100 m from roads, gas wells, fences, and power lines because habitat use by grassland birds is often influenced by anthropogenic disturbance (Sutter et al. 2000, Thompson et al. 2015). Plots that contained ≥ 50% shrub cover were moved to a nearby area with < 50% shrub cover when possible (With 1994, Lipsey 2015). Plots were removed from the study when there was no location within 300 m of the plot that met the criteria for soil, vegetation, or anthropogenic structures. Removal of 21 plots during ground truthing resulted in 100 useable plots, but limitations of time made it impossible to effectively survey all 100 sites within a single field season. I randomly selected 50 of these to survey during the 2017 season and reserved the remaining 50 for survey during 2018. Prior to the start of the 2018 season, I created an additional 31 plots on private lands using the previously described random sampling methods. Of these 31, I was granted permission to access only six plots. In 2018, I repeated field inspections of all plots to ensure plot conditions had not changed during the year. Examples of such changes might include the construction of new oil derricks, fences, or power lines. Six of the BLM plots for 2018 were removed from the study to allow for the addition of the six new private land plots while keeping the total number surveyed to 100 (Fig. 3).

Sampling

I conducted point count surveys for the four focal species of grassland birds at 50 study plots within the study area during May 2017 and another 50 plots during May 2018. Each point-count location was positioned in the center of each plot to ensure that no individuals holding territory partially outside the plot were counted. I conducted 3, 5-minute point counts for target species at each plot. Replicated surveys at each site occurred on the same survey morning to assure population closure. I recorded all birds detected by sight and sound within 100 m of the point during each 5-minute period (Hutto et al. 1986). At each survey location, the observer recorded date and time, percent cloud cover, precipitation, temperature, and wind speed. Other data recorded included sex (dichromatic species only), group size, vocalization, and behavior of each species identified. At each survey location, the observer recorded date and time, percent cloud cover, precipitation, temperature, and wind speed. Point count surveys were conducted

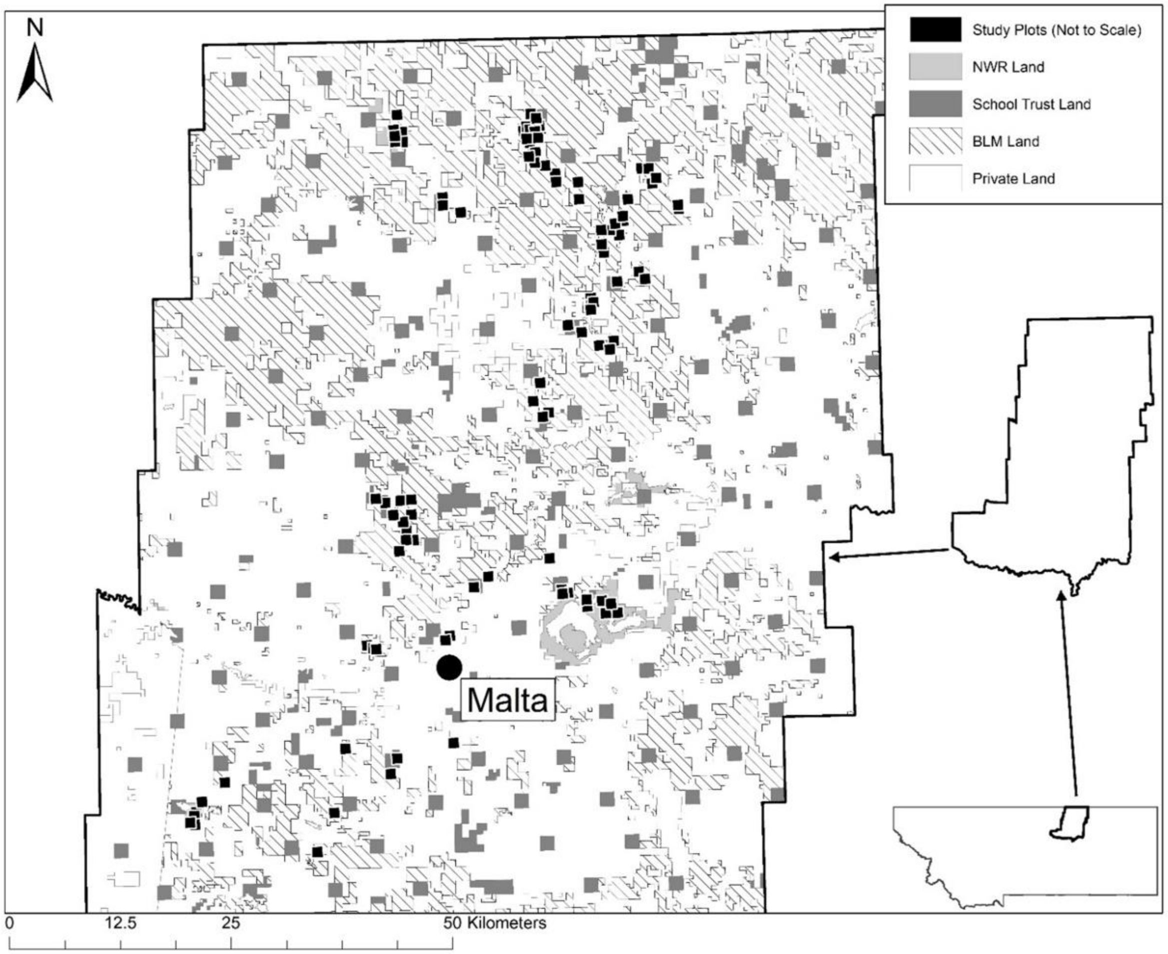

Figure 3. Study plots on Bureau of Land Management (BLM), National Wildlife Refuge (NWR), Montana State Trust (ST) land, and private land in Phillips County, Montana. Inserts show a closeup of some plots in the northern and southern parts of the county.

from one-half hour before sunrise through no later than 1000h MDT. Surveys were not conducted if average wind speed exceeded 25 kph or during rainfall.

To assess vegetation conditions within the survey plots, I generated 15 random points within each of the 100 study plots. I conducted vegetation surveys from late May – July 2017 and 2018. I began by conducting vegetation surveys at five of these points, I then calculated the mean and standard deviation of % grass and used the following equation to determine the necessary sample size needed to accurately represent variation in vegetation measurements within each plot:

$$n = (Z_{\alpha})^2 (s)^2 \div (B)^2$$

where n = the uncorrected sample size, Z_{α} is the standard normal coefficient calculated for a confidence interval of 90% (1.64), s is the sample standard deviation and B is the sample mean multiplied by the desired precision (0.15). With the mean and standard deviation along with standard values for Z_{α} and precision, I calculated the uncorrected sample size. This value was then compared to the table given in Elzinga et al. (1998; Appendix 7) to assess whether sampling effort was sufficient to accurately reflect plot-level variation. If the corrected sample size was greater than the current number of points surveyed, I continued to survey vegetation at additional random points until the necessary sample size was reached to adequately assess plot-level vegetation conditions. I used this formula at each of the 100 plots individually so that each plot had enough vegetation surveys to account for the variability of structure within it, with more variable plots having more surveys. I acknowledge that it would have been more accurate to use the formula for each of the 13 vegetation covariates separately and then use the highest number of surveys called for across all covariates, but logistical constraints on time prevented calculating sampling effort for each individual vegetation measurement. I chose to use grass cover because it was the most abundant cover type.

Prior to vegetation sampling each day, I calibrated my ability to visually estimate biomass within a 20 × 50 cm Daubenmire frame (Daubenmire 1959) by estimating, clipping, and taking the mass of 5–10 samples prior to conducting surveys (Coulloudon et al. 1999). At each vegetation sampling site, I recorded visual obstruction reading (VOR) to the nearest cm from each of the four cardinal directions at a distance and height of 4 m and 1 m, respectively (Robel et al. 1970). I quantified overlapping canopy coverage at random points using 5, 20 × 50 cm Daubenmire frames, with one frame centered on the randomly selected point, and the remaining four placed 0.5 m in each cardinal direction (Winter 1999, Whalley and Hardy 2000). I estimated percent canopy coverages of current growing season grass, residual grass, forbs, shrubs, litter, bare ground, and exotic grass to six coverage bins (0 – 5, 5 – 25, 25 – 50, 50 – 75, 75 – 95, and 95 – 100%). I made a distinction between current growing season grass and residual grass from the previous year because all four of my study species use residual grass in their nest construction. Residual grass cover may also be useful to conceal nests from predators early in the breeding season. Residual grass and litter were distinguished by structure, grass that still maintained an upright stature, similar to what it had when alive was counted as residual grass, grass that was no longer attached to the ground or was lying flat against the ground was included in litter. When evaluating live or residual grass cover both exotic and native grasses were lumped together, but when evaluating exotic grass cover only exotic grasses were included. At each sampling point, I recorded an ocular estimate of the herbaceous biomass, recorded the litter depth, slope (measured with a clinometer), and average height of grass, forbs, and shrubs within the frame.

To establish the relationship between green herbaceous biomass and dry herbaceous biomass, I collected all the standing herbaceous vegetation within the northern Daubenmire frame at the first three plot scale vegetation points in each plot. Samples were placed in paper sacks and stored it in a shed to air dry. Weekly I measured the mass of all the samples and recorded the dry mass of the sample when mass stabilized. I calculated a mean difference between estimated green mass and measured green mass for each field observer and applied that calibration to all estimated samples for each observer to estimate dry mass for each sample (Lipsey and Dreitz 2014).

Statistical Analysis

I built and evaluated binomial N-mixture models of avian abundance to test hypotheses regarding the effects of plot-scale vegetation conditions on the abundance of the four focal species using program R package ‘unmarked’ (Royle 2004; Fiske and Chandler 2011). The binomial N-mixture model simultaneously estimates detection probability and abundance of unmarked individuals identified during spatially replicated counts, operating under the assumption of population closure, where births/deaths and emigration/immigration are equal to zero for the duration of the surveying period (Royle 2004). Because I only measured vegetation conditions previously shown to influence grassland bird abundance or detectability, I used stepwise model selection techniques to identify the factors influencing detection probability and abundance for each grassland bird species. I started with a fully parameterized model including all uncorrelated vegetation predictor variables (Table 1) and eliminated uninformative parameters based on their lack of influence on detection probability or abundance. Submodels related to species-specific detection probabilities were fit prior to fitting models for local abundance. I used Akaike's Information Criterion corrected for small sample size (AIC_c) to compare models and identify important variables to include in the final detection or abundance model for each grassland bird species. Supported models with large model weights (w_i) and AIC_c values ≤ 2 from the best-fit model were considered parsimonious (Burnham et al. 2011). When a supported model differed from the top model by a single parameter, I considered the additional parameter to be uninformative (Arnold 2010).

Table 1: Non corelated variables included in candidate model sets for abundances of Baird's sparrow, chestnut-collared longspur, McCown's longspur, and Sprague's pipit in 100 9-ha plots in Phillips County MT, during May – July of 2017 and 2018.

Model Covariates	Term Description
Detection	
Temperature	Ambient temperature at the time of the survey (°C)
Wind Speed	Wind speed at the time of the survey (kph)
Observer	The technician conducting the survey
Precipitation	Level of precip during survey (fog, or light rain)
Slope	Plot averaged slope (°)
Biomass	Plot averaged dry herbaceous biomass (kg/ha)
Abundance	
Biomass	Plot averaged dry herbaceous biomass (kg/ha)
Biomass SD	Plot specific standard deviation of biomass
Residual Grass Cover	Ground cover of previous growing season grass (%)
Forb Cover	Ground cover of forbs (%)
Shrub Cover	Ground cover of shrubs (%)
Litter Cover	Ground cover of litter (%)
Exotic Grass Cover	Ground cover of exotic grasses (%)

Variables considered to influence detection probability of grassland birds were observer, temperature, cloud cover, wind speed, day of the survey (Julian day), average slope, and biomass within the plot. Plot-averaged biomass and slope were not used in models for Sprague's pipit detection probability as all detections except one for this species were from males singing during their flight display, so ground level conditions like vegetation structure and topography are unlikely to have an effect on detection probability for this species. Vegetation biomass as indexed by visual obstruction reading, grass coverage and height, litter depth, bare ground, and forb and woody vegetation prevalence have previously been cited as important correlates of grassland bird abundance (Grant et al. 2004, Fisher and Davis 2010, Thompson et al. 2014). For each covariate included in detection and abundance submodels, I first evaluated whether a linear, quadratic, or pseudo-threshold effect was best supported for its influence on avian detection probability or abundance and included only the most supported functional form in subsequent analysis (Franklin et al. 1999).

Prior to fitting models, I first tested for multicollinearity among predictor variables by calculating Pearson's correlation coefficient (r) for each combination of vegetation measures. I considered two variables to be correlated if $|r| \geq 0.7$. I found significant correlations between biomass and the heights of live and residual grass (r = 0.87 and 0.80 respectively), as well as exotic cover (r = 0.77), and visual obstruction reading (VOR) (r = 0.93). VOR is a common index of herbaceous biomass and an important determinant of grassland bird abundance (Davis et al. 1999, Madden et al. 2000, Davis 2004, Fisher and Davis 2010). However, biomass is a more common condition informing rangeland management I therefore retained biomass as an independent variable and removed the others from further analyses. I was particularly interested in the effect of exotic grasses on bird abundances, so I retained exotic cover as a covariate but did not include it in any candidate models that also included biomass (Kalnins 2018). Shrub cover was correlated with shrub height (*r* = 0.85); I retained shrub cover as a predictor variable and excluded shrub height due to previously observed associations of grassland birds with shrub coverage (With 1994, Davis et al. 1999, Madden et al. 2000, Davis 2004, Lipsey and Dreitz 2014). Litter cover was inversely correlated with bare ground cover (*r* = -0.71) because litter cover and depth are often associated with bird abundance, I retained litter cover over bare ground cover (Fisher and Davis 2010). I also included the standard deviation of biomass within the plot as a potential covariate representing within plot vegetation heterogeneity. The heterogeneity of vegetation structure has been demonstrated to be related to bird species diversity (Fuhlendorf et al. 2006, Hovick et al. 2014).

Collinearity between biomass and exotic grass cover (*r* = 0.77) prohibited including both terms in the same candidate model. Therefore, I built and evaluated two sets of candidate models for each species, one set containing biomass and one set containing exotic cover. Exotic cover was not correlated with residual grass (*r* = 0.20), forb (*r* = 0.16), shrub (*r* = 0.16), and litter covers (*r* = 0.28). For bird species where an effect of exotic grass cover was supported, I used AIC_c to compare the top model from the biomass model set and the top model from the exotic cover model set to evaluate which effect had more relative support from the data.

An initial screening revealed that detection probabilities of three of my four focal species were highly variable among observers and across species. To reduce the number of parameters in my candidate models, I calculated an average detection probability for all observers for each species, and separated observers into two groups based on their individual detection probabilities relative to the group mean (high detection probability and low detection probability); I combined individual observers into two groups of relative observer skill reduced the number of parameters in detection models from 10 to 1 while retaining potentially important observer effects on detection probability.

I evaluated potential overdispersion in the data by comparing support for three highly-parameterized models, one with a Poisson distribution, one with a negative binomial distribution, and one with a zero-inflated Poisson distribution. Each model included all possible parameters for both detection probability and abundance. Models were then compared using corrected AIC_C, and the most supported error distribution was used for all future models for that species. For Baird's sparrow and Sprague's pipit a Poisson distribution was supported, a zero-inflated Poisson was supported for chestnut-collared longspur, and for McCown's longspurs a negative binomial distribution was supported. After accounting for overdispersion, I used the most parameterized model of abundance for each species to evaluate model fit to the data using the *Nmix.gof.test* function in R package 'AICcmodavg' (Mazerolle 2017). I used 500 simulations to generate a distribution of chi-squared statistics and estimate the variance inflation factor ($\hat{c}$). A $\hat{c} < 2.0$ indicates suitable model fit (Mazerolle 2017).

Results

I conducted 300 point-count surveys at 100 survey points in 2017 and 2018. The largest number of observations overall was chestnut-collared longspur, followed by Baird's sparrow, Sprague’s pipit, and then McCown’s longspur. I observed 304 chestnut-collared longspurs (x̄ per point = 3.04 ± 2.30 SD), 104 Baird’s sparrows (1.04 ± 1.01), 88 Sprague’s pipits (0.88 ± 0.88), and 41 McCown’s longspurs (0.41 ± 0.98).

Across all 100 study plots I conducted a total of 776 vegetation surveys. The observed exotic grasses included crested wheatgrass (*Agropyron cristatum*), smooth brome (*Bromus inermis*), and Kentucky bluegrass (*Poa pratensis*).

Baird’s Sparrow

I detected Baird’s Sparrows at 63 survey plots with an average detection probability of 0.73 (± 0.03 SD). I found support for three models of Baird’s sparrow detection probability (Table 2), which contained an effect of observer and plot-scale slope, but two of the models also included cloud cover and temperature. The probability of detecting a Baird’s sparrow was variable across observers, decreased with average plot slope (β = -0.66 ± 0.23 SE) and cloud cover (β = -0.28 ± 0.16), and increased with ambient temperature during the survey (β = 0.24 ± 0.16). After accounting for variable detection probability, the top model for abundance of Baird’s sparrows included a positive effect of litter cover (β = 0.21 ± 0.09) and residual grass cover (β = 0.20 ± 0.09; Figs 4 and 5; Table 2). The goodness of fit test indicated relatively good model fit for the

Table 2: Model selection results for Baird's sparrow detection and abundance in 100, 9 ha plots in Phillips County, Montana during May – July of 2017 and 2018. The number of parameters (K), AIC_c values, ΔAIC_c values, and model weights (AIC_cWt) are reported.

