THESIS

GRAZING FOR GRASSLAND BIRDS: ASSESSING HOW MANAGEMENT AND

ENVIRONMENTAL CONDITIONS AFFECT ABUNDANCE IN COLORADO'S

SHORTGRASS STEPPE

Submitted by

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ABSTRACT

GRAZING FOR GRASSLAND BIRDS: ASSESSING HOW MANAGEMENT AND

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Rangelands are temporally and spatially complex socio-ecological systems on which the predominant land use is livestock production. In North America, rangelands also contain approximately 80% of remaining habitat for grassland birds, a guild of species that has experienced precipitous declines since the 1970s. Some evidence suggests livestock grazing can be managed to benefit certain grassland bird species by generating the vegetation structure/density they prefer. These benefits, however, appear to be ecosystem-specific, are equivocal even for species predicted to benefit from grazing (e.g., those that prefer short, sparse vegetation), are rarely considered in conjunction with the full suite of environmental factors known to influence grassland birds (e.g., precipitation, vegetation composition), and are poorly understood for species breeding in the shortgrass steppe. To address these research gaps, I evaluated how two grazing management systems – continuous, season-long grazing and adaptive, rest-rotational grazing – and environmental characteristics (e.g., vegetation structure, vegetation composition, precipitation and topography) affected grassland bird abundance in Colorado's shortgrass steppe. I fit hierarchical distance sampling models that accounted for temporary emigration in a Bayesian framework to five years of point count data (2013-2017) for five focal grassland bird species collected from an ongoing grazing experiment on the Central Plains Experimental Range, a USDA experimental range site, in northeastern Colorado. I first examined grazing impacts on grassland bird abundance

in conjunction with ecological sites, which represent local soil and plant characteristics. When grazing management was evaluated in conjunction with spatial variation in ecological sites, I found two of our five focal bird species responded to grazing management: McCown's longspur abundance decreased and grasshopper sparrow abundance increased in pastures rested from grazing for the entire previous year. In addition, abundances of all focal species varied across ecological sites. To evaluate environmental influences on grassland bird abundance, I first used model selection (deviance information criterion; DIC) to identify temporal scales of precipitation and spatial scales of topography that best predicted grassland bird abundance. I then fit two environmental models – 1) a full environmental model with the best topographic and precipitation scale and vegetation structure and composition covariates for each species, and 2) a full environmental model where I replaced the precipitation scale with a categorical effect of year. Finally, I used model selection (DIC) to evaluate the predictive capacity of my grazing models compared to my environmental models for each species. I found precipitation had the largest magnitude of effect on the abundance of lark bunting and grasshopper sparrow. Vegetation structure had the largest magnitude of effect on the abundance of McCown's longspur, and vegetation composition had the largest magnitude of effect on the abundance of western meadowlark. Vegetation structure and precipitation had the largest magnitude of effect on horned lark abundance. Precipitation strongly and positively affected the abundance of all focal species except western meadowlark, where the effect was strong but negative. Vegetation structure strongly affected the abundance of all species except grasshopper sparrow, and characterized species by their preferred vegetation structure/density (e.g., sparse grass-preferring species' abundances decreased and dense grass-preferring species' abundances increased with vegetation structure). Responses to vegetation composition were generally species specific, but cover of

standing dead vegetation and shortgrass affected the abundance of two of my five focal species. Only McCown's longspur responded to topography. Although my focal species responded to multiple environmental characteristics considered in my environmental models, the grazing models had greater predictive capacity than the environmental models for some of my focal species that prefer more moderate to tall/dense vegetation on the landscape – lark bunting and western meadowlark – and the grazing and environmental models had equal predictive capacity for grasshopper sparrow. This study suggests the factors influencing grassland bird abundance in the shortgrass steppe are complex and diverse. Grazing management alone can predict patterns in grassland bird abundance, but these species also responded to specific components of vegetation composition, vegetation structure and precipitation. Thus, grazing impacts on grassland birds may be context-dependent and managers should consider local environmental conditions (e.g., ecological sites, precipitation conditions, vegetation composition) when developing grazing management for grassland birds. My study occurred during historically wet and average precipitation years, so repeating these analyses in drought would reveal additional and important insight into drivers of grassland bird abundance in the shortgrass steppe. Ultimately, my results suggest cattle production on rangelands can continue to support human economic needs while also supporting grassland bird populations in the shortgrass steppe.

ACKNOWLEDGEMENTS

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Introduction

North America's temperate grasslands, most of which occur in the central Great Plains region of the United States and Canada, are among the most endangered ecosystems on the continent (Samson et al. 2004, Hoekstra et al. 2005). Once covering almost half the landmass (approximately one billion acres) of the continental United States, North America's grasslands declined markedly following the Homestead Act of 1862 in the United States and similar federal acts in Canada. These acts incentivized steady and extensive agricultural conversion that has reduced grasslands to less than 20% of their pre-settlement distribution across North America (Knopf 1994), and in some regions less than 0.1% (Samson et al. 2004). Conversion rates remain high – in the U.S. Western Corn Belt, grasslands continue to be converted to agriculture at similar rates to deforestation in the Brazilian Amazon (Wright and Wimberly 2013).