Detection	K	AIC_c	ΔAIC_c	AIC_cWt
Observer + Slope	4	521.62	0	0.36
Observer + Slope + Cloud Cover	5	521.97	0.35	0.30
Observer + Slope + Cloud Cover + Temp	6	522.35	0.73	0.25
Observer + Julian Day	4	524.73	3.11	0.07
Null	2	526.26	4.64	0.03
Observer + Slope + Temp + Wind + Cloud Cover + Biomass	8	526.55	4.94	0.03
Obs + Julian Day + Slope + Temp + Wind + Cloud Cover + Biomass + Precip	10	530.37	8.76	0.004
Abundance with Biomass				
Litter Cover + Residual Cover	8	514.23	0	0.37
Litter Cover	7	515.73	1.39	0.18
ln(Biomass) + Litter Cover	8	515.97	1.73	0.15
Residual Cover	7	516.95	2.71	0.09
ln(Biomass) + Residual Cover	8	517.25	3.01	0.08
ln(Biomass)	7	518.71	4.47	0.04
ln(Biomass) + Shrub Cover	8	520.65	6.42	0.02
ln(Biomass) + SD Biomass	8	520.65	6.42	0.01
ln(Biomass) + Forb Cover	8	521.44	7.21	0.01
Null	6	522.35	8.12	0.01
ln(Biomass) + Resid Cover + Shrub Cover + Forb Cover	10	522.43	8.20	0.01
Shrub Cover	7	523.03	8.79	0.005
ln(Biomass) + Resid Cover + Shrub Cover + Forb Cover + Litter Cover	12	523.20	8.97	0.004
SD Biomass	7	524.47	10.23	0.002
Forb Cover	7	524.64	10.41	0.002
Abundance with Exotic Cover				
Litter Cover + Residual Cover	6	513.19	0	0.49

Table 2: continued

Abundance with Exotic Cover	K	AIC$_c$	ΔAIC$_c$	AIC$_c$Wt
Litter Cover	5	515.28	2.09	0.17
Residual Cover	5	515.84	2.66	0.13
Exotic Cover + Litter Cover	6	516.71	3.52	0.08
Exotic Cover + Residual Cover	6	517.28	4.1	0.06
Exotic Cover	5	520.61	7.42	0.01
Exotic Cover + Residual Cover + Forb Cover + Shrub Cover + Litter Cover	9	521.28	8.09	0.01
Null	4	521.62	8.43	0.01
Shrub Cover	5	521.75	8.56	0.01
Exotic Cover + Shrub Cover	6	521.76	8.57	0.01
Exotic Cover + Residual Cover + Forb Cover + Shrub Cover	8	521.89	8.7	0.01
Exotic Cover + Forb Cover	6	523.18	9.99	0.003
Forb Cover	5	523.7	10.51	0.003

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

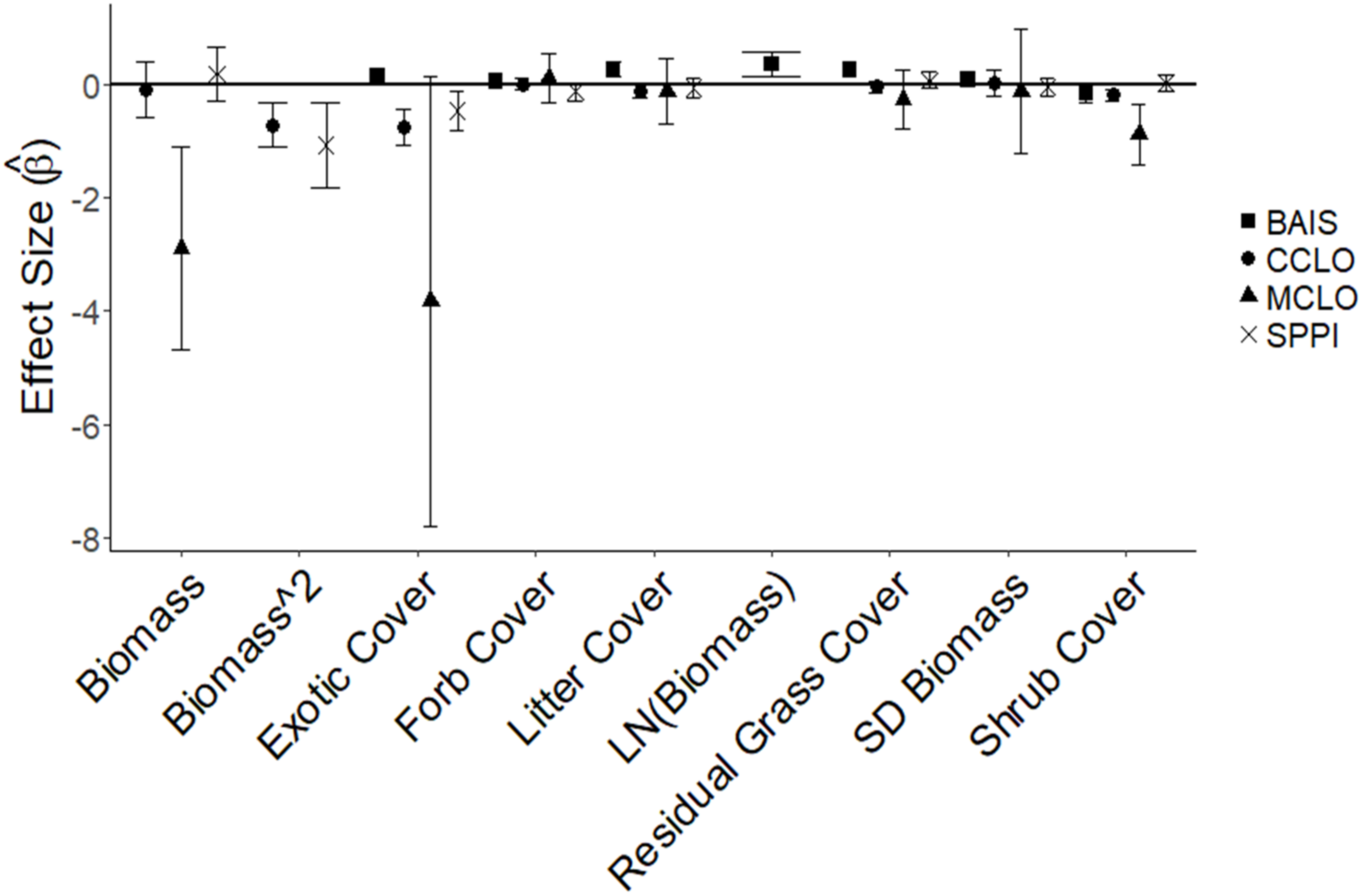

Figure 4. Scaled effect size for covariates with 85% confidence intervals from univariate models on abundances of Baird’s sparrow (BAIS), chestnut-collared longspur (CCLO), McCown’s longspur (MCLO), and Sprague’s pipit (SPPI) in 100 9-ha plots in Phillips county Montana during May – July of 2017 and 2018.

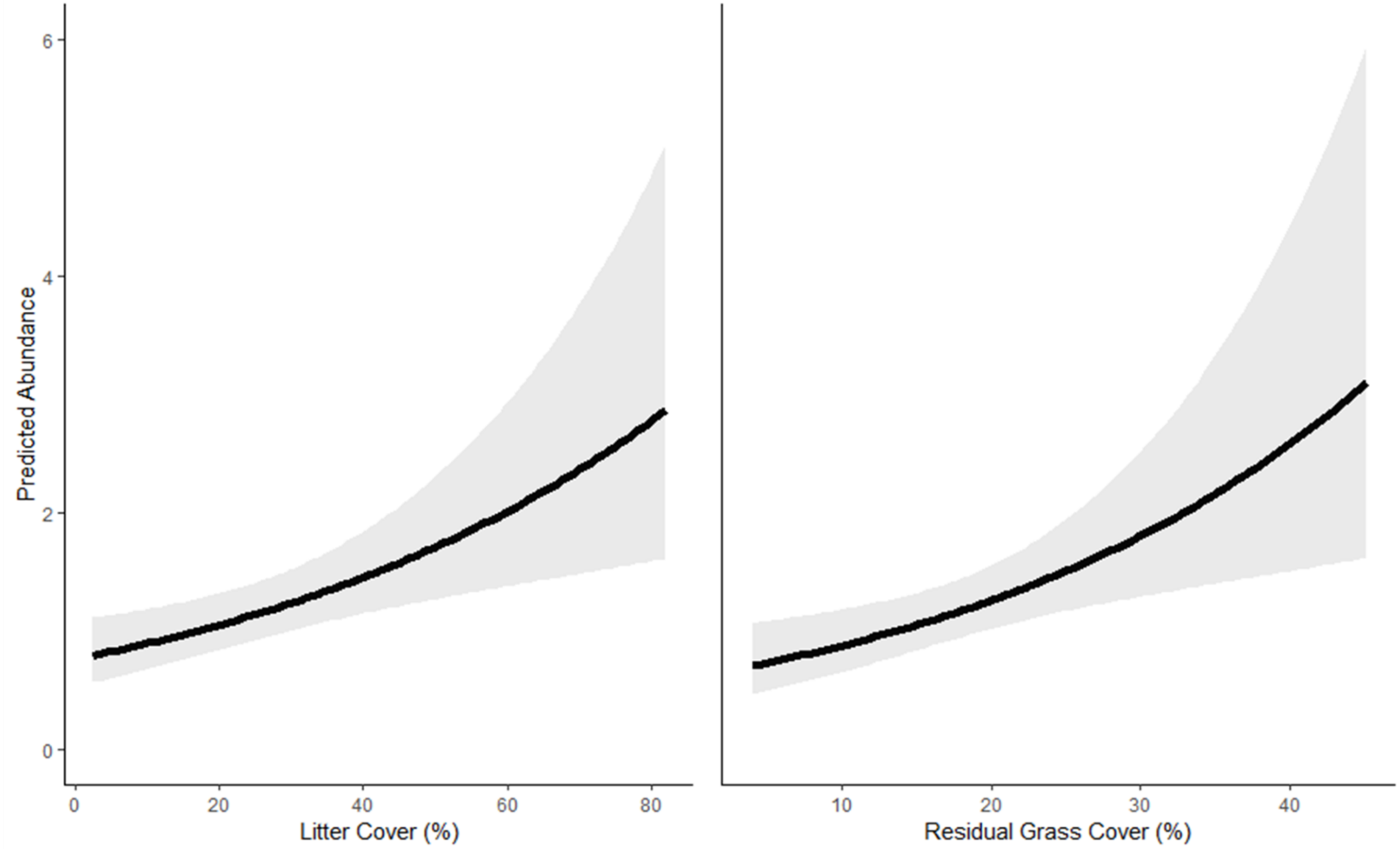

Figure 5. Predicted abundance of Baird’s sparrow as a function of the percent of litter and residual grass cover at the plot scale in 100 9-ha plots in Phillips County, Montana during May – July of 2017–2018. Shaded regions represent 95% confidence intervals.

global model ($\chi^2 = 235.95$, $\hat{c} = 0.85$, $p = 0.92$). A candidate model set where exotic grass cover replaced biomass yielded similar results; Baird's sparrow abundance increased with both residual and litter cover, and an effect of exotic grass cover had little support ($\Sigma w_i = 0.18$; Table 2).

Chestnut-collared Longspur

I detected chestnut-collared longspurs at 80 survey plots. The average (± SE) probability of detecting a chestnut-collared longspur was 0.56 ± 0.05. The top model for detection had 70% of the relative support of the data and included terms for cloud cover, observer, plot-scale biomass, slope, and temperature (Table 3); however the 85% confidence intervals about the coefficient estimates for temperature and slope overlapped zero (-0.07 – 0.24 and -0.33 – 0.12 respectively; Table 3). The probability of detecting a chestnut-collared longspur decreased with cloud cover ($\beta = -0.31 \pm 0.10$) and biomass ($\beta = -0.94 \pm 0.20$). After accounting for imperfect and variable detection probability, a model that included a quadratic effect of biomass and linear effects of shrub and residual grass cover had 97% of the relative support (Table 3). Residual grass cover ($\beta = -0.17 \pm 0.08$) and shrub cover ($\beta = -0.27 \pm 0.07$) were negatively associated with local abundance. Local abundance was maximized when herbaceous biomass was ca. 1300 kg ha^{-1} (Figs. 4 and 6). The goodness of fit test indicated good fit of the global model ($\chi^2 = 333.09$, $\hat{c} = 0.96$, $p = 0.61$).

Table 3: Model selection results for chestnut-collared longspur detection and abundance in 100, 9 ha plots in Phillips County, Montana during May – July of 2017 and 2018. The number of parameters (K), AIC_C values, ΔAIC_C values, and model weights (AIC_CWt) are reported.

Detection	K	AIC_c	ΔAIC_c	AIC_cWt
Temp + Observer + Biomass + Slope + Cloud Cover	8	962.58	0	0.70
Temp + Observer + Biomass + Slope + Cloud Cover + Precipitation	9	965.38	2.74	0.17
Temp + Observer + Biomass + Slope	7	966.77	4.19	0.09
Observer + Julian Day	5	970.13	7.55	0.02
Null	3	970.45	7.86	0.01
Temp + Obs + Biomass + Slope + Cloud Cover + Precip + Wind + Julian Day	11	971.43	8.84	0.008
Abundance with Biomass				
Biomass + $Biomass^2$ + Residual Grass Cover + Shrub Cover	10	936.69	0	0.97
Biomass + $Biomass^2$ + SD Biomass + Resid + Shrub + Forb + Litter	13	943.95	7.26	0.03
Biomass + $Biomass^2$	8	747.12	10.44	0.005
Biomass + $Biomass^2$ + Litter Cover	9	948.74	12.06	0.002
Forb Cover + Litter Cover + Shrub Cover	9	950.52	13.83	< 0.001
Litter Cover	7	957.59	20.91	< 0.001
Null	6	957.83	21.02	< 0.001
Shrub Cover	7	959.45	22.76	< 0.001
Residual Grass Cover	7	960.08	23.40	< 0.001
SD Biomass	7	960.51	23.83	< 0.001
Forb Cover	7	960.54	23.86	< 0.001
Abundance with Exotic Cover				
Exotic Cover + Residual Grass Cover + Forb Cover + Shrub Cover + Litter Cover	11	945.33	0	0.55
Exotic Cover + Residual Grass Cover + Shrub Cover	9	946.85	1.52	0.26
Forb Cover + Shrub Cover + Litter Cover	9	948.02	2.68	0.14

Table 3: continued

Abundance with Exotic Cover	K	AIC_c	ΔAIC_c	AIC_cWt
Exotic Cover + Litter Cover	8	950.88	5.55	0.03
Exotic Cover	7	953.28	7.95	0.01
Litter Cover	7	956.14	10.81	0.002
Null	6	956.78	11.45	0.002
Shrub Cover	7	958	12.67	0.001
Residual Grass Cover	7	958.63	13.3	0.001
Forb Cover	7	959.09	13.76	0.001

^{2} Variable indicates a quadratic effect

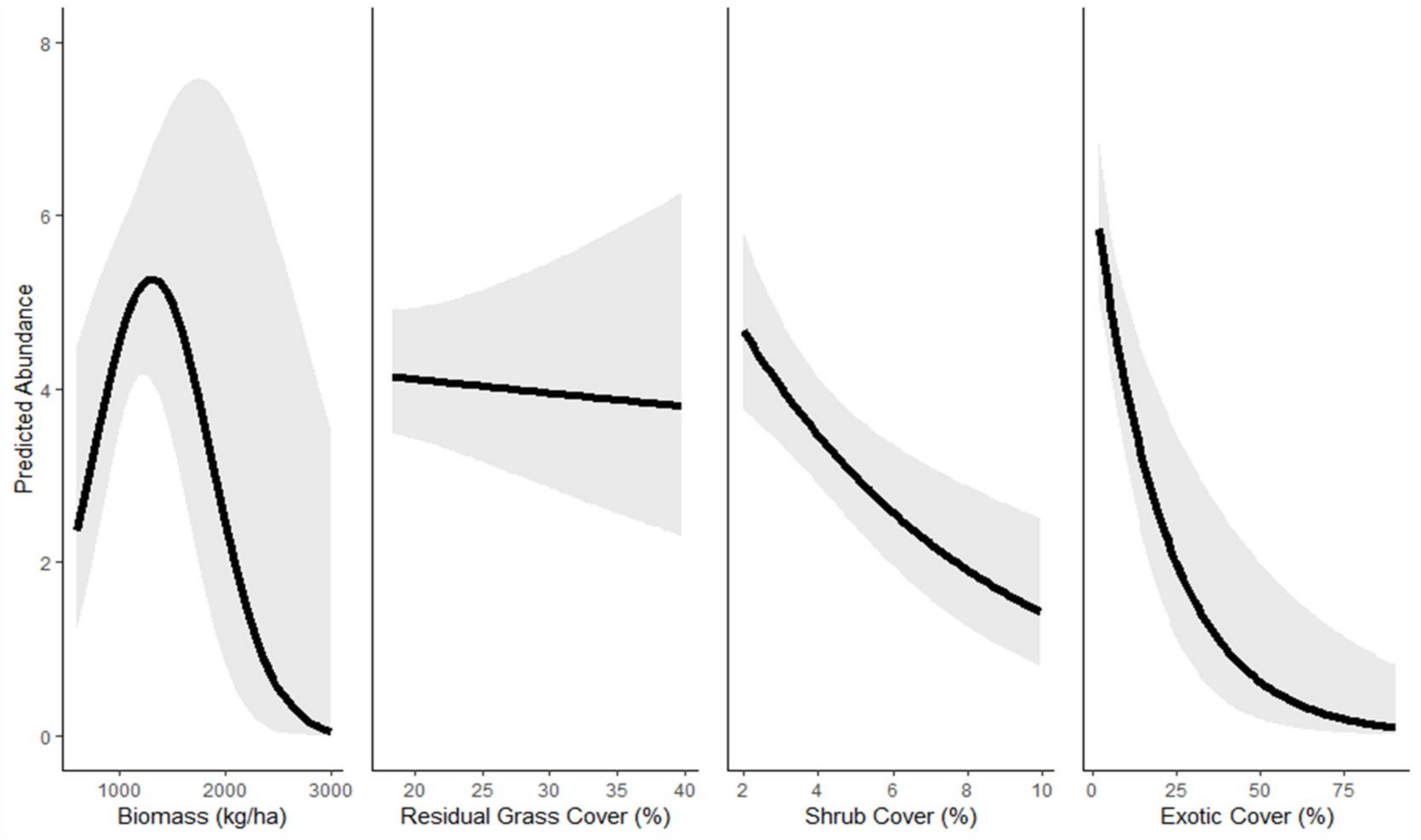

Figure 6. Predicted abundance of chestnut-collared longspur adults as a function of plot averaged biomass and coverage of residual grass and shrubs shaded regions in Phillips County, Montana during May – July of 2017–2018. Shaded areas represent 95% confidence intervals.

When running the analysis with the exotic cover model set, I found support for two models of abundance ($\Delta AIC_C = 1.52$; Table 3) containing effects for the percent cover of exotic grasses, residual grasses, forbs, shrubs, and litter. However, 85% confidence intervals around the effects for residual grass cover (-0.21 – 0.03) and forb cover (-0.17 – 0.07) overlapped 0 and considered uninformative. The abundance of chestnut-collared longspurs declined with exotic cover ($\beta = -0.75 \pm 0.21$SE), shrub cover ($\beta = -0.24 \pm 0.07$), and litter cover ($\beta = -0.19 \pm 0.09$). The quadratic effect of biomass on the local abundance of chestnut-collared longspurs was much more informative than exotic grass; the top model for the set including biomass had 49 times (0.98/0.02) more support than the top model in the exotic grass model set (Table 4).

McCown's Longspur

I detected McCown's longspurs at 22 sites with an average detection probability of 0.44 (± 0.10 SE). The top model for McCown's longspur detection had 68% of the relative support of the data and included terms for cloud cover, wind speed, and plot biomass. The probability of detecting a McCown's longspur was negatively influenced by cloud cover ($\beta = -0.98 \pm 0.49$ SE), wind speed ($\beta = -0.60 \pm 0.37$), and biomass ($\beta = -2.61 \pm 0.86$; Table 5). After accounting for probability of detection, three models of McCown's abundance were supported (Table 5). All three models included an effect of shrub cover, two included an effect of biomass, and the last also had an effect of litter cover. However, an 85% confidence interval on the effect of litter cover on local abundance overlapped 0 (-0.97 – 0.16), suggesting the factor was uninformative. The

Table 4. Model selection results of top models from biomass candidate model set and exotic cover candidate model set for chestnut-collared longspur abundance in 100 9-ha plots in Phillips County, Montana during May – July of 2018 and 2018. The number of parameters (K), AIC_c values, ΔAIC_c values, and model weights (AIC_cWt) are reported.

	K	AIC_c	ΔAIC_c	AIC_cWt
Biomass + $Biomass^2$ + Shrub Cover + Residual Grass Cover	10	936.69	0	0.98
Exotic Cover + Shrub Cover + Litter Cover	9	944.09	7.40	0.02

^{2} Variable indicates a quadratic effect

Table 5: Model selection results for McCown’s longspur detection and abundance in 100, 9 ha plots in Phillips County, Montana during May – July of 2017 and 2018. The number of parameters (K), AIC_C values, ΔAIC_C values, and model weights (AIC_CWt) are reported.

Detection	K	AIC_c	ΔAIC_c	AIC_cWt
Cloud Cover + Wind + Biomass	6	270.27	0	0.68
Cloud Cover + Wind + Biomass + Temperature	7	272.64	2.36	0.21
Cloud Cover + Wind + Biomass + Temperature + Slope	8	275.09	4.81	0.06
Null	3	277.08	6.81	0.02
Cloud Cover + Wind + Biomass + Temperature + Slope + Precipitation	9	277.96	7.69	0.01
Julian Day	4	278.97	8.69	0.009
Cloud Cover + Wind + Biomass + Temp + Slope + Precip + Obs + Julian Day	11	284.72	14.00	< 0.001
Abundance with Biomass				
Shrub Cover + Biomass	8	265.21	0	0.36
Shrub Cover	7	265.88	0.67	0.26
Shrub Cover + Biomass + Litter Cover	9	267.16	1.95	0.14
Biomass	7	268.3	3.08	0.08
Shrub Cover + Biomass + Litter Cover + Forb Cover	10	270.05	4.84	0.03
Null	6	270.27	5.06	0.03
Biomass + Forb Cover	8	270.61	5.39	0.02
Biomass + Residual Cover	8	270.62	5.41	0.02
Biomass + Litter Cover	8	270.09	5.87	0.02
Residual Cover	7	272.38	7.17	0.01
Forb Cover	7	272.87	7.66	0.008
Litter Cover	7	272.89	7.68	0.008
SD Biomass	7	276.16	10.95	0.002
Shrub Cover + Biomass + Litter Cover + Forb Cover + Residual Cover + SD Biomass	12	276.16	10.95	0.002

Table 5 continued

Abundance with Exotic Cover	K	AIC_c	ΔAIC_c	AIC_cWt
Shrub Cover	7	265.88	0	0.32
Exotic Cover + Shrub Cover	8	266.1	0.22	0.29
Exotic Cover + Shrub Cover + Litter Cover	9	267.19	1.31	0.17
Exotic Cover	7	269.35	3.47	0.06
Null	6	270.27	4.39	0.04
Exotic Cover + Forb Cover + Shrub Cover + Litter Cover	10	270.31	4.42	0.04
Exotic Cover + Residual Cover	8	271.51	5.63	0.02
Exotic Cover + Litter Cover	8	271.83	5.95	0.02
Exotic Cover + Forb Cover	8	272.19	6.31	0.01
Residual Cover	7	272.38	6.5	0.01
Exotic Cover + Residual Cover + Forb Cover + Shrub Cover + Litter Cover	11	272.78	6.9	0.01
Forb Cover	7	272.87	6.99	0.01
Litter Cover	7	272.89	7.00	0.01

local abundance of McCown's longspurs was negatively associated with both shrub cover (β = -0.81 ± 0.36) and biomass (β = -2.36 ± 1.18; Figs 4 and 7). The goodness of fit test indicated relatively good model fit for the global model ($\chi^2 = 313.58$, $\hat{c} = 1.09$, $p = 0.2$).

A set of candidate models with exotic cover instead of biomass gave similar results, there was equal support for three models for abundance of McCown's longspur (Table 5), all including exotic cover and one also including shrub cover and the other including litter cover (Table 5). The 85% confidence intervals for the effects of exotic cover (-7.09 – 0.96) and litter cover (-1.10 – 0.02) overlap 0. McCown's longspur abundance declined with shrub cover (β = -0.89 ± 0.37).

Sprague's Pipit

Sprague's pipits were detected at 59 sites with an average detection probability of 0.66 (± 0.04 SE). I found support for three models evaluating variation in Sprague's pipit detection probability (Table 6), all of which contained an effect of observer but with two containing temperature and one containing cloud cover; 85% confidence intervals on the effect of cloud cover overlapped 0 (-0.02 – 0.60) so this effect was considered uninformative. Accounting for detection probability, I found support for three models of Sprague's pipit abundance (Table 6). All models contained a quadratic form of biomass, with one also containing residual grass cover and another also containing forb cover. The 85% confidence intervals on the effects of residual grass and forb covers overlapped 0 (-0.01 – 0.37, and -0.33 – 0.02 respectively), I therefore considered these factors to be uninformative. Local abundance of Sprague's pipits was maximized when plot-level

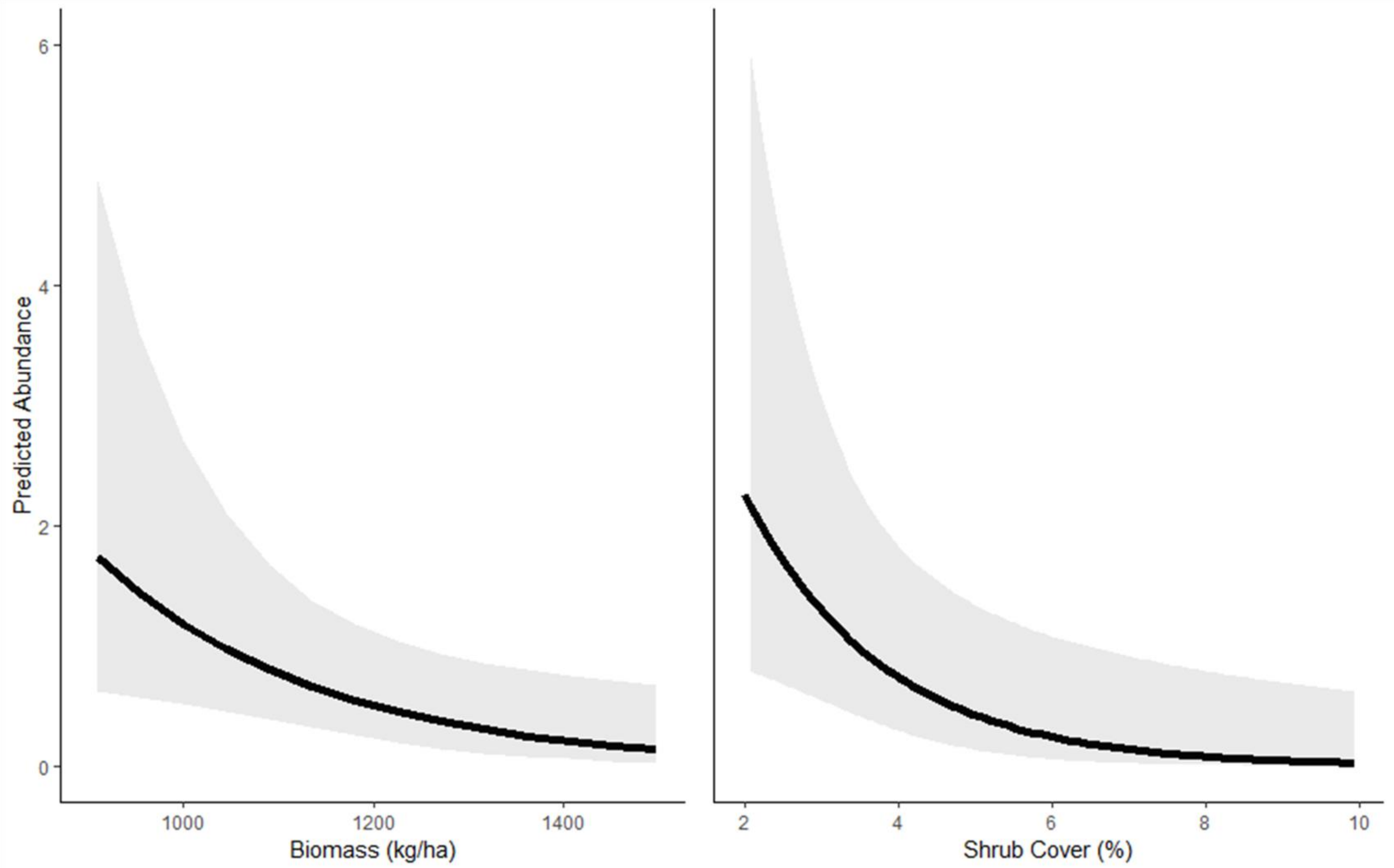

Figure 7. Predicted abundance of McCown’s longspurs as a function of plot scale biomass and shrub cover in Phillips County, Montana during May – July of 2017–2018. Shaded regions represent 95% confidence intervals.

Table 6. Model selection results for Sprague's pipit detection and abundance in 100, 9 ha plots in Phillips County, Montana during May – July of 2017 and 2018. The number of parameters (K), AIC_C values, ΔAIC_C values, and model weights (AIC_CWt) are reported.

Detection	K	AIC_c	ΔAIC_c	AIC_cWt
Observer	3	497.57	0	0.38
Observer + Temperature	4	498.06	0.49	0.30
Observer + Temperature + Cloud Cover	5	498.89	1.32	0.20
Observer + Temperature + Cloud Cover + Precipitation	6	501.03	3.46	0.068
Null	2	502.45	4.87	0.033
Julian Day	3	504.71	7.14	0.009
Observer + Temperature + Cloud Cover + Precipitation + Wind + Julian Day	8	506.05	8.48	0.005
Abundance with Biomass				
Biomass + $Biomass^2$	6	485.71	0	0.34
Biomass + $Biomass^2$ + Residual Cover	7	486.49	0.77	0.23
Biomass + $Biomass^2$ + Forb Cover	7	486.76	1.05	0.20
Biomass + $Biomass^2$ + Shrub Cover	7	488.19	2.48	0.10
Biomass + $Biomass^2$ + Litter Cover	7	488.24	2.52	0.10
Biomass + $Biomass^2$ + Forb Cover + Litter Cover + Shrub Cover	9	491.16	5.44	0.02
Biomass + $Biomass^2$ + Forb Cover + Litter Cover + Shrub Cover Residual Cover + SD Biomass	11	494.71	9.00	0.003
Null	4	497.69	11.98	< 0.001
Forb Cover	5	498.44	12.73	< 0.001
Litter Cover	5	499.62	13.91	< 0.001
Residual Cover	5	499.83	14.12	< 0.001
SD Biomass	5	499.88	14.17	< 0.001
Shrub Cover	5	500.09	14.37	< 0.001
Abundance with Exotic Cover				
Exotic Cover	5	492.95	0	0.32

Table 6: continued

Abundance with Exotic Cover	K	AIC_c	ΔAIC_c	AIC_cWt
Exotic Cover + Forb Cover	6	493.95	1.00	0.20
Exotic Cover + Residual Cover	6	493.95	1.01	0.20
Exotic Cover + Litter Cover	6	495.52	2.58	0.09
Exotic Cover + Shrub Cover	6	495.54	2.59	0.09
Null	4	497.69	4.75	0.03
Forb Cover	5	498.44	5.50	0.02
Exotic Cover + Forb Cover + Shrub Cover + Litter Cover	8	498.28	6.33	0.01
Litter Cover	5	499.62	6.68	0.01
Residual Cover	5	499.83	6.89	0.01
Shrub Cover	5	500.09	7.14	0.01
Exotic Cover + Residual Cover + Forb Cover + Shrub Cover + Litter Cover	9	500.75	7.80	0.01

[2] Variable indicates a quadratic effect

biomass averaged 1400 kg ha^{-1} (Figs 4 and 8). The goodness of fit test indicated very good model fit: estimated $\chi^2 = 261.68$, $\hat{c} = 0.99$, $p = 0.52$.

Using exotic cover in place of biomass, I found support for three models (Table 6), all including exotic cover but two also including residual grass cover and forb cover respectively, however 85% confidence intervals around the effect sizes of these last two parameters overlap 0 (forb cover: -0.33 – 0.02, residual cover: -0.02 – 0.33) suggesting these terms are uninformative. Sprague's pipit abundance declined with exotic cover ($\beta = -0.48 \pm 0.24$). The quadratic effect of biomass on local abundance of Sprague's pipits were much more informative than that of exotic grass; the top model from the set including biomass had 32 times (0.97/0.03) more support from the data than the top model in the exotic grass model set (Table 7).

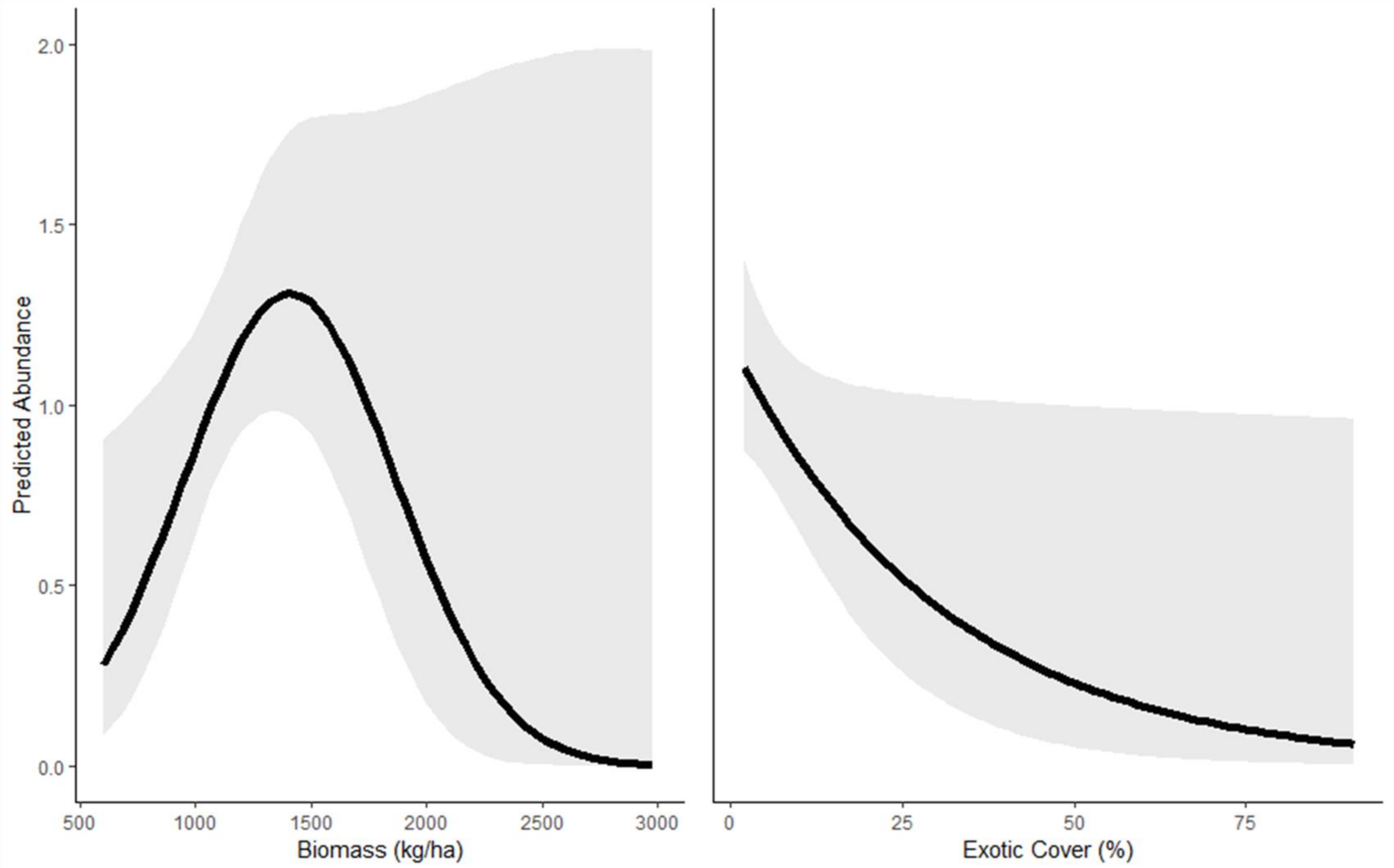

Figure 8. Predicted abundance of Sprague’s pipits as a function of plot scale biomass in Phillips County, Montana during May – July of 2017–2018. Shaded regions represent 95% confidence intervals.

Table 7. Model selection results of top models from biomass candidate model set and exotic cover candidate model set for Sprague's pipit abundance in 100 9-ha plots in Phillips County, Montana during May – July of 2018 and 2018. The number of parameters (K), AIC_C values, ΔAIC_C values, and model weights (AIC_CWt) are reported.