In addition to loss of area, North America's grasslands have lost much of the heterogeneous, dynamic disturbance processes under which they evolved. Physical characteristics (e.g., climate, topography, soils) and dynamic disturbance processes (e.g., fire, herbivore grazing) drive vegetation heterogeneity in grassland plant communities (Lauenroth et al. 1999). Grasslands are inherently heterogeneous because of the spatio-temporal variability of these drivers at different scales (Toombs et al. 2010, Fuhlendorf et al. 2017). For example, unpredictable, episodic precipitation events resulting in high intra- and inter-annual weather variation define vegetation patterns on the Great Plains and likely influenced historic grazer behavior and pressure (Samson et al. 2004, Fuhlendorf et al. 2006, Skagen and Adams 2012). Pre-European settlement, bison (*Bison bison*) grazed nomadically on the Great Plains by preferentially foraging on high-quality regrowth in recently burned areas (created by natural or anthropogenic fires). Unburned areas,

which received less grazing pressure and where vegetation growth was likely more influenced by rainfall, contained more abundant fuel and would be more likely to burn in subsequent fires. Thus, fire and grazing pressure interactively affected plant composition and structure by creating a "shifting mosaic" of different patch types across a landscape (Fuhlendorf et al. 2006). Today, cattle grazing has replaced bison and prairie dog grazing in most grasslands, and fire regimes are significantly altered such that fire occurs more frequently and uniformly on tallgrass prairie in the east yet is largely absent from shortgrass prairie in the west (Augustine et al. 2010). Maintaining heterogeneity in the western Great Plains (i.e., in shortgrass steppe) is likely even more important given these grasslands are relatively less structurally and compositionally diverse compared to others in the Great Plains region (Toombs et al. 2010).

Much of the remaining grasslands in the United States are rangelands – arid and semiarid systems characterized by low plant productivity and high precipitation variability, including frequent drought, that are unsuited to cultivation (Stoddard et al. 1975, Briske et al. 2015). Livestock grazing is the primary land use on rangelands (Briske et al. 2015) and grasslands directly support this industry; over 95% of the lands necessary to maintain beef cattle in the Great Plains and western U.S. are grasslands (Conner et al. 2001) and over 80% of remaining grasslands are privately owned (North American Bird Conservation Initiative U.S. Committee 2013).

Livestock management on rangelands is generally described by grazing system (Briske et al. 2008). Grazing systems define how grazing is applied on a landscape and are often intended to increase key forage species and cattle production (Briske et al. 2008). They are characterized by stocking rate, timing and duration of grazing and livestock distribution (Briske et al. 2011, Ranellucci et al. 2012). Grazing systems predominately fall into two categories – rotational and continuous. Rotational grazing systems are diversely implemented, but fundamentally describe

systems where livestock are rotated through different pastures throughout the growing season (generally from mid-March to August/September in grasslands). Under continuous grazing systems, livestock remain in the same pastures for the entirety of the growing season.

Rotational grazing systems are often touted as the most effective land management strategy in rangelands because they are assumed to reduce grazing pressure by spatially varying livestock presence on the landscape, thus supporting a fundamental assumption of all grazing systems that rest and deferment promote plant growth (Briske et al. 2008). Briske et al. (2008), however, summarized extensive experimental research that indicated rotational grazing systems are not superior to continuous grazing for a variety of plant and animal responses. The authors suggest multiple reasons for these findings: rotational grazing may have been introduced with unrealistic expectations that were not evidence-based, and grazing systems are constrained by having to optimize competing ecological processes under limited and erratic precipitation and production characteristics of rangelands worldwide. Perhaps most importantly, however, is that many grazing experiments tested effects at very small scales utilizing stocking rates that were too high and rest periods that were too short. The authors suggested grazing system research could benefit from testing the effects of these systems on plants and animals at larger and longer scales with standardized stocking rates (Briske et al. 2008, 2011).

Grassland birds are one suite of species known to respond to grazing management, and the conservation of these species is of high management concern. Grassland birds have experienced the sharpest population declines of almost all guilds of birds in North America (Brennan and Kuvlesky 2005, Sauer et al. 2017). There are nine endemic grassland species of the Great Plains and more than 20 that are more widespread nationally but have a "strong affinity" for the region (Knopf 1996). Approximately half of the 46 species that breed in grasslands are species of

conservation concern and are declining (North American Bird Conservation Initiative U.S. Committee 2009, North American Bird Conservation Initiative 2016). Given that approximately 80% of remaining grassland bird habitat occurs on private lands managed for cattle production (North American Bird Conservation Initiative U.S. Committee 2013), slowing or stopping population declines will require collaborative efforts with private landowners to understand grazing impacts on these species.