	K	AIC_c	ΔAIC_c	AIC_cWt
Biomass+Biomass[2]	6	485.71	0	0.97
Exotic Cover	5	492.95	7.23	0.03

[2] Variable indicates support for a quadratic effect

Discussion

Generally, the local abundances of Baird's sparrows, chestnut-collared longspurs, McCown's longspurs, and Sprague's pipits were associated with biomass, residual grass cover, litter cover, and shrub cover, but direction and magnitude of these effects varied among species. Baird's sparrow abundance was positively associated with litter cover and residual grass cover. The abundance of chestnut-collared longspurs was negatively associated with residual grass cover and shrub cover and had a quadratic relationship with biomass, with abundance reaching a maximum around 1300 kg ha^{-1}. McCown's longspur abundance was negatively associated with biomass and shrub cover. The abundance of Sprague's pipits was maximized with a biomass of approximately 1400 kg ha^{-1}.

The observed effects of biomass on abundance of chestnut-collared longspurs, McCown's longspurs, and Sprague's pipit are consistent with previous studies (Davis et al. 1999, Madden et al. 2000, Green et al. 2002, Davis 2005, With 2010, Davis et al. 2014, Lipsey 2015). McCown's longspurs showed the strongest disassociation with plot-scale biomass, with chestnut-collared longspurs and Sprague's pipits showing a quadratic relationship with biomass around an apparent preferred level, and pipits having a slightly higher preferred biomass than the longspurs. The quadratic relationship between biomass and Sprague's pipit abundance is consistent with previous studies (Madden et al. 2000), but the relationship has not been previously observed in chestnut-collared longspurs. Conceptually, the relationship between local abundance of all four of my study species and biomass is likely quadratic in nature, with each species preferring a window of biomass (Knopf 1996). However, successfully observing this relationship requires surveying across a full range of biomass, including not only areas where the species occurs but also areas that are too bare and too dense for occurrence. Thus, the effect sizes documented in my study are only appropriate for evaluating vegetation relationships in areas already determined to be suitable for focal species. Future studies interested in observing the full scope of this relationship for McCown's longspurs will likely need to survey areas of extremely sparse vegetation, as this species has been observed to occupy fallow fields in northern Montana (personal observation).

In contrast to previous work, I found no relationship between biomass and Baird's sparrow abundance (Madden et al. 2000, Sliwinski and Koper 2015). This may be because I did not survey plots with enough variation in biomass to observe changes in Baird's sparrow abundance. However chestnut-collared longspur are known to prefer sparser vegetation than Baird's sparrow and was my most commonly observed species, suggesting that plots captured at least the lower end of Baird's sparrow biomass preference (Sliwinski and Koper 2015). While most studies don't directly evaluate plot biomass, it is common to use VOR as a biomass index. Madden et al. (2000) observed Baird's sparrow occurrence declined when VOR exceeded 10 cm suggesting that this is the upper limit of Baird's sparrow preference. However, I surveyed plots with average VOR as high as 40 cm. A more likely explanation then, is that while overall herbaceous biomass may be important, the specific structure of vegetation may be more important. My biomass estimates included all standing herbaceous vegetation, including residual grass. The relative support for residual grass cover over biomass suggests that this structural form is more important to Baird’s sparrow abundance than other biomass contributors such as live grass or forbs.

The difference between chestnut-collared longspurs apparent preference for relatively sparse vegetation and the Baird’s sparrows’ preference for denser vegetation is also reflected in the contrasting impact of residual grass cover for these species. Baird’s sparrows had a positive association with residual grass while chestnut-collared longspurs had a negative association. My findings are consistent with the work of Davis et al. (1999) who found that on native prairie in southern Saskatchewan, Baird’s sparrow abundance was associated with higher density of grasses, whereas chestnut-collared longspurs were associated with lower density of grasses. In North Dakota, Madden et al. (2000) also found a positive association between Baird’s sparrow occurrence and plot grass cover.

I found a positive association between litter cover and Baird’s sparrow abundance. The role of litter cover in bird habitat use is not well understood (Fisher and Davis 2010). This species may be taking litter cover as a sign of improved nutrient cycling and good range health overall (Pyke et al. 2002). Alternatively, Baird’s sparrows may be using litter cover as a more direct index for arthropod availability (Bultman and Uetz 1984).

All four species have previously been found to disassociate with shrubs (With 1994, Davis 2005, Lipsey et al. 2016). However, I only observed a significant negative effect of shrub cover on abundances of chestnut-collared longspur and McCown’s longspur. I did not find support for an effect of shrub cover on the abundance of Baird’s sparrow or Sprague’s pipits, which may be due to a limited range of shrub coverage across study plots; shrub cover never exceeded 10% on any plot. When Madden et al. (2000) observed a negative association with shrub cover they surveyed sites with shrub coverage from 0 – 90%. Other studies that demonstrated a negative association with shrubs used different methods to quantify shrub presence on study sites such as recording distance to nearest shrub (Davis et al. 1999, Davis 2004) making it difficult to assess how their study sites compared with mine. Nevertheless, shrub cover of less than 10% did not negatively affect the local abundance of Baird’s sparrows and Sprague’s pipits on my study area.

Findings related to the effect of exotic grasses on the abundance and demography of my focal species have been inconsistent (Lloyd and Martin 2005, Davis et al. 2016). The correlation between biomass and exotic cover in my data makes it difficult to interpret the effects of exotic vegetation on the abundance of my species. Alternative model comparison using models with exotic cover but not biomass found support for negative effects of exotic cover on chestnut-collared longspurs and Sprague’s pipits, but I cannot say with certainty that these patterns are not influenced by differences in biomass across plots. It should also be noted that while some of my study plots were uniformly non-native, many were combinations of native and non-native grasses being native pasture where exotic grasses had encroached. Previous studies into the effects of non-native grasses typically studied more homogenous planted fields (Lloyd and Martin 2005, Davis et al. 2016). This mix of exotic and native grasses in my study plots could have mitigated any effect of exotic grasses on bird abundances.

The probability of detection for all our focal species was significantly less than perfect, giving good evidence that inference that does not account for imperfect detection may be biased. I found evidence for an effect from both survey specific factors (cloud cover, wind speed, observer) and site-specific factors (biomass and slope) on detection. The effects of cloud cover, wind speed, and observer are consistent with assumptions of standard point count protocols (e.g. don’t survey in very high speed wind, training for technicians is very important) and have also been empirically observed (Ralph et al. 1993, Diefenbach et al. 2003, Thompson et al. 2016). Contrary to some previous studies I found no support for an effect of Julian day on detection (Thompson et al. 2016). This is likely due to the relatively brief window of time between our first and last point count survey within each season. I completed all of our point counts within one-week periods during both survey years. Buskirk and McDonald (1995) also did not observe a difference in detection between survey days when conducting point count surveys in Indiana within a 13-day period.

The effect of the plot slope and biomass on detection probability have some interesting implications for future studies. I found that slope was only an important factor for Baird’s sparrow detection. My results suggest that biomass can negatively impact detection for both chestnut-collared and McCown’s longspurs. Given Sprague’s pipits long duration aerial display I did not expect biomass to influence their detection, but the lack of an effect of biomass on the detection of Baird’s sparrows is more surprising. Biomass, typically indexed by VOR, is a common covariate in grassland bird habitat studies (Madden et al. 2000, Davis 2005, Fisher and Davis 2010), but an effect of biomass on detection for grassland birds could confound the true relationship between biomass and abundance if its effect is not taken into account.

Future research should anticipate less than perfect and spatially variable detection for these species. While the effects of weather and observer skill on detection can be mitigated with survey restrictions during certain weather conditions and extensive technician training respectively, the effects of local topography and vegetation will be harder to control. In the likely event that researchers cannot limit their study sites to flat bare areas, topography and biomass should be measured and these measurements used to correct for their impact on detection. Researchers interested in establishing the preferred range of biomass for each species will need to ensure that they are surveying across a gradient of biomass that encompasses the suspected preference for their species of interest. In the case of McCown's longspur this may require including some fallow fields in the study sites. To separate the effects of biomass and exotic grasses researchers will need to survey sites with highly variable biomass and exotic cover to avoid correlation between these effects.

Management Implications

My results and those of previous studies suggest that McCown's and chestnut-collared longspurs prefer areas with relatively sparse vegetation and few shrubs. Pastures managed to consist of roughly 1300 kg ha^{-1} of herbaceous biomass during the nesting season will benefit chestnut-collared longspurs. Sprague's pipits seem to prefer pastures with approximately 1400 kg ha^{-1}. Baird's sparrows prefer areas with high amounts of residual grass and litter cover. Chestnut-collared longspurs and Sprague's pipits may also be disassociated with the encroachment of exotic grasses, but that assertion still requires further study.

Promoting habitat with the apparent ideal biomass for chestnut-collared longspur or Sprague's pipits would require controlling disturbance to the pasture either in the form of livestock grazing or controlled burning, although grazing vegetation down to a target level is probably a more practical method than burning an area and anticipating that vegetation will grow back to desired levels by the following breeding season. Biomass is influenced not only by disturbance but also by soil productivity, precipitation, and the local plant community. The ideal livestock stocking rate in a given area to reach targeted biomass will therefore depend on the local ecological site type and soil productivity. Stocking rates will also need to vary temporally to compensate for variation in annual precipitation and transition between ecological states (Lipsey and Naugle 2016). The northern mixed-grass prairie has a mix of cold season and warm season grasses and of bunch grasses and sod-forming grasses. The relative dominance of a given grass species or growth form can have implications for the biomass of that area, for example, areas dominated by taller bunchgrasses may have more biomass overall than those dominated by sod-forming grasses. Areas dominated by cool season grasses will begin producing biomass as early as April 1st, well before breeding begins for study species, allowing for an early boost to local biomass (National Resource Conservation Service 2019). Current and historic management and recent drought or fire can change the local plant community and impact future biomass production and how the area will respond to grazing. State and transition models (Stringham et al. 2003) supplied by the NRCS, can aid managers in anticipating how fire, precipitation, and grazing will interact with the local plant community.

One advantage of controlled burning is a reduction in woody plant encroachment, which is beneficial to chestnut-collared and McCown's longspurs (Bragg and Hulbert 1976, Van Auken 2009). However, burning will reduce litter cover as well, and so may be detrimental to Baird's sparrow abundance in the first year post-burn. Promoting habitat for all four species with the same management strategy may not be possible at a fine scale but promoting structural heterogeneity across a pasture may benefit species with disparate habitat needs (Fuhlendorf et al. 2006, Hovick et al. 2014). Given that controlled burns are generally viewed negatively in the region (Sliwinski 2017) controlled grazing may the more palatable option for managers to promote or maintain structural heterogeneity.

CHAPTER THREE

EFFECTS OF VEGETATION CONDITIONS ON NEST DENSITY AND NEST SURVIVAL OF NORTHERN MIXED-GRASS PRAIRIE SONGBIRDS

Introduction

Grassland bird populations in the Great Plains have declined more severely than any other avian group during the past 40 years (North American Bird Conservation Initiative 2014, Sauer et al. 2015). This decline is often attributed to the degradation and fragmentation of grassland habitats due to conversion to row crop agriculture and the encroachment of shrubs and exotic plants (Samson et al. 2004, Hoekstra et al. 2005). In the northern mixed-grass prairies, four species of grassland songbird are of particular interest for conservation and management due to their severe rates of population decline. Baird's sparrows (*Centronyx bairdii*), chestnut-collared longspurs (*Calcarius ornatus*), McCown's longspur (*Rynchophanes mccownii*), and Sprague's pipits (*Anthus spragueii*) are all experiencing annual population declines of 2.9 – 6.2% (Sauer et al. 2015). One possible reason for this decline may be low nest survival resulting from high rates of nest predation or paucity of appropriate nesting habitat (Davis and Sealy 1998, Davis 2005). Land management strategies aimed at counteracting these declines need to maximize habitat supporting large numbers of at-risk species successfully producing offspring.

Previous research on vegetation associations of grassland songbirds typically evaluate vegetation conditions at the nest-site and a few random points or transects immediately adjacent to the nest (Winter 1999, Davis 2005, Davis et al. 2016).

Evaluating vegetation at this fine scale is of limited utility to managers interested in improving habitat for at risk species. To assist managers, there is a need for an evaluation of associations between birds and vegetation conditions at scales large enough for reasonable implementation of management.

The structure and composition of vegetative ground cover has been shown to influence reproductive effort and success (Davis 2005, Lipsey and Dreitz 2014). Grass is used as a nest substrate, whereas forbs and shrubs provide concealment from predators or perch points for singing males. The value of plant litter to bird habitat is less understood but litter may be associated with improved nutrient cycling, soil retention, and better rangeland health (Pyke et al. 2002). Plant vertical height and density may also allow for concealment from predators. Vegetation structure and composition naturally vary in most grassland ecosystems due to spatial and temporal variation in soils, topography, precipitation, and disturbances (Fuhlendorf and Engle 2001, Lipsey and Naugle 2016). Many grassland bird species have evolved to specialize in specific niches on a landscape with spatially and temporally varying vegetation conditions (Knopf 1996). It is therefore unlikely that a single optimal condition for all grassland bird species exists. Previous studies suggest that biomass and horizontal and vertical cover are associated with nest density of many grassland birds, though the direction and magnitude of associations vary across species (Sutter 1997, Davis 2005, Lipsey and Dreitz 2014). Evidence for associations between plant structure and nest survival for these species is less conclusive (Davis 2005). A study of grassland birds outside of the northern-mixed grass prairie also found some evidence that the local topography may influence nest placement and weak evidence that it may influence nest survival (Frey et al. 2008).

In addition to local vegetation structure, plant composition may also play a role in reproductive success of grassland birds. Exotic grasses have been intentionally introduced throughout the northern Great Plains due to their higher nutritive value to livestock and greater tolerance for drought and cold (Lesica and DeLuca 1996). Exotic vegetation in the pasture may negatively impact bird reproductive output though studies on this effect have produced inconsistent results (Lloyd and Martin 2005, Davis et al. 2016). Grassland birds nesting in exotic grass fields can experience higher predation rates, lower renesting rates and fewer fledged juveniles per nest (Lloyd and Martin 2005, Davis et al. 2016).

The suitability or quality of habitat for breeding grassland birds is often inferred from the associations between fine-scale vegetation conditions at nest sites and nest survival, under the assumption that higher nest survival translates to higher bird productivity in the population (Davis 2003, Lloyd and Martin 2005). Recommendations for habitat management based solely on nest survival may be inappropriate for grassland bird conservation, however, if the vegetation conditions influencing pasture-level nest density differ from local conditions affecting nest survival. Vegetation conditions associated with increased nest density may be more important for population-level productivity than those associated with nest survival because productivity of a unit area is determined by a combination of nest density and nest success (Bock and Jones 2004). Thus, nest density and survival should be studied simultaneously to infer habitat drivers of grassland bird productivity and to test assumptions of nest survival as an appropriate index for evaluating the effects of habitat management on population productivity.

To address the gaps in knowledge related to breeding habitat associations for these sensitive species of grassland birds, I evaluated the effects of vegetation conditions on nest density and nest survival of Baird's sparrow, chestnut-collared longspur, McCown's longspur, and Sprague's pipit in an area of northern Montana representing the core of their extant distributions. Specifically, my objectives were to evaluate 1) relationships between local nest densities and plot-level vegetation conditions, 2) effects of local (nest site) and plot-level vegetation conditions on daily nest survival and 3) compare the magnitude of the associations between local nest density and nest survival. I expect nest density and nest survival of the two longspur species to favor areas with low biomass, and higher bare ground or litter coverage (With 2010, Bleho et al. 2015). Baird's sparrows and Sprague's pipits will likely nest in higher densities in more densely vegetated areas and show positive associations with grass cover and biomass (Sutter 1997, Green et al. 2002, Davis et al. 2014). All four species are believed to be disassociated with shrubs (With 1994, Davis et al. 1999, Davis 2004, Grant et al. 2004, Lipsey and Dreitz 2014); however, recent work in Montana has suggested conflicting positive associations between shrub cover and nest survival for chestnut-collared longspurs and Sprague's pipits (Lipsey and Dreitz 2014). Previous work has indicated negative associations between breeding densities of grassland obligate birds and the amount of exotic grass cover (Frey et al. 2008, Davis et al. 2016); however, others have found no significant effect of exotic cover (Lloyd and Martin 2005, Lipsey and Dreitz

2014). The structure and density of grasses may be more important than species composition (Sutter and Brigham 1998). I expect correlates of nest density and nest survival to be similar for each species and for plot-level nest density to be correlated with nest survival.

Methods

Study Area

My study area was located in northern Phillips county Montana, ranging from 24 km south of Malta, MT to eight km south of the Canadian border. This region contains one of the largest tracts of intact native mixed-grass prairie in the country (Cooper et al. 2001). A simulation of population distribution for my study species conducted by the U.S. Fish and Wildlife Service predicted that Phillips county contains some of the highest densities of my study species throughout their range (M. Sather, unpublished data). The region is dominated by gently rolling grassy hills. The climate is semi-arid with short hot summers and long cold winters. Average annual precipitation typically comes as rain in May – July (Cooper et al. 2001). Total precipitation ranges from 193 – 493 mm per year (1981 – 2015; PRISM 2019). The dominant grasses are western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Stipa comate*), prairie junegrass (*Koeleria macrantha*), green needlegrass (*Stipa viridula),* and Sandberg bluegrass (*Poa secunda*) (Charboneau et al. 2013). Almost 75% of the region is managed for livestock grazing (Lipsey 2015). In areas where the native mixed-grass prairie is relatively intact, grassland bird populations are still relatively stable (Cooper et al. 2001).

Site Selection. I used a stratified random sampling approach to control for possible confounding factors that may influence the abundance and productivity of birds, including soil characteristics (soil type, productivity), expected annual precipitation, and distance to roads (Sutter et al. 2000, Lipsey and Naugle 2016). Natural Resource Conservation Service (NRCS) soil survey data were used to identify and select areas in northern Phillips county identified as having silty soils, with 250 – 330 mm of average precipitation and at least 1,120 kg ha^{-1} of vegetation productivity in a normal year. I selected sites based on these parameters because they describe the conditions known to support all four of my focal species (M. Sather, U.S. Fish and Wildlife Service, personal communication). I further stratified sites by ownership, land use, and distance to roads. To ensure study sites represented the gradients of vegetative conditions and livestock use, I selected study sites occurring on private and public lands known to have diverse land and livestock management. I limited selection of study sites to lands managed by Bowdoin National Wildlife Refuge (NWR), the Bureau of Land Management (BLM), Montana state trust lands and private owners. To incorporate private lands into my sample, I selected several potential sites based on the above characteristics as potential study sites conditional on access being granted by the owner. To make it feasible to drive to study sites, I limited my search to within 40 miles of Bowdoin NWR. I then used ArcMap (ESRI 2016) to select broad areas that contained the selected soil conditions and land uses and were close enough together to allow for the access of multiple sites in a given field day. I then used ArcMap to randomly generate 300 × 300 m plots within these areas. Of the generated plots, I selected only plots that fit predefined soil conditions, were completely within one land ownership type (BLM, NWR, Montana state trust, or private), were not within 200 m of a road, and did not overlap one another. In total I generated 12 potential plots on school trust land, another 12 on NWR land, 97 on BLM, and 31 on private land. The disparity in the number of plots generated for each land use type is due to the difference in abundance for each type. In Phillips county within 40 miles of Bowdoin NWR, there are approximately 215,218 ha (72% of public land) of BLM land, 76,578 ha (26% of public land) of school trust land, and only 6,819 ha (2% of public land) of NWR land.

Beginning with an initial set of 121 plots on BLM, NWR, and state trust land, I ground-truthed all plots in 2017 prior to sampling. I examined plots for features that may negatively impact bird use of the area. These included features for which I did not have any data on their location (e.g., interior fences roads). When possible, I moved plots ≥ 100 m from roads, oil wells, fences, and power lines because habitat use by grassland birds is often influenced by anthropogenic disturbance (Sutter et al. 2000, Thompson et al. 2015). Plots that contained ≥ 50% shrub cover were moved to a nearby area with < 50% shrub cover when possible (With 1994, Lipsey 2015). Plots were removed from the study when there was no location within 300 m that met the criteria for soil, vegetation, or anthropogenic structures. After truthing I had 100 useable plots, but limitations of time made it impossible to effectively survey all 100 sites within a single field season. I randomly selected 50 of these to survey during the 2017 season and reserved the remaining 50 for survey during 2018. Prior to the start of the 2018 season, I created an additional 31 plots on private lands using the previously described random sampling method. Of these 31, I was granted permission to access only six plots. In 2018, I repeated field inspections of all plots to ensure plot conditions had not changed during the year. Examples of such changed might include the construction of new oil derricks, fences, or power lines. Six of the BLM plots for 2018 were removed from the study to allow for the addition of the six new private land plots while keeping the total number surveyed to 100 (Fig. 9).

Sampling

I conducted rope dragging surveys during May and June of 2017 and 2018 to locate songbird nests at the 100 survey plots. Rope dragging surveys were conducted with a weighted 20-m rope and occurred during morning (06:00–10:00 MDT) and evening (17:00–20:00 MDT) hours. To estimate detection probability of nests, I surveyed each plot multiple times; 71 plots were surveyed three times and the remaining 29 were surveyed twice. I began each rope dragging survey at a systematically selected corner of the study plot, and then systematically searched the plot using standard rope-dragging protocols (Labisky 1957). To control for possible differences in nest density as the breeding season progressed, I randomized the order of surveys among plots; however, all replicated surveys within a plot were conducted within 30-d period to ensure population

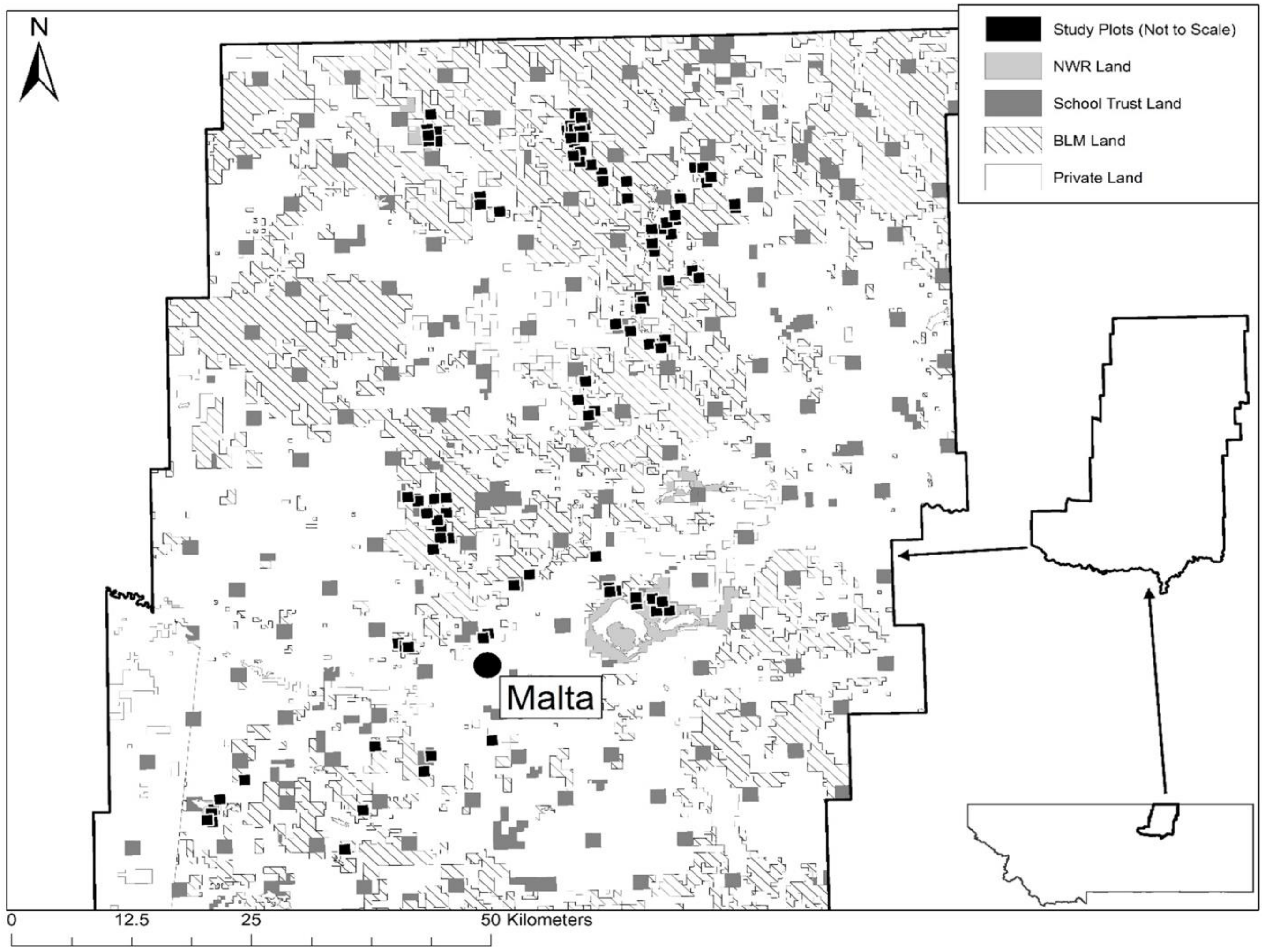

Figure 9. Study plots on Bureau of Land Management (BLM), National Wildlife Refuge (NWR), Montana State Trust (ST) land, and private land in Phillips County, Montana. Inserts show a closeup of some plots in the northern and southern parts of the county.

closure. To control for the possible diurnal effects in nest detection, the time of surveys within each plot (morning or evening) was alternated among replicated surveys.

In the event of a bird flush during rope-dragging or incidentally within a plot, observers searched the area to locate a nest. For each detected nest, I recorded the GPS coordinates and marked the site with bamboo stakes approximately 25 cm in length located 2 m north and east of the nest to aid in relocating the nest during nest monitoring. Nests of focal species discovered incidentally within my study plots during site truthing or point counts were also marked and monitored. In addition to the number of nests for each species found, I also recorded the temperature, wind speed, and cloud cover during the survey, and date and time of the survey.

I recorded the number of eggs or nestlings in nests at nest discovery. Subsequent nest visits occurred approximately every 3 days until the nest failed or fledged young. Nests were considered successful if they fledged ≥ 1 young bird, as evident from observations of fledglings, parental feeding post-fledging, parental persistent alarm calling in the area of an empty nest, or the presence of fledgling feces in or near nest (Martin and Geupel 1993, Ralph et al. 1993). Nests that did not fledge ≥ 1 young were classified as failed. Nests fail because of abandonment, depredation, or parasitism in which the nest fledged only young of the parasite species. Nests with eggs were classified as abandoned when the total number of days I observed a nest exceeded the maximum incubation period of that species. I would have also classified nests in the nestling stage as abandoned if the nest was found to contain dead nestlings with no sign of injury, suggesting they died of starvation, however this did not occur at any of the nests I found during the study. Nests were classified as failed due to depredation if eggs were suddenly absent from the nest with or without eggshells present, or if the nestlings were absent from the nest prior to the earliest possible fledge date, or if the nestlings were gone from the nest at an age when they could have fledged but none of the above evidence of fledging was present. My protocol may underestimate nest success, but a conservative approach was preferred to potentially overestimating nest success (Williams and Wood 2002). Accurate estimation of nest success is further complicated by a wide window of potential fledge dates in the case of my focal species (Green et al. 2002, With 2010, Davis et al. 2014, Bleho et al. 2015). Chestnut-collared longspurs and Baird's sparrows can fledge (i.e., leave the nest) when their primaries are only half unsheathed and they are unable to fly (personal observation). The possibility of nestlings fledging while they are still apparently immature prevented us from assuming successful fledging based solely on the nestlings age. Nests failed due to parasitism if brown-headed cowbirds laid an egg in the nest and the cowbird nestling removed all the host eggs or chicks such that no host chicks fledged.

Vegetation Surveys. To assess vegetation conditions within the survey plots, I generated 15 random points within each of the 100 study plots. I began by conducting vegetation surveys at five of these points, I then calculated the mean and standard deviation of % grass and used the following equation to determine the necessary sample size needed to accurately represent variation in vegetation measurements within each plot:

$$n = (Z_{\alpha})^2(s)^2 \div (B)^2$$

where n = the uncorrected sample size, Z_{α} is the standard normal coefficient calculated for a confidence interval of 90% (1.64), s is the sample standard deviation and B is the sample mean multiplied by the desired precision (0.15). With the mean and standard deviation along with standard values for Z_{α} and precision, I calculated the uncorrected sample size. This value was then compared to the table given in Elzinga et al. (1998; Appendix 7) to get the corrected sample size of vegetation survey points needed. If the corrected sample size was greater than the current number of points surveyed, then I continued to survey vegetation at additional random points until the necessary sample size was reached to adequately assess plot-level vegetation conditions. I used this formula at each of the 100 plots individually so that each plot had enough vegetation surveys to account for the variability of structure within it, with more variable plots having more surveys. I acknowledge that it would have been more accurate to use the formula for each of the 13 vegetation covariates separately and then use the highest number of surveys called for across all covariates. As I was using this formula in the field and individually for each plot, I did not consider using the formula 13 times per plot to be a good use of time, I chose to use it only once per plot based on variation in the grass cover. I chose grass cover because it was the most abundant cover type in each plot so variations in other cover types like shrub cover would result in increasing variability in grass cover, since anywhere there was a shrub growing that ground would not have grass cover.

Prior to vegetation sampling each day, I calibrated my ability to visually estimate biomass within a 20 × 50 cm Daubenmire frame (Daubenmire 1959) by estimating, clipping, and taking the mass of 5–10 samples prior to conducting surveys (Coulloudon et al. 1999). At each vegetation sampling site and nest location, I recorded visual obstruction (VOR) to the nearest cm from each of the four cardinal directions at a distance and height of 4 m and 1 m, respectively (Robel et al. 1970). I quantified overlapping canopy coverage at random points using 5, 20 × 50 cm Daubenmire frames, with one frame centered on the randomly selected point, and the remaining four placed 0.5 m in each cardinal direction (Winter 1999). I estimated percent canopy coverages of current growing season grass, residual grass, forbs, shrubs, litter, bare ground, and exotic grass to six coverage bins (0 – 5, 5 – 25, 25 – 50, 50 – 75, 75 – 95, and 95 – 100). I made a distinction between current growing season grass and residual grass from the previous year because all four of my study species use residual grass in their nest construction. Residual grass cover may also be useful to conceal nests from predators early in the breeding season. Residual grass and litter were distinguished by structure, grass that still maintained an upright stature, similar to what it had when alive was counted as residual grass, grass that was no longer attached to the ground or was lying flat against the ground was included in litter. When evaluating live or residual grass cover both exotic and native grasses were lumped together, but when evaluating exotic grass cover only exotic grasses were included. I included overlapping cover in my estimation, meaning I estimated the understory cover (litter, bare ground, etc.) underneath taller vegetation (grass, shrubs, etc.) because grassland songbirds are small and spend most of their time on the ground it is possible that understory structure is important to them. I also estimated the herbaceous biomass, recorded the litter depth, slope (recorded with clinometer), and average height of grass, forbs, and shrubs within the frame.

To establish the relationship between green herbaceous biomass and dry herbaceous biomass, I collected all the standing herbaceous vegetation within the northern Daubenmire frame at the first 3 plot scale vegetation points in each plot after other vegetation surveys had been completed. These samples were placed in paper sacks and stored it in a shed to air dry. Weekly I measured the mass of all the samples to determine if any have completely dried out, at which point I record the dry weight of the sample. A sample is considered to have completely dried if the mass from the current week matched that of the previous week. After all vegetation surveys were completed, I calculated a mean difference between estimated green weight and measured green weight for each field observer and applied that calibration to all estimated samples for that observer. I used the same method to establish a mean difference between green weight and dry weight for all samples, I then used this calibration to convert all estimated green weights to calibrated dry weight.

In addition to surveying vegetation at the plot scale I also conducted vegetation surveys at nest sites within 3 days of fledging or expected fledge date for failed nests. These surveys were identical to the plot scale vegetation surveys described above except that the point was centered on the nest rather than on a randomly generated point. To account for changes in growth of vegetation between the time when a nest finishes and the time when I conducted plot scale vegetation surveys, each nest vegetation survey was paired with two parallel vegetation surveys at two randomly selected locations within the same survey plot, and all three surveys occurred on the same day.

Statistical Analysis

I evaluated the effects of plot-scale vegetation conditions on the nest density (nests per 300 x 300-m plot) using N-mixture models to simultaneously estimate detection probability and abundance in the R package ‘unmarked’(Royle 2004, Fiske and Chandler 2011). Binomial or N-mixture models provide accurate estimates of the detection probability and abundance of unmarked individuals identified during spatially replicated counts during a period of population closure.

Prior to fitting models, I first tested for multicollinearity among vegetation covariates to ensure only uncorrelated variables were included in candidate models of nest density. I calculated the Pearson’s correlation coefficient (r) for each combination of vegetation covariates. I considered variables to be correlated if $r \geq 0.7$. I found significant correlations between biomass several other vegetation covariates including: VOR (r = 0.93), heights of live grass (r = 0.87) and residual grass (r = 0.80), and the proportional coverage of exotic grasses (r = 0.77). Visual obstruction reading (VOR) is a commonly used index of herbaceous biomass and an important determinant of grassland bird abundance (Davis et al. 1999, Madden et al. 2000, Davis 2004, Fisher and Davis 2010). Because biomass is a more common condition informing rangeland management, I retained biomass and removed VOR and the heights of live and residual grass from further analyses. I was particularly interested in the effects of exotic grasses on nest density and nest survival, so I retained its proportional cover as a covariate but never included both biomass and proportion exotic grass in the same candidate model (Kalnins 2018). Shrub cover was correlated with shrub height (*r* = 0.85); I retained shrub cover as a predictor variable and excluded shrub height due to previously observed associations of grassland birds with shrub coverage (With 1994, Davis et al. 1999, Madden et al. 2000, Davis 2004, Lipsey and Dreitz 2014). Litter cover was inversely correlated with bare ground cover (*r* = -0.71); litter cover and depth are often associated with bird abundance so I removed bare ground cover from analyses (Fisher and Davis 2010). I also included the plot standard deviation of biomass as a potential covariate. The heterogeneity of vegetation structure has been demonstrated to be related to bird species diversity (Fuhlendorf et al. 2006, Hovick et al. 2014). While the association between structural heterogeneity and diversity does not necessarily mean individual species benefit from heterogeneity, it is possible that some species make use of various structures for nesting, foraging, and concealment from predators. Potential covariates for nest abundance and daily survival included all uncorrelated vegetation measures. Covariates for detection of nests included survey date and time, wind speed, temperature, and cloud cover during the survey, and plot averaged biomass and shrub cover.

To evaluate the relationships between nest density and plot-scale vegetation variables, I built and evaluated a candidate set of models using Akaike's Information Criterion adjusted for finite samples for each species (AIC_c). Supported models with large model weights (w_i) and AIC_c values ≤ 2 from the best-fit model were considered parsimonious (Burnham et al., 2011). The vegetation and survey conditions we measured in the field were previously shown to influence grassland bird detection probability or local abundance (Fisher and Davis, 2010; Ahlering and Merkord, 2016), and I used backward stepwise model selection to identify parsimonious models. Uncorrelated vegetation variables considered in model sets for each species included biomass, proportion forb cover, proportion shrub cover, proportion litter cover, proportion residual grass cover, and slope. I evaluated potential overdispersion in the count data by comparing support for three highly-parameterized models among three different distributions for each species: the Poisson, negative binomial, and zero-inflated Poisson.

Models evaluating detection probabilities of each species were fit assuming constant nest density prior to fitting models of abundance. I used 85% confidence intervals to examine predictive strength of each variable for the best-fitting model (Arnold et al. 2010) and assessed the goodness-of-fit for the top model for each species with a parametric bootstrap procedure ($n = 500$ iterations) using the *Nmix.gof.test* function in the AICmodavg package (Mazerolle 2017); $P > 0.05$ indicated adequate model fit to the data.

Exotic grass cover was correlated with biomass and I could not include both covariates in the same model (Kalnins 2018). Therefore, I evaluated two candidate model sets for each species, one set containing biomass and one set containing exotic cover with all other uncorrelated variables. The two top models from each set were then compared using AIC_c and relative support compared.

I used the nest survival model in program MARK (White and Burnham 1999) to model the daily nest survival rate (DSR) as a function of vegetation covariates collected at two spatial scales: the nest site and the plot. I conducted three separate analyses, one using vegetation data from the nest site, one using vegetation data at the plot-scale, and the last being a multi-scale analyses including vegetation covariates at both nest sites and plot-scale. Possible factors affecting nest survival at the nest and plot scales included all non-collinear vegetation characteristics. I included a term for survey year to account for possible differences in nest survival between years. At the plot-scale I also included the standard deviation (SD) of each vegetation covariate across each plot. After completing the analyses at the nest and plot scales, I took covariates from parsimonious models from each candidate set and evaluated each possible pair for collinearity. When two covariates were collinear ($r \geq 0.7$), I constructed a univariate model for each covariate and compared them using AIC_c to assess which had more support from the data. All supported or non-collinear covariates were used in a multi-scale candidate model set. I also fit a null model to estimate an average daily survival rate for all nests. To estimate the probability of a nest surviving the entire exposure period then raised estimated daily survival rate to a power equal to the maximum number of days for a nest to successfully fledge young. The standard error of this estimate was derived using the delta method (Powell 2007).