While the population declines of many grassland bird species are concerning, multi-species management for grassland birds in the Great Plains is complicated because these species differentially utilize a gradient of vegetation structure and density generated by disturbance patterns (Knopf 1996). Some species prefer short, sparse vegetation created by heavy grazing, recent fire and/or drought conditions, whereas others prefer tall, dense vegetation created by lighter grazing regimes, high precipitation and/or an absence of fire (Wiens 1973, Knopf 1996). Vegetation structure can also influence grassland bird populations directly via nest site selection and success (With 1994, Winter et al. 2005, Skagen et al. 2018). Some grassland birds respond to vegetation composition as well as structure, particularly cover of grasses, bare ground, forbs, dead vegetation, and litter (Fisher and Davis 2010). Recent research suggests grassland birds also respond directly to precipitation patterns; precipitation can be a significant driver of grassland bird abundance at local and regional scales (Niemuth et al. 2008, Ahlering and Merkord 2016, Gorzo et al. 2016, Lipsey and Naugle 2017). Precipitation, rather than grazing intensity or vegetation characteristics, may even drive abundance or constrain the effects of grazing in some systems (Ahlering and Merkord 2016, Lipsey and Naugle 2017). Gaining a better understanding of how grazing and environmental characteristics affect grassland bird populations is imperative to effective conservation and management for these species.

Research to-date has found mixed effects of grazing on grassland bird abundance, where effects are species- and ecosystem-specific (Coppedge et al. 2008, Augustine and Derner 2015a, Ahlering and Merkord 2016), grazing was examined concurrent with and without fire (Sliwinski and Koper 2015, Ahlering and Merkord 2016), and studies employed variable stocking rates and grazing regimes (Johnson et al. 2012, Ranellucci et al. 2012, Sliwinski and Koper 2015). For example, previous studies found higher abundance, no difference, and lower abundance of grasshopper sparrows on rotationally vs. continuously grazed pastures in mixed-grass prairie (Kempema 2007). In a study in tallgrass prairie, average abundance of grasshopper sparrows was highest in traditionally managed pastures (i.e., pastures burned annually and grazed at a standard stocking rate for the region) compared to patch-burned pastures (where cattle could selectively forage between burned and unburned areas; Coppedge et al. 2008). In contrast, grasshopper sparrows were only found in unburned areas in the shortgrass steppe (Augustine and Derner 2015a). Grazing impacts on grassland bird abundance are equivocal even for species that might be expected to benefit most from grazing practices, i.e., species that nest in short, sparse vegetation. In two separate studies, higher stocking rates and grazing with prescribed fire did not increase densities of horned larks (Johnson et al. 2011, Augustine and Derner 2015a), and higher cattle utilization and grazing with prescribed fire did not increase McCown's longspur densities (Augustine and Derner 2015a, Lipsey and Naugle 2017).

Grassland birds are known to respond to factors other than grazing management, but most studies investigating drivers of grassland bird abundance examine only one or two factors. For example, most grassland bird studies have investigated the influences of vegetation characteristics and grazing (Wiens 1973, Knopf 1996, Derner et al. 2009, Augustine and Derner 2015a, Golding and Dreitz 2017) or climate/weather (Niemuth et al. 2008, Langham et al. 2015, Gorzo et al. 2016)

on grassland bird abundance, but rarely the joint effect of grazing, vegetation and climate/weather (though see Lipsey and Naugle 2017). Given that these species evolved under the complex disturbance and climate patterns that define grasslands, developing strategies to mitigate population declines will be best informed by jointly, rather than individually, examining the influence of grazing, vegetation and climate/weather on these species.

Additionally, most research to-date on grazing impacts and habitat preferences of grassland birds has occurred in the Great Plains' mixed-grass and tallgrass prairie (Fuhlendorf et al. 2006, Ranellucci et al. 2012, Sliwinski and Koper 2015, Ahlering and Merkord 2016, Golding and Dreitz 2017, Lipsey and Naugle 2017). Few studies have examined factors driving grassland bird abundance in the shortgrass steppe (Augustine and Derner 2015a), which is the driest and warmest region of the Great Plains. The shortgrass steppe is characterized by having the most inter- and intra-annually variable precipitation regime and the shortest vegetation structure of the Great Plains' grasslands. Its variable climate has resulted in a native vegetation community that is uniquely drought- and grazing-adapted (Lauenroth et al. 1999). This system also contains some of the most extensive grasslands that remain in the Great Plains (Samson et al. 2004), making it particularly important for grassland bird conservation. Grazing impacts on grassland birds have been shown to be ecosystem specific (Coppedge et al. 2008, Augustine and Derner 2015a, Ahlering and Merkord 2016); thus, a thorough understanding of what drives grassland bird abundance in the shortgrass steppe is a critical missing piece for grassland bird conservation across the Great Plains.

Given these research needs, my main thesis objective was to jointly examine how grazing, vegetation, topography and precipitation affect grassland bird abundance on the Central Plains Experimental Range (CPER), a U.S. Department of Agriculture experimental range site, in

Colorado's shortgrass steppe. As part of an ongoing grazing experiment comparing the effects of rotational grazing to continuous, season-long grazing on a variety of ecosystem services, I fit a hierarchical distance sampling model that accounted for temporary emigration in a Bayesian framework to calculate the abundance of five breeding grassland bird species on the CPER – lark bunting (*Calamospiza melanocorys*), McCown's longspur (*Rhynchophanes mccownii*), western meadowlark (*Sturnella neglecta*), horned lark (*Eremophila alpestris*), and grasshopper sparrow (*Ammodramus savannarum*). In my first chapter, I examined how the experimental grazing treatments (season-long grazing; intensive, short-duration rotational grazing; or rest), ecological sites and year affected abundance of these focal species. I also tested whether an interaction of grazing and ecological site affected abundance. In my second chapter, I used the same model structure as in the first chapter to evaluate how fine-scale vegetation data, topography and precipitation affected abundance. I used an information theoretic criterion approach (deviance information criterion [DIC]; Spiegelhalter et al. 2002) to select scales of topographic and precipitation covariates, and to determine whether grazing or environmental conditions most strongly predicted grassland bird abundance on the CPER.