I used the *predict* function in R package umarked (Fiske and Chandler 2011) with the most parsimonious model for nest density to predict the true number of nests within each plot based on the local vegetation measurements. There was no model for nest survival that was better supported than the null model so I fit a model with all covariates from any model that with equal support to the null model and used that model to predict the nest DSR for each plot based on the local vegetation conditions. I then compared the two predictions to see what relationship existed between nest density and nest survival. I used Pearson's correlation coefficient to evaluate the correlations between predicted nest survival and nest density for each species.

Results

I conducted a total of 272 rope drag surveys during both 2017 and 2018. I found a total of 273 nests of my focal species, including 19 confirmed Baird's sparrow nests, 237 chestnut-collared longspur nests, 10 McCown's longspur nests, and seven Sprague's pipit nests. I also found an additional one Baird's sparrow nest, 28 chestnut-collared longspur nests, and six McCown's longspur nests opportunistically while conducting other surveys. The average ± SD number of nests per plot was 0.20 ± 0.67 for Baird's sparrow, 2.65 ± 2.72 for chestnut-collared longspurs, 0.16 ± 0.63 for McCown's longspurs, and 0.07 ± 0.26 for Sprague's pipits.

Across all 100 study plots I conducted a total of 776 vegetation surveys at random points in addition to the vegetation surveys at each nest site. The observed exotic grasses included crested wheatgrass (*Agropyron cristatum*), smooth brome (*Bromus inermis*), and Kentucky bluegrass (*Poa pratensis*).

The relatively small number of nests detected during rope drag surveys for Baird's sparrow and McCown's longspurs (19 and 10 respectively) prohibited the fitting of any complex models for nest density for these species. However fitting null models allowed for the estimation of average detection probability of nests for each species. The average probability of detecting a nest was 0.17 ± 0.12 SE for Baird's sparrow nests and 0.15 ± 0.11 for McCown's longspur nests. Small sample sizes of nests for Sprague's pipits (n = 7) precluded analyses.

The average detection probability for chestnut-collared longspur nests was 0.24 ± 0.05 SE. I found that models with Poisson, negative binomial, and zero-inflated Poisson had equal support from the data, so I used the standard Poisson distribution for all future models as it was the simplest. Two models for detection received approximately equal support (Table 8), both including biomass and shrub cover and one also including temperature. Detection probability of nests was negatively associated with biomass (β = -0.94 ± 0.19), shrub cover (β = -0.42 ± 0.10), and ambient temperature during a survey (β = -0.12 ± 0.07).

After accounting for spatially-variable detection probability, I found support for two models of chestnut-collared nest abundance; both models contained an effect of biomass and one also including an effect of slope (Table 8). Chestnut-collared nest abundance was negatively associated with plot averaged herbaceous biomass (β = -1.65 ± 0.53), and slope (β = -0.16 ± 0.09; Figs 10 and 11). The goodness of fit test indicated little overdispersion but only moderate model fit $\chi^2 = 305.06$, $\hat{c} = 1.24$, $p = 0.02$.

When using a candidate model set for nest density including terms for exotic cover instead of biomass, the top model included terms for exotic cover and slope (Table 8). Chestnut-collared longspur nest density declined with exotic cover (β = -0.75 ± 0.32 SE) and slope (-0.19 ± 0.09; Figs 10 and 12). The effect of exotic grass cover on nest

Table 8: Model selection table for nest detection probability and nest density of chestnut-collared longspurs from 272 rope drag surveys of 100 9-ha plots in Phillips County, MT during May – June of 2017 and 2018. The number of parameters (K), AICc values, ΔAICc values, and model weights (AICcWt) are reported.[a]

Detection	K	AICc	ΔAICc	AICc Wt
Shrub Cover + Biomass + Temp	5	670.91	0	0.47
Shrub Cover + Biomass	4	671.26	0.35	0.39
Shrub Cover + Biomass + Temp + Date	6	673.44	2.53	0.13
Shrub Cover + Biomass + Slope + Date + Time + Temp + Cloud Cover + Wind	10	679.41	8.50	0.01
Null	2	721.70	50.79	< 0.001
Density with Biomass				
Biomass + Slope	7	667.90	0	0.27
Biomass	6	668.88	0.99	0.17
Slope	6	669.85	1.95	0.10
Biomass + Litter Cover	7	670.64	2.74	0.07
Biomass + Shrub Cover	7	670.73	2.83	0.07
Biomass + Forb Cover	7	671.17	3.28	0.05
Null	4	671.26	3.36	0.05
Biomass + Residual Cover	7	671.38	3.48	0.05
Biomass + SD Bio	7	671.44	3.54	0.05
Litter Cover	6	672.00	4.11	0.04
Shrub Cover	6	673.07	5.17	0.02
Residual Cover	6	673.09	5.2	0.02
SD Bio	6	673.30	5.4	0.02
Biomass + Residual Cover + Forb Cover	8	673.84	5.95	0.01
Litter Cover + Shrub Cover	7	674.30	6.41	0.01
Density with Exotic Cover	K	AICc	ΔAICc	AICc Wt
Exotic Cover + Slope	7	664.97	0	0.51
Exotic Cover	6	667.73	2.76	0.13

Table 8: continued

Density with Exotic Cover	K	AICc	ΔAICc	AICc Wt
Exotic Cover + Litter Cover	7	668.38	3.41	0.09
Slope	6	669.85	4.88	0.04
Exotic Cover + Shrub Cover	7	669.98	5.01	0.04
Exotic Cover + Residual Cover	7	670.07	5.10	0.04
Exotic Cover + Forb Cover	7	670.29	5.32	0.04
Exotic Cover + Resid Cover + Litter Cover + Forb Cover + Shrub Cover +Slope	11	670.73	5.76	0.03
Null	5	670.91	5.94	0.03
Litter Cover	6	672.00	7.03	0.02
Exotic Cover + Residual Cover + Forb Cover	8	672.79	7.82	0.01
Shrub Cover	6	673.07	8.10	0.01
Residual Cover	6	673.09	8.12	0.01
Litter Cover + Shrub Cover	7	674.30	9.33	0.01

[a] Only models with Akaike weights (AICc Wt) ≥ 0.01 are presented, except for the null model.

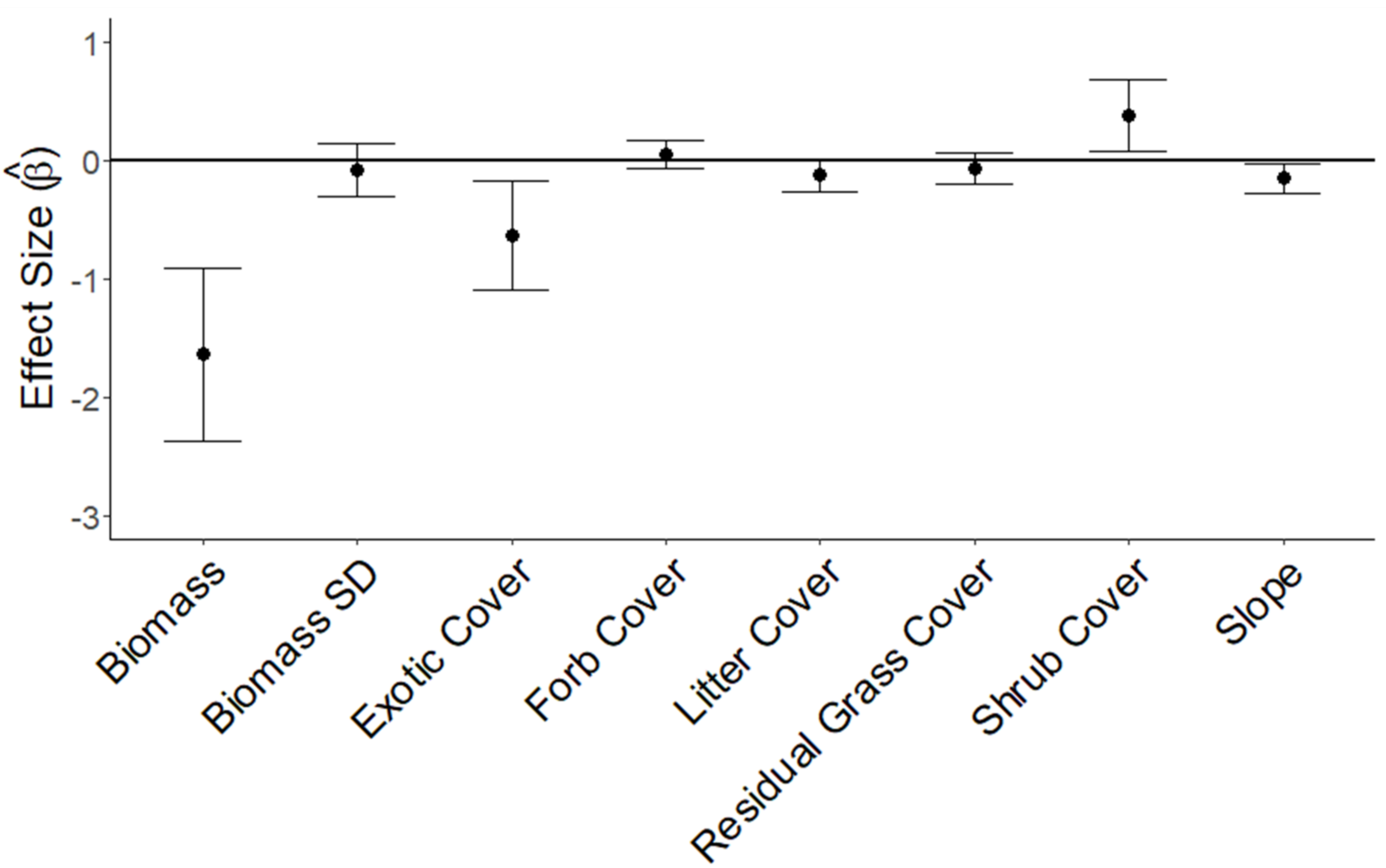

Figure 10. Estimated effect sizes with 85% confidence intervals from plot scale covariates on density of chestnut-collared longspur nests in 100 9-ha plots in Phillips County, MT during May – June of 2017 and 2018.

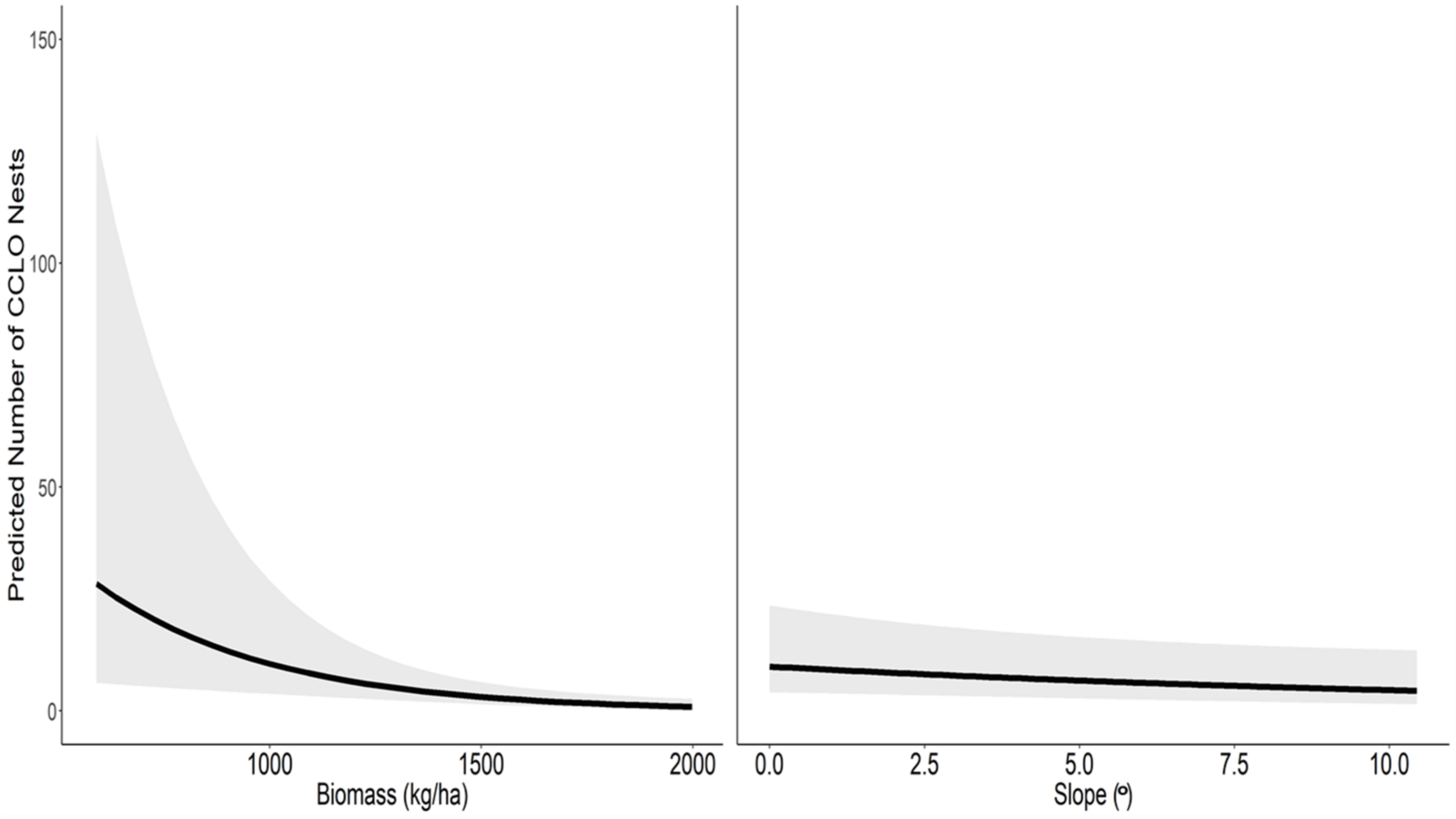

Figure 11. Predicted effect of plot-scale biomass on the number of chestnut-collared longspur nests in Phillips County, Montana during May – June 2017–2018. Shaded areas represent 95% confidence intervals.

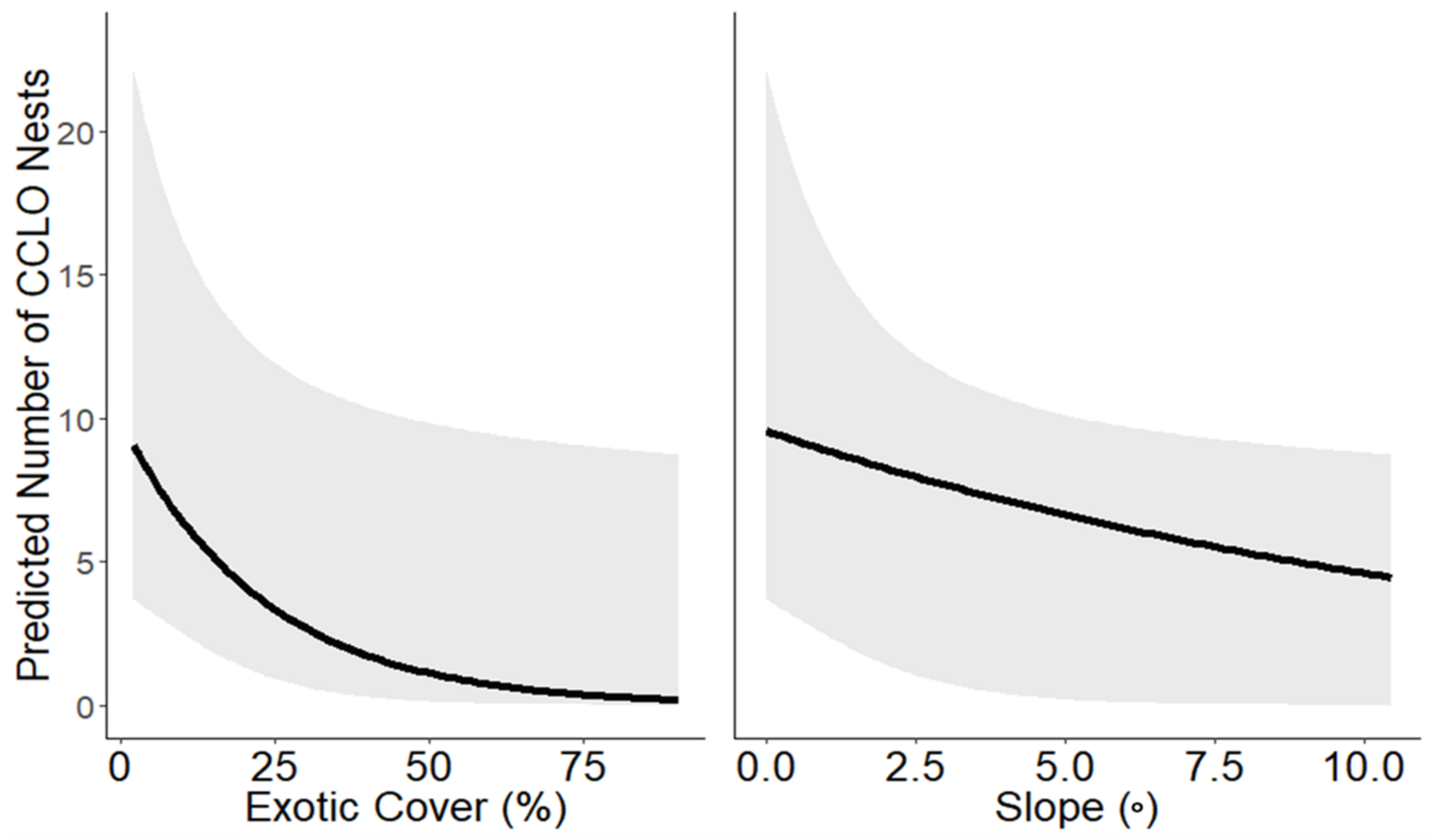

Figure 12. Predicted effect of plot-scale exotic grass cover and slope on the number of chestnut-collared longspur nests in Phillips County, Montana during May– June 2017–2018. Shaded areas represent 95% confidence intervals.

density was more informative than biomass, the top model for the set including exotic cover had four times (0.81/0.19) more support than the top model in the biomass set (Table 9).

Nest Survival

Apparent nest success was 30% (6/20), 29% (76/263), 38% (6/16), and 29% (2/7) for Baird's sparrow, chestnut collared longspur, McCown's longspur, and Sprague's pipit, respectively. Average estimated daily nest survival for all chestnut-collared longspur nests was 0.93 ± 0.01 SE. Estimated nest survival for the entire nest exposure period (30 days, Bleho et al. 2015) was 0.12 ± 0.02.

When evaluating vegetation at the nest site, the null model had approximately equal support as the top model (ΔAICc = 0.91; Table 10), indicating little support for vegetation characteristics at this scale on the daily survival rate of chestnut-collared longspur nests. Covariates in models with equal support to the Null model (ΔAICc < 2) included survey year, biomass, forb cover, litter cover, and exotic cover (Table 10; Fig 13).

Similarly, the null model was equally supported as the top model of plot-level effects on nest survival (ΔAICc = 0.78; Table 10). Models that were equally as supported by the data as the null model (ΔAICc < 2) contained covariates for survey year, biomass, litter cover, residual grass cover, shrub cover, and exotic cover, as well as the standard deviations (SD) for biomass, litter cover and exotic cover (Table 10; Fig 14). I found no

Table 9: Model selection results of top models from biomass candidate model set and exotic cover candidate model set for chestnut-collared longspur nest density from 272 rope drag surveys of 100 9-ha plots in Phillips County, MT during May – June of 2017 and 2018. The number of parameters (K), AICc values, ΔAICc values, and model weights (AICcWt) are reported.

	K	AICc	ΔAICc	AICc Wt
Exotic Cover + Slope	7	664.97	0	0.81
Biomass + Slope	7	667.90	2.93	0.19

Table 10: AICc Model selection table for daily survival rate of 263 chestnut-collared longspur nests in 100 9-ha plots in Phillips County, MT, during May – July of 2017 and 2018. Vegetation characteristics are evaluated at both the nest-site and plot scale[a]

Nest-site vegetation	K	AICc	ΔAICc	AICc Wt
Forb	2	929.16	0	0.13
Year	2	929.29	0.13	0.13
Year + Forb	3	929.35	0.18	0.12
Year + Exotic	3	930.07	0.91	0.09
Null	1	930.08	0.91	0.09
Year + Litter	3	930.43	1.26	0.07
Year + Biomass	3	930.59	1.42	0.07
Exotic	2	930.63	1.47	0.06
Year + Residual Grass	3	931.28	2.11	0.05
Year + Shrub	3	931.3	2.13	0.05
Linear Biomass	2	931.75	2.59	0.04
Residual Grass	2	932.02	2.85	0.03
Shrub	2	932.04	2.88	0.03
Litter	2	932.07	2.91	0.03
Biomass + Residual Grass	3	933.74	4.58	0.01
Plot scale vegetation				
Year	2	929.29	0	0.09
Biomass	2	930.07	0.78	0.06
Null	1	930.08	0.78	0.06
Litter	2	930.27	0.98	0.06
Biomass + Year	3	930.78	1.49	0.04
Biomass + Litter	3	930.97	1.68	0.04
Biomass SD	2	931	1.71	0.04

Table 10: continued

Plot scale vegetation^b	K	AICc	ΔAICc	AICc Wt
Exotic + Year	3	931.01	1.71	0.04
Litter SD	2	931.03	1.74	0.04
Exotic SD	2	931.12	1.83	0.04
Shrub Cover + Year	3	931.16	1.87	0.04
Residual Grass + Year	3	931.2	1.91	0.03
Litter + Year	3	931.2	1.91	0.03
Litter + Litter SD	3	931.28	1.98	0.03
Shrub Cover	2	931.49	2.2	0.03
Biomass + Residual Grass	3	931.57	2.28	0.03
Forb Cover	2	931.77	2.48	0.03
Slope	2	931.83	2.53	0.03
Forb SD	2	931.86	2.56	0.03
Residual Grass	2	931.87	2.58	0.02
Shrub SD	2	931.91	2.62	0.02
Slope SD	2	931.96	2.67	0.02
Biomass + Biomass SD	3	932.04	2.75	0.02
Exotic Grass Cover	2	932.07	2.78	0.02
Residual Grass SD	2	932.07	2.78	0.02
Exotic Grass Cover + Litter	3	932.21	2.91	0.02
Exotic Grass Cover + Exotic Grass SD	3	933.12	3.83	0.01
Shrub Cover + Shrub Cover SD	3	933.33	4.04	0.01
Forb Cover + Forb SD	3	933.64	4.34	0.01
Slope + Slope SD	3	933.64	4.34	0.01
Residual Grass + Residual Grass SD	3	933.77	4.48	0.01
Exotic Grass Cover + Residual Grass	3	933.86	4.57	0.01

Table 10: continued

Multi-scale Vegetation[c]	K	AICc	ΔAICc	AICc Wt
Year	2	929.29	0	0.20
Null	1	930.08	0.78	0.13
Nest Forb Cover + Plot Shrub Cover	3	930.79	1.49	0.09
Nest Biomass + Plot Biomass	3	930.85	1.56	0.09
Nest Forb Cover + Plot Residual Grass Cover	3	930.9	1.61	0.09
Nest Exotic Grass Cover + Plot Cover Litter	3	931.02	1.73	0.08
Nest Exotic Grass Cover + Plot Exotic Grass SD	3	931.54	2.25	0.06
Nest Litter Cover + Plot Litter Cover	3	931.8	2.51	0.06
Nest Biomass + Plot Biomass SD	3	932.47	3.18	0.04
Nest Biomass + Plot Biomass + Plot Shrub Cover	4	932.58	3.29	0.04
Nest Exotic Grass Cover + Plot Exotic Grass Cover	3	932.61	3.31	0.04
Nest Exotic Grass Cover + Plot Litter Cover + Plot Exotic Grass Cover	4	932.75	3.46	0.03
Nest Litter Cover + Plot Litter SD	3	933.03	3.74	0.03
Nest Exotic + Plot Residual + Plot Exotic Grass	4	934.51	5.21	0.01

[a] Only models with Akaike weights (AICc Wt) ≥ 0.01 are presented

[b] Variables ending in SD indicate the standard deviation of that variable at the plot-scale

[c] Variables at the nest-site are denoted with Nest and variables at the plot-scale are denoted with Plot

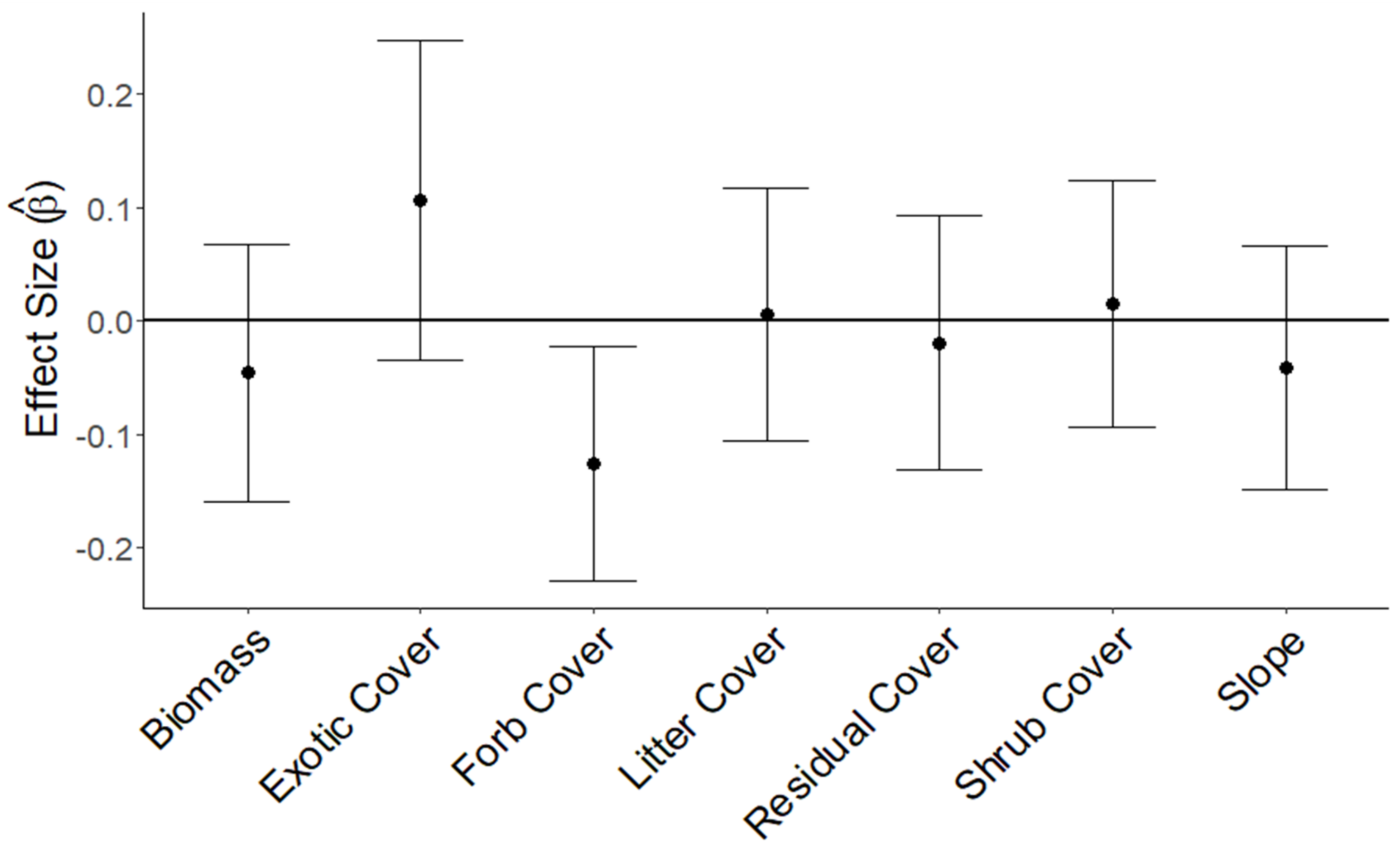

Figure 13. Estimated effect sizes from standardized covariates measured at the nest site on daily survival of 263 chestnut-collared longspur nests in 100 9-ha plots in Phillips County, MT, during May – July of 2017 and 2018.

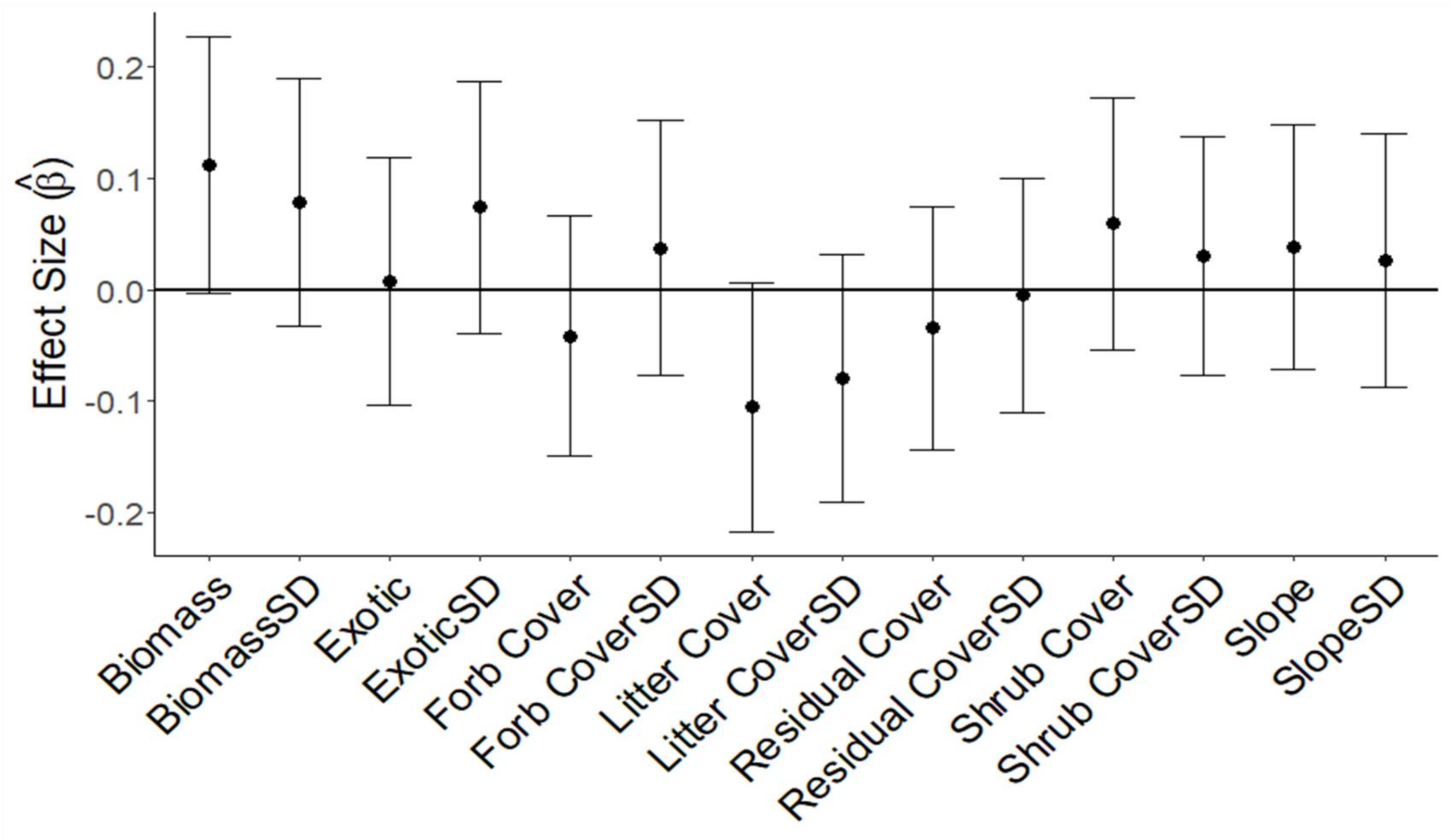

Figure 14. Estimated effect sizes from standardized covariates measured at the plot scale on daily survival of 263 chestnut-collared longspur nests in 100 9-ha plots in Phillips County, MT, during May – July of 2017 and 2018. Covariates ending in SD represent the effect of the standard deviation of the covariate at the plot scale.

collinearity ($r < 0.7$) among supported covariates at both the nest-site and plot scale so the multi-scale candidate set included all supported terms from the first two scales. In this model set, the null model was also equally supported (ΔAICc = 0.78; Table 10).

There was moderate but significant negative correlation between the predicted number of chestnut-collared longspur nests in each plot and the predicted daily nest survival of those nests based on the local vegetation conditions ($r = -0.57$, $p < 0.05$; Fig 15).

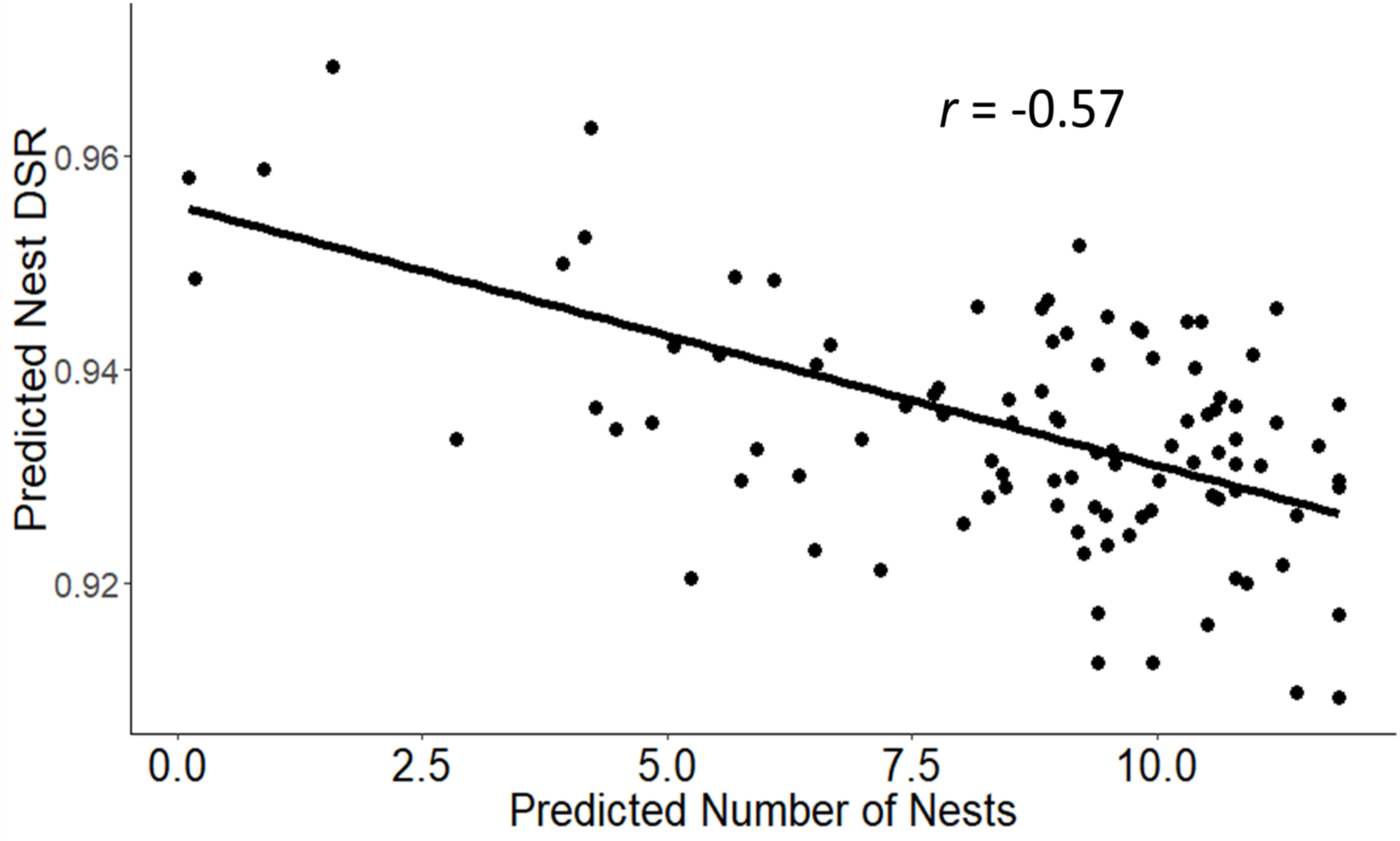

Figure 15. Predicted number of chestnut-collared longspur nests and nest daily survival rate (DSR) in 100, 9-ha plots in Phillips County, MT during May – July of 2017 and 2018 based off of top models for each response. The Pearson's correlation coefficient (*r*) is also reported.