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Chapter 1 – Can Adaptive Rangeland Management Benefit Birds? An Experimental Application in the Shortgrass Steppe

Introduction

Rangelands comprise approximately 40% of the earth's terrestrial surface and today are managed primarily in ways that allow native vegetation to support domestic livestock production (Holechek et al. 2011, Sayre et al. 2013). Domestic livestock production on rangelands currently supports the livelihoods of an estimated 1 billion people, and an estimated 2 billion people rely on products from rangelands (Sayre et al. 2013, Briske et al. 2015). While rangelands of Africa and Asia have supported domestic livestock, often in conjunction with a diversity of native herbivores, for thousands of years, rangelands of North and South America have undergone a transformation over the past 200 years from dominance by native grazers and browsers to dominance by domestic livestock. Despite this focus on livestock production, these systems remain ecologically diverse (Briske et al. 2015) and livestock can potentially serve as critical ecological surrogates for native grazers depending on how their abundance and spatiotemporal distribution are managed (Derner et al. 2009, Allred et al. 2011). For example, livestock management practices can enhance native wildlife populations, such as ungulates in Africa (Odadi et al. 2017, Russell et al. 2018) and birds in Australia and North America (Commonwealth of Australia 2016, Golding and Dreitz 2017, Lipsey and Naugle 2017). The degree to which grazing practices promote biodiversity and the potential economic tradeoffs for producers, however, rarely has been studied in an experimental framework. Furthermore, evidence suggests trends of current agricultural yields are not sufficient to support the world's future population (Ray et al. 2013). With a projected global population increase of 2-4 billion people by 2050 (Cohen 2010), understanding how to balance livestock production needs with biodiversity conservation in grazed systems is increasingly important.

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In the wake of shifting management paradigms, rangelands are increasingly recognized as spatially, temporally and ecologically complex agroecosystems (Fuhlendorf et al. 2012, 2017). In North America, rangeland management historically emphasized practices that created a more uniform pattern of forage utilization across landscapes to most efficiently utilize forage without degrading plant communities (Fuhlendorf et al. 2017, Sayre 2017). To the extent that this leads to structural and compositional homogenization of rangelands, such practices can also potentially lead to declines in the capacity for rangelands to support native biological diversity. As a result, land management agencies and conservation organizations have recommended heterogeneous applications of grazing, such as patch-burn grazing management and rotational grazing systems that include both intense grazing and long-term rest from grazing, to support native biodiversity (Fuhlendorf et al. 2006, Toombs and Roberts 2009). Rotational grazing systems are posited to generate heterogeneity by providing vegetation a sufficiently long release from grazing pressure to recover and attain structural characteristics that support different wildlife species as compared to recently grazed communities (Briske et al. 2011). Rotational grazing systems are currently widespread across North America's rangelands, but the temporal and spatial pattern of livestock movement can vary widely across individual ranches, with unknown implications for sustaining biodiversity (Briske et al. 2008, Roche et al. 2015).

Despite the widespread adoption of various forms of rotational grazing systems in rangelands, experimental evidence for benefits to wildlife has been lacking (Briske et al. 2011). A review of grazing experiments comparing rotational grazing (i.e., heterogeneous management) to continuous, season-long grazing (i.e., homogenous grazing management) indicated rotational grazing is not superior to continuous, season-long grazing for a variety of plant and animal responses (Briske et al. 2008, 2011). This contradicts experiential knowledge of some managers

and producers (Teague et al. 2013, Roche et al. 2015), as well as other evidence suggesting the heterogeneous application of grazing can support biodiversity and wildlife populations on rangelands (Toombs et al. 2010, Ahlering and Merkord 2016, Golding and Dreitz 2017, Lipsey and Naugle 2017). Two important limitations of grazing experiments conducted to date are that experiments occurred in artificially small pastures that prevented livestock from expressing the types of foraging behavior that typically occur on ranches (Briske et al. 2008, Teague and Barnes 2017), and the rest periods implemented in these studies were too short. With short rest periods (e.g., where pastures could be grazed multiple times a growing season), rotational grazing could potentially produce more homogenous vegetation structure because vegetation would not have sufficient time to regrow between rest periods (Fuhlendorf and Engle 2001). There is a clear need to test the effects of grazing management on plants and animals at larger and longer scales with standardized stocking rates and longer rest periods (Briske et al. 2008, 2011).

The few grazing experiments that have examined management for heterogeneous vegetation structure and wildlife have primarily occurred in the tallgrass and mixed-grass ecosystems of North America's Great Plains (Fuhlendorf et al. 2006, Derner et al. 2008, Briske et al. 2011, Golding and Dreitz 2017, Teague and Barnes 2017). Much less is known about the effects of grazing management on biodiversity in semi-arid ecosystems, such as the shortgrass steppe of North America. The shortgrass steppe occupies the driest and warmest region of the Great Plains, and experiences more intra- and inter-annually variable precipitation than the eastern Great Plains (Lauenroth et al. 1999). This results in a unique, drought- and grazing-adapted vegetation community containing the shortest vegetation structure of North America's grasslands (Lauenroth et al. 1999). The shortgrass steppe also contains some of the largest intact rangelands in the Great Plains (Samson et al. 2004). This is important because grassland conversion to agriculture and

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urban development in the Great Plains has likely caused notable sharp declines in wildlife populations. For example, grassland birds breeding in the Great Plains are one of the most threatened guilds of birds in North America (Brennan and Kuvlesky 2005, Sauer et al. 2017). They also differentially utilize a gradient of vegetation structure for breeding habitat, where some species prefer tall, dense structure while others prefer short, sparse structure (Knopf 1996). Research in the cooler and/or wetter mixed-grass and tallgrass prairie has shown some grassland bird species benefit from increased vegetation heterogeneity created by heterogeneous grazing management (Fuhlendorf et al. 2006, Hovick et al. 2012, Ahlering and Merkord 2016). These studies, however, have primarily investigated the interactive effect of fire and grazing (e.g., patch-burn grazing) on grassland birds rather than grazing alone. Fire is a much less common management tool on rangelands in the shortgrass steppe than in the rest of the Great Plains, though patch-burn grazing in the shortgrass steppe can create habitat for some declining grassland bird species (e.g., mountain plover; Augustine and Derner 2015). It is currently unknown whether grazing alone can benefit grassland birds breeding in the shortgrass steppe.

To examine how grazing management can sustain wildlife populations, we implemented a grazing experiment on the Central Plains Experimental Range in Colorado's shortgrass steppe. This experiment is examining the effects of traditional grazing (i.e., continuous, season-long grazing) versus collaborative adaptive rotational grazing on multiple ecosystem services, including grassland bird abundance. One of the explicit goals of this experiment is to maintain or increase populations of five grassland birds breeding on the Central Plains Experimental Range – grasshopper sparrow (*Ammodramus savannarum*), western meadowlark (*Sturnella neglecta*), lark bunting (*Calamospiza melanocorys*), horned lark (*Eremophila alpestris*) and McCown's longspur (*Rhynchophanes mccownii*). We predicted grassland bird species would respond to grazing

management in the manner hypothesized by Knopf (1996), where species that prefer taller vegetation structure (e.g., western meadowlark, grasshopper sparrow; Vickery 1996, Davis and Lanyon 2008) would be more abundant in recently rested pastures of the rotational grazing treatment, while species that prefer shorter vegetation structure (e.g., horned lark, McCown's longspur; Beason 1995, With 2010) would be more abundant in recently intensively grazed pastures of the rotational grazing treatment. Lark buntings prefer more moderate amounts of vegetation structure (Shane 2000), and because we expected vegetation structure to be more homogenous in our traditional treatment, we predicted buntings would be most abundant in traditionally grazed pastures.

Methods

Study area

The Central Plains Experimental Range (CPER) is a 6,270-ha experimental range site managed by the USDA and located outside of Nunn, CO (40°50´N, 104°43´W) in the semiarid shortgrass steppe. Mean daily max and min temperatures range from -12-4°C in January and 15-26°C in July (Skagen et al. 2018). Long-term mean annual precipitation on the CPER is 340 mm (Augustine and Derner 2015a), greater than 80% of which occurs during the growing season of April through September (Lauenroth and Sala 1992). Topography is flat to gently rolling; soils range from fine sandy loams on upland plains to alkaline salt flats bordering a large drainage running north-south in the eastern portion of the site. Two C_4 shortgrass species – blue grama (*Bouteloua gracilis*) and buffalograss (*Bouteloua dactyloides)* – comprise over 70% of aboveground net primary productivity at the CPER (Lauenroth and Burke 2008). C_3 perennial grasses (*Pascopyrum smithii*, *Hesperostipa comata*, and *Elymus elymoides*), C_4 bunchgrasses

(*Aristida longiseta*, *Sporobolus cryptandrus*), plains pricklypear cactus (*Opuntia polyacantha*), subshrubs (*Gutierrezia sarothrae*, *Eriogonum effusum*, *Artemisia frigida*), and saltbush (*Atriplex canescens*) are less abundant but widespread and generate taller structure on the landscape (Augustine and Derner 2015a).

Experimental design

The collaborative adaptive rangeland management (CARM) experiment began in 2013 to contrast the effects of continuous, season-long grazing management (traditional rangeland management [TRM]) with a collaborative form of rotational, multi-paddock grazing management on multiple ecosystem services, including grassland bird diversity, abundance and reproductive performance (Wilmer et al. 2018). For this experiment, ten pairs of 130-ha pastures were established where each pair was similar in terms of the proportion of soil and plant characteristics (i.e., ecological sites), topographic patterns as measured by a topographical wetness index (TWI; a remotely sensed index of water flow on a landscape (Beven and Kirkby 1979)) and prior management history of season-long grazing at moderate stocking rates. One pasture in each pair was randomly assigned to the TRM treatment. Each TRM pasture was grazed throughout the growing season (mid-May to early October) by a single herd of yearling steers. The other pasture in each pair was assigned to a collaborative adaptive rangeland management treatment (CARM; Figure 1). Whereas the TRM pastures were grazed by 10 small herds that occupy each pasture
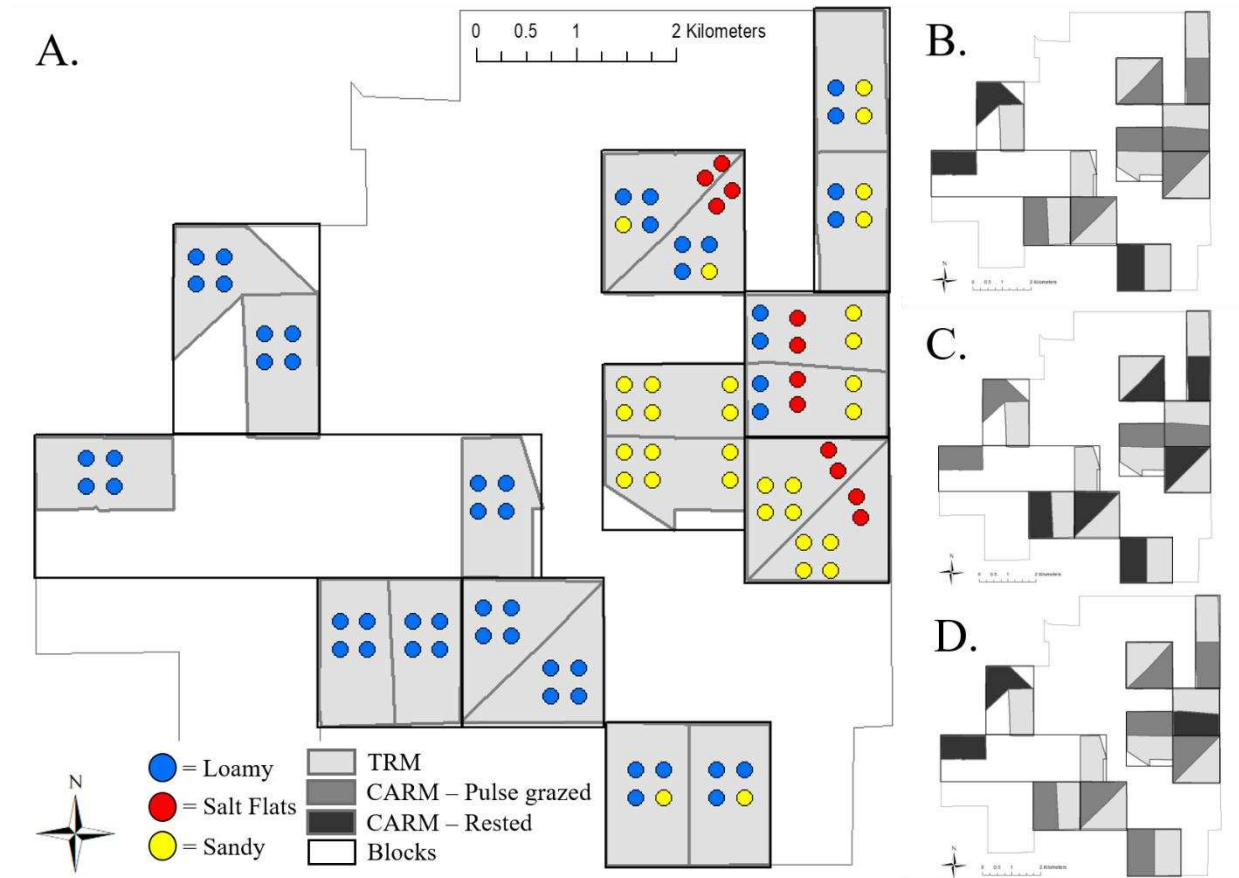
Figure 1. Illustration of the number of monitoring plots on each ecological site (loamy plains, sandy plains, salt flats) and the treatments applied to 10 pasture pairs (blocks). One pasture in each pair received the collaborative adaptive rangeland management (CARM; either intensive, short-duration grazing [pulse grazing] or a lack of grazing [rest]) treatment and one received a traditional rangeland management (TRM) treatment at the Central Plains Experimental Range in eastern Colorado. The light gray line represents the boundary of the CPER. The experiment began with a pretreatment year in 2013, so grazing treatments were first applied in 2014. Because grazing treatments were applied within weeks of conducting the bird surveys, we considered treatments to have a lagged effect on bird abundance. Thus, for the purposes of our analyses, all pastures were labeled with the TRM treatment for 2013 and 2014 (A). Plots B-D show the grazing treatments applied to the site prior to the 2015 – 2017 growing seasons, respectively, illustrating how the two components of the CARM treatment varied by year.

separately, the CARM pastures were grazed by a single large herd of yearling steers managed with

an adaptive, rotational grazing system.

Details of the cattle management strategy applied to the CARM pastures were decided by

an 11-member stakeholder group that developed an initial grazing management plan in 2013, and

subsequently met three times annually during 2014 – 2017 to review results from prior grazing seasons and decide on the stocking rate and grazing sequence for the subsequent grazing season. This stakeholder group included ranchers, stewardship biologists from non-profit conservation organizations, and land managers from federal and state agencies, who collectively made decisions based on consensus or supermajority (see Wilmer et al. 2018 for details). The stakeholder group decided to manage the CARM pastures using a single large herd of yearling steers that would move among 8 pastures each year, contingent on weather patterns, with the remaining 2 pastures planned for year-long rest. The same total number of steers grazed in the CARM and TRM pastures each year, which was set at 214 yearlings in 2014 based on the recommended moderate stocking rate for the ecological sites present in the study area (equivalent to 0.61 AUM ha^{-1}; USDA-NRCS 2007a, 2007b, 2007c). The stakeholder group adjusted the stocking rate annually in subsequent years, depending on past vegetation conditions and weather forecasts for the upcoming grazing season, with the annual stocking rate set in April of each year prior to the May 15th grazing start date. Due to favorable weather conditions in 2014 and 2015, stakeholders increased stocking rate 5% each year to 0.64, 0.67, and 0.70 AUM ha^{-1} in 2015, 2016 and 2017 respectively. The TRM stocking rate was also adjusted each year to match the CARM stocking rate, such that pastures in the two treatments differed only in the spatiotemporal pattern of cattle grazing intensity. Pre-treatment data were collected in 2013, when all 20 pastures received the TRM treatment.

Management of the CARM pastures during 2014-2017 was designed to apply two contrasting grazing intensities to pastures, consisting of either (1) intense but short-duration grazing by the large cattle herd (at 10 times greater stocking density than TRM pastures, which we hereafter refer to as pulse grazing), or (2) year-long lack of grazing (which we hereafter refer to as rest). Which CARM pastures received the pulse grazing treatment and which were rested from

grazing varied across years and depended on the grazing sequence planned by the stakeholders, as well as on-the-ground, weather-dependent conditions (i.e., forage biomass and cattle behavior) measured weekly during the grazing season. Based on weather and vegetation conditions experienced during our study, we applied year-long rest to 3, 6, 3, and 1 of the CARM pastures during 2014 – 2017 respectively, with the remaining 7, 4, 7, and 9 pastures receiving pulse grazing (Figure 1). The larger number of rested pastures in 2015 was a result of above-average forage production in both 2014 and 2015.

Environmental data

To evaluate vegetation and avian responses to grazing management, pastures were stratified by ecological site and monitoring plots were randomly placed within these strata in each pasture. Pastures encompassed 3 types of ecological sites: loamy plains, sandy plains, and salt flats (see USDA-NRCS 2007a, 2007b, 2007c for details on soil series and plant communities associated with each ecological site). The loamy ecological site is most prevalent but least productive, while the salt flats ecological site is most productive but least prevalent on the CPER. We established four monitoring plots in each pasture that only contained loamy and sandy ecological sites, and six monitoring plots in pastures that additionally contained the salt flat ecological site. Each plot contained a systematic grid of four 25-meter transects oriented north-south and spaced 106 m apart, where we measured various vegetation metrics, including vegetation height-density (see below). Avian point count locations were placed in the center of each plot, such that vegetation surrounding the point count location was quantified along with avian abundance.

We used visual obstruction readings (VOR) to quantify vegetation height-density. We measured VOR by placing a Robel pole (Robel et al. 1970) that was modified with 1-cm

increments at eight locations spaced every 3 m along the transects in each plot and recorded the highest band on the pole that was partially or entirely obscured by vegetation. We measured VOR annually in June and calculated the mean VOR for each avian point count location per year.

Avian data

We collected avian abundance data using a standard six-minute point count (Hanni et al. 2013; Figure 1). Point count locations were surveyed between sunrise and ~10:30 am twice during the breeding season between May 26 and June 16. One survey of all points was conducted by the same observer each year (hereafter, survey 1), and a second survey of all points was conducted by a different observer that also changed each year (hereafter, survey 2). Observers used a rangefinder to record the distance to all individual birds detected (i.e., the point count had no fixed radius) and recorded the method of detection for (e.g., aural, visual) and the sex (if determinable) of each individual.

Statistical analyses

We fit hierarchical (*N*-mixture) distance sampling models (Amundson et al. 2014, Royle and Kéry 2016) using repeated counts to estimate temporary emigration (Chandler et al. 2011) to examine the effect of grazing management on grassland bird abundance. Temporary emigration describes the process by which birds enter and leave sampling plots across sampling periods. Incorporating temporary emigration into *N*-mixture models relaxes the assumption of geographic closure common to models for imperfect detection (e.g., distance sampling) by assuming only a subset rather than the entirety of a focal species' population is available for detection during a survey. Relaxing the assumption of constant availability allows for unbiased density estimates

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because the probability of detection given presence and the probability of presence are not confounded (Chandler et al. 2011).

We modeled the abundance of each species at site k (site being a unique combination of year and point count location; N_k), as a function of a Poisson random variable with mean abundance (λ_k) per site:

$N_k \sim \text{Poisson}(\lambda_k)$

We modeled mean abundance per site (λ_k) as a function of a block-specific intercept ($\beta_{0,\text{block}}$; to account for unmodeled heterogeneity among points within blocks) plus categorical effects of year, treatment and ecological site for all species except McCown's longspur. For McCown's longspur, we used a pasture-specific intercept ($\beta_{0,\text{pasture}}$) because the parameters associated with the block random term would not converge when we constrained the longspur data to the loamy plains ecological site. We used a categorical effect of year in our models because preliminary investigation of the raw data revealed that yearly changes in abundance were not linear. We included three treatment effects – the two components of the CARM treatment, pulse grazed and rested, and the traditional, continuous, season-long grazing treatment (TRM). We treated grazing management as a lagged effect on abundance because birds were surveyed each year at the beginning of the growing season, when grazing treatments had only been implemented for a few weeks. We did not examine the contrast between TRM versus all CARM pastures because we hypothesized that pulse grazing and rest would have substantially different and species-specific effects on bird abundance. Our ecological sites included the three dominant ecological sites on the CPER (described above) – loamy plains, sandy plains and salt flats. This resulted in the following treatment model for species-specific abundance:

$$\log(\lambda_k) = \beta_{0,\text{block/pasture}} + \beta_1\,2014_k + \beta_2\,2015_k + \beta_3\,2016_k + \beta_4\,2017_k + \beta_5\,\text{pulse grazed}_k + \beta_6$$

$\text{rested}_k + \beta_7\,\text{salt flats}_k + \beta_8\,\text{sandy plains}_k$

We specified vague normal priors (Normal(0, 10)) for the coefficients for mean abundance per site (λ_k). We specified the same vague normal prior for the mean of the block random terms and the mean of the pasture random terms. We specified a uniform prior from 0 to 10 for the standard deviation of the block and pasture random terms.

We used distance sampling with a hazard rate detection function to model detection probability (p_d; Buckland et al. 2001). We used a generalized linear model with a log-link function to model detection covariates on the scale parameter of the detection function (σ; Amundson et al. 2014). These covariates varied by site k and survey j. We considered fixed effects of VOR and survey, random terms for year and observer, and combinations of these as potentially influencing detection. Because observers who conducted the second survey varied each year, we did not consider observer and year in the same detection model. We truncated the distance sampling data by 10% (*sensu* Buckland et al. 2001) before fitting models and we specified vague normal priors on the coefficients for the detection model. We specified either a weakly-informative half-cauchy (Gelman 2006) or vague uniform(0, 10) priors for the standard deviations of the random terms. We chose a final detection model based on visually assessing trace plots, the Gelman-Rubin statistic for parameter convergence (Gelman et al. 2013), and a chi-square discrepancy goodness of fit test (Amundson et al. 2014, Royle and Kéry 2016). We considered parameters with Gelman-Rubin statistics ≤1.10 as converged (Gelman et al. 2013). Our goodness of fit test evaluated model fit using posterior predictive distributions to calculate a Bayesian *p*-value. We considered Bayesian *p*-values ≤0.1 or ≥0.9 to indicate a lack of fit (Amundson et al. 2014).

Depending on the species, we included either an effect of VOR on temporary emigration, a null model on temporary emigration (p_a; Chandler et al. 2011), or no temporary emigration. In support of parsimony, we first fit models without temporary emigration. If parameters did not converge or the model did not fit, we added temporary emigration to the model. For models that included temporary emigration, we assumed observed counts y_{kj} were the outcome of a binomial distribution conditioned on true abundance N, detection probability $p_{d,kj}$, and temporary emigration probability $p_{a,k}$,

$$y_{kj} \sim \text{Binomial}(N_k, p_{d,kj}\, p_{a,k})$$

We specified covariates on the logit scale to model covariate effects on temporary emigration,

$$\text{logit}(p_{a,k}) = \delta_0 \text{ or}$$

$$\text{logit}(p_{a,k}) = \delta_0 + \delta_{1k}\text{VOR}_k$$

We specified either vague normal priors on both the linear coefficients of the temporary emigration model (i.e., δ_0 and δ_1), or a Jeffreys prior on the intercept (δ_0; Lunn et al. 2012) and a normal vague prior on the linear coefficient for VOR (δ_1). For models that did not include temporary emigration, we assumed observed counts y_{kj} were the outcome of a binomial distribution conditioned on true abundance N_k and detection probability $p_{d,kj}$.

Once we identified a detection and emigration model, we fit a model for each species with the covariates on abundance as described above and a model with an interaction between treatment and ecological site. We considered an interaction between treatment and ecological site because previous research found soil productivity explained grazing effects on grassland birds (Lipsey and Naugle 2017), and the ecological sites on the CPER differ in terms of productivity (USDA-NRCS