Discussion

Small sample sizes for Baird's sparrow, McCown's longspur, and Sprague's pipit (20, 14, and 7, respectively) prevented evaluation of associations between vegetation conditions and nest density or survival. The much larger sample size of chestnut-collared longspur nests allowed for the comparison of a full suite of models. I found that the density of chestnut-collared longspur nests within a study plot was negatively associated with the plot scale biomass, exotic grass cover, and slope. I found little evidence for nest site or plot-level vegetation effects on the daily survival of chestnut-collared longspur nests.

The negative effect of plot scale biomass on the density of chestnut-collared longspur nests is in keeping with common perceptions of the species favoring sparsely vegetated areas (Bleho et al. 2015). However, I found even greater support for an effect of exotic cover on nest density.

The effects of exotic vegetation are more typically studied in monocultures fields seeded to 100% exotic cover (Lloyd and Martin 2005, Davis et al. 2016). My results suggest that even low levels (< 10% cover) of exotic grass has negative effects on nest densities of chestnut-collared longspurs. In contrast, I was unable to detect an effect of exotic cover on nest survival suggesting disconnects between the correlates of nest density and nest survival. The negative effect of exotic vegetation on reproductive productivity may therefore manifest itself in ways besides nest survival. For example, Lloyd and Martin (2005) found that chestnut-collared longspur nestlings in monocultures of exotic crested wheatgrass grew more slowly and fledged at a lower body weight than nestlings in native prairie, likely resulting in lowered recruitment rates. Thus, assessments of nest survival without consideration of nest density may yield improper inferences regarding the effects of spatially-explicit vegetation conditions on overall avian productivity. A negative correlation between predicted plot-level nest survival and nest density provided additional evidence that nest survival data should be supplemented with information on nest density when considering best habitat management practices for grassland birds. However, model uncertainty in my nest survival models suggest estimates of plot-level nest survival should be interpreted cautiously.

The topography of Phillips County is one of gently rolling hills. Most of my study plots (71/100) were on relatively flat ground with average slope ≤ 2°. However a few plots (10/100) were on hills with a combination of flat areas and steep slopes resulting in higher average slopes (≥ 10°). Frey et al. (2008) found a preference among some bird species for different topographies in tallgrass prairie. They measured topography differently than I did, treating it as a categorical variable (flat lowlands and uplands and sloped midlands). To my knowledge there is no similar study on my focal species but I suspect there is some maximum slope above which they are not willing to nest. That there was a negative effect of plot average slope on nest density gives some evidence for this, but the effect, while significant at the 85% level, was still weak. Assessing preference for topographic patterns was not a primary objective of this study and plots were not chosen to maximize statistical power around this covariate. A future study interested in this effect would be better served to choose study plots that are entirely made up of steep slopes rather than the mix of slope and flat areas that I had in my plots as this limits the ability to detect this effect.

While I found that shrub cover reduced the detection of nests, it did not affect nest density. Davis (2005) observed that some grassland birds in Saskatchewan, while avoiding areas with tall dense shrubs, will sometimes place nests close to small shrubs. Despite this observation, he found a positive association between chestnut-collared longspur nest placement and distance from the nest to nearest shrub, suggesting these birds avoided shrub cover around their nest. Working with McCown's longspurs in Colorado, With (1994) observed that half of all nests (14/28) in a moderately grazed pasture were placed beside shrubs and that these nests were 2-3 times more likely to be predated than those not placed next to shrubs. Only 18% (49/263) of the chestnut-collared longspur nests I found had a shrub within one meter of the nest and my analysis did not support a negative effect of shrub cover on either nest density or nest survival. One possible reason for this contrast could be the negative effect that shrub cover had on nest detection, it is possible that previous studies observed fewer nests in areas of moderate shrub cover not because there were fewer nests in those areas but because the shrub cover made it more difficult to locate nests.

The probabilities of detecting the nests of Baird's sparrow, chestnut-collared longspur, and McCown's longspur were all significantly less than perfect, meaning that detection naïve estimates of nest density are likely downward biased. For chestnut-collared longspurs, the probability of detecting a nest was negatively associated with biomass, shrub cover, and ambient temperature during the survey. We found no significant effect of time of day, day of the field season, or wind speed. A previous study similarly found no significant effect of time of day or day of the season but contrary to my results also found no support for an effect of vegetation density (Giovanni et al. 2011).

While to my knowledge no other study has demonstrated a negative relationship of biomass on nest detection, this has long been hypothesized by other researchers (Kirsch 1969). Nest searching protocols differ between studies, but they differ in how observers narrow their search from the entire male's territory down to a relatively small area that is then searched systematically. All nest searching protocols ultimately end with an observer needing to visually locate the nest within a small area. In grassland systems, bird nests are built on the ground and camouflaged by the surrounding vegetation. Areas with higher overall biomass will have taller and denser vegetation making nests harder to locate for both researchers and potential nest predators.

Ambient temperature during the survey had a negative effect on nest detection. This is likely because the rope drag method of nest searching relies on females sitting on their nests at the time of the survey. When the temperature is cool, females are more likely to be on the nest to ensure that the eggs and nestlings do not get hypothermic. When temperatures are warm females can afford to be off nest for longer periods, allowing them to spend more time foraging. It is therefore unsurprising that nest detection declined as ambient temperatures increased.

To my knowledge the effect of shrub cover on detection rate has not been tested before, but I found that shrubs would interfere with rope dragging by catching the drag rope, forcing me to raise the rope up over the shrub before continuing with the survey. Bypassing shrubs in this way likely led to small patches of herbaceous vegetation surrounding shrubs that was not thoroughly searched using the drag rope and may have contained nests.

It is important to note that the N-mixture model I used for the nest density analysis was designed to model counts of living animals, not nests. As such some of the inherent assumptions of these models may not be met when counting nests. A primary assumption is that all replicated surveys take place within a period of population closure, during which no individuals are born, die, immigrate, or emigrate from the survey area. Bird nests do not move so immigration and emigration will be non-existent, but births and deaths should be considered. Nests aren't "born" and don't "die" but nests fail, and new nests are initiated. The rope drag method of nest searching I used can only detect active nests with female birds currently sitting on them. As such, if a nest at a given plot is predated between the repeat surveys then it is not eligible for detection during the second survey and its absence should not be used in estimation of detection probability. My methods did not directly compensate for this potential source of bias. However all four of my study species are known to make second nesting attempts after the completion of the first nest, though the delay period between completion of the previous nest and initiation of the second nest is variable and for some species not well understood (Green et al. 2002, With 2010, Davis et al. 2014, Bleho et al. 2015).

I randomized the survey order of plots so the number of days between repeat surveys varied between plots ($\bar{x}$ = 10.64 ± 3.79 SD, range: 1 – 22), but was long enough on average to allow for birds to make a second nest attempt. I could have standardized the order of surveys such that the time between visits was equal to or greater than the maximum observed time between first and second breeding attempts for all species, however this would have introduced another problem. The number of nests available for detection is not uniform throughout the breeding season, even if nests failure is relatively constant, the date of nest initiation is not. Lipsey and Dreitz (2014) estimated the nest initiation date for grassland songbird nests in Phillips County, MT in 2014 and found that there were two peak periods of nest initiation in late May and mid-June. The first peak corresponds to when most breeding pairs initiate their first nest and the second peak corresponds to the second nest. During these peak periods, the number of nests on the landscape would reach its maximum, then decline as nests fail or succeed. A standard order of plot surveys would result in some plots being surveyed close to the peak period when there are more nests available for detection, while some plots would be surveyed between the peaks when there are fewer nests, introducing bias into the data and interfering with our ability to detect the effect of other factors in nest density. Even if it were possible to ensure that all surveys always gave the birds enough time to renest, this does not preclude the possibility that between visits the first nest of a given breeding pair will fail, they will make a second nest, and then that nest will also fail, all before the next survey. Ultimately no survey order can completely remove the possibility that some nests will not be eligible for detection on repeat visits, but I attempted to mitigate this issue as much as possible.

There are alternatives to the N-mixture models that could be considered. Distance sampling (Buckland 1993) is perhaps the most common approach to accounting for imperfect detection. This method requires walking transects and measuring the distance between the transect and any detected individual, then modeling detection as a function of distance from the transect. Walking transects to find grassland songbird nests is already an established method (Basore et al. 1986) and would not require much modification to include distance sampling. However, this method has its own assumptions and, like N-mixture models, was originally intended for counting animals not nests. Notably, distance sampling models assume that detection varies only with distance and not with any feature of the landscape. This assumption may be appropriate when counting singing adults in an open field, where the landscape is relatively homogenous, but it is likely inappropriate to a heterogenous landscape like the northern mixed-grass prairie. Indeed, my results suggest that biomass and shrub cover both negatively impact nest detection and these characteristics were certainly not homogenous in our plots even at a fine spatial scale. While I concede that nest detection very likely declines with distance from an observer, the inability to account for other factors in detection makes this method less useful in a heterogenous landscape. Despite its flaws I believe that N-mixture models are still preferable when counting bird nests in the northern mixed-grass prairie.

I found no significant evidence for an effect of any of the vegetation covariates measured on the daily survival rate of chestnut-collared longspur nests regardless of scale of assessment. Previous studies also only found weak or insignificant effects of vegetation structure and composition on nest survival (Davis 2005, Lipsey and Dreitz 2014). One explanation for this result is that the fine scale vegetation conditions I measured are less important to nest survival than the large-scale landscape features for which I controlled. When selecting field sites I intentionally controlled for the presence of roads, fences, and power lines which have been shown to negatively affect bird abundance (Sutter et al. 2000, Davis 2004). While controlling for these factors I found that fine scale vegetation conditions at both the nest-site scale and the 9-ha plot scale had no discernable effect on nest survival, suggesting that patch size may be more important than these fine scale vegetation features. This is not to say that fine scale vegetation features are irrelevant however, as I detected effects of plot scale vegetation features on nest density which still impacts overall productivity.

Management Implications

My results demonstrate the importance of accounting for imperfect detection when evaluating nest density for ground nesting grassland songbirds. Consistent with other studies, I found that chestnut-collared longspurs seem to prefer to nest in areas with relatively sparse vegetation. I found an association between nest density for chestnut-collared longspurs and plot biomass, exotic grass cover, and topography. Chestnut-collared longspurs nested in higher density in flatter areas, but realistically it is unlikely that managers will be able to change landscape topography. Instead I would suggest that this result merely shows that managers should target their management action on relatively flat areas, as hilly regions will not be able to support as many nests. Reducing biomass in a region can be done with either livestock grazing or controlled burning, though producers in eastern Montana tend to be resistant to burning (Sliwinski 2017). The elimination of exotic grasses can be done with targeted herbicide (Cox and Allen 2008), mowing, or burning (Diboll 1986). However managers should consider that long-term control of exotics will require multiple years of treatment and that annual precipitation may be more favorable to exotics species over native species in some years (Cox and Allen 2008). The lack of any effect of nest-site or plot-scale vegetation on nest survival suggests that managers should either focus on improving nest density or should focus on increasing patch size (Vickery et al. 1994, Davis 2004).

The contrast between vegetation conditions relevant to nest density and those relevant to nest survival suggests a disconnect between nest site selection and nest-site characteristics that improve nest survival. It is tempting to assume that evolution has adequately prepared bird species to select habitat that maximizes their survival and productivity. However this is not always the case as there are documented cases of maladaptation (Hollander et al. 2011, Piper et al. 2013). If the goal of managers is to maximize species productivity, then my results suggest that evaluating nest density or nest survival alone may be of limited value.

CHAPTER FOUR

CONCLUSION

Grassland birds populations have declined more in the past 40 years than any other avian guild (Knopf 1996, Sauer et al. 2015). In the northern mixed-grass prairie, four species have attracted particular attention due to severe population declines. Baird's sparrow, chestnut-collared longspur, McCown's longspur, and Sprague's pipits are all experiencing annual population declines of 2.9 – 6.2% (Sauer et al. 2015). These declines have attracted the attention of landscape managers interested in improving habitat quality throughout these species' ranges with the goal of slowing or stopping these declines. However, such strategies are currently limited by a lack of knowledge of vegetation associations at spatial scales relevant to management.

Previous studies of vegetation associations for these species have attempted to relate local vegetation structure and composition to species abundance or nest survival. However, these studies typically evaluate vegetation at a fine scale, which is of limited use to management strategies. Typically vegetation is measured at survey locations or nest-sites and at nearby random points or transects (Sutter 1997, Winter 1999, Madden et al. 2000, Davis 2005, Davis et al. 2016). While this spatial scale may be biologically meaningful, landscape managers do not implement practices on patches of land the size of a songbird nest. To provide useful associations for managers, vegetation conditions and bird responses need to be evaluated at spatial scales relative to land management activities.

In addition, abundance or density of birds alone may be a misleading index of habitat quality (van Horne 1986) and evaluation of demographic responses in tandem to abundance is necessary to make appropriate management recommendations. Previous evaluations of grassland bird vegetation relationships are often limited to a local abundance or nest survival, but rarely both. These two metrics are both important to population persistence and there is reason to suspect that they are not linked (Madden et al. 2000, Bock and Jones 2004). Furthermore, the survival rate of nests may be independent of the density of nests within an area (Hollander et al. 2011, Piper et al. 2013), so an understanding of both is necessary to understand the total productivity of a bird population relative to habitat management activities that occur on a unit-area basis.

To help address this gap in knowledge, I conducted surveys within 9-ha study plots. Within each plot, I estimated adult abundances using point counts, nest density and nest survival from nest searching and monitoring, and evaluated both mean and variation in vegetation conditions. Point counts and nest searching surveys were replicated within a period of population closure to allow for estimation and compensation for imperfect detection probabilities. My objectives were to evaluate the relationships between broad scale vegetation structure and composition and abundance, nest density, and nest survival for Baird’s sparrow, chestnut-collared longspur, McCown’s longspur, and Sprague’s pipit.

Plot-level biomass, residual grass cover and litter cover were positively associated with Baird’s sparrow abundance. The abundance of chestnut-collared longspurs was negatively associated with residual grass cover, shrub cover and exotic grass cover and exhibited a quadratic relationship with biomass. McCown's longspur abundance was negatively associated with biomass and shrub cover. The abundance of Sprague's pipits was negatively associated with exotic grass cover and had a quadratic relationship with biomass. Unfortunately, small samples sizes for nests of Baird's sparrows, McCown's longspurs, and Sprague's pipits prevented the estimation of nest density and nest survival. However, sample sizes of chestnut-collared longspur nests were large and nest density was negatively associated with plot-level biomass, exotic grass cover and slope. Contrasting with these findings, nest survival of chestnut-collared longspurs did not appear to be associated with any nest site- or plot-scale vegetation conditions.

Other studies have also found few and weak associations between local vegetation conditions and nest survival for these species (Davis 2005, Lipsey and Dreitz 2014). Nonetheless, this result raises the question of what if anything does impact nest survival. Some obvious possible explanations include an insufficient sample size or a lack of sufficient variation in vegetation conditions to allow for observation of the relationship between these metrics. However, my sample size for chestnut-collared longspur nests was reasonably higher or similar to other studies of this species and vegetation conditions were highly variable both within and between study plots. It has been demonstrated that these species are associated with large-scale landscape features including a positive association with patch size or distance to landscape edge (Davis 2004) and are negatively associated with anthropogenic landscape features such as roads (Sutter et al. 2000) and oil wells (Thompson et al. 2015). When selecting field sites, I attempted to control for variation in large scale landscape features to better be able to detect the effects of local vegetation. The lack of evidence for an effect of these vegetation conditions on nest survival may indicate that these landscape features are more relevant to nest survival than local vegetation. However, to my knowledge there are not currently any studies that examine this relationship, as the studies into these landscape features have only examined bird abundance or occupancy.

The negative and quadratic effects of plot biomass on the abundances of chestnut-collared longspur, McCown's longspur, and Sprague's pipit demonstrate that management strategies for these species will need to limit plant biomass. For managers this will mean that some level of controlled vegetation disturbance will be necessary, either through prescribed fire or livestock grazing. However, local edaphic conditions, precipitation, and plant communities can mediate the effects of livestock grazing and management decisions related to grassland bird conservation should be made at a local level (Lipsey and Naugle 2016). Contrasting vegetation associations among species likely makes ineffective a single local management strategy that improves habitat for all four species. The natural heterogeneity of vegetation structure and composition of the northern mixed-grass prairie may be an asset here, as a large heterogenous landscape could conceivably provide suitable habitat for all four species (Fuhlendorf et al. 2006, Hovick et al. 2014). My study species are nomadic like other grassland birds (Igl and Johnson 1997). Low breeding site fidelity is likely driven by annual changes in precipitation (George et al. 1992). Unusually wet or dry years will increase or decrease local biomass respectively, but while this may displace bird species that occupy a given area in normal precipitation years, it will also allow species with different preferred levels of biomass to move in. Thus, the best approach to preserving a variety of grassland songbird species may be to maintain large patches of grassland with variable productivity such that temporal variations in precipitation will nevertheless result in suitable habitat for all species. Managers interested in promoting or maintaining structural and compositional heterogeneity within grassland habitats may need to induce variable disturbance to the landscape either using patch burning or specialized grazing systems.

The disconnect between relevant covariates to nest density and nest survival suggest possible maladaptation of chestnut-collared longspurs (Hollander et al. 2011). While I observed a simple negative association between exotic grass cover and nest density, if you were to combine estimates of nest density and nest survival into an index of species productivity, then the relationship to local covariates would likely be different. If it is productivity that managers are ultimately concerned with, then an examination of either nest density or nest survival alone may yield spurious results. A useful understanding of productivity for these species may require an evaluation of both metrics.

My results also underscore the importance of accounting for imperfect detection in evaluations of adult abundances or nest densities. Future researchers should be aware that not accounting for detection for these species will likely result in downward biased estimates of abundance and nest density. Furthermore, future studies interested in exploring vegetation associations for these or similar species should consider that plot level topography and vegetation characteristics can influence detection and obscure the true relationship between species abundances and vegetation characteristics. To my knowledge this study is the first to use N-mixture models to model bird nest density and nest detection as functions of plot level and survey specific characteristics. While I have some concerns about the application of some of the assumptions of these models to counting nests (see chapter 3 Discussion), ultimately, I believe that future research should address the confounding influence of spatially-variable detection probabilities of nests.

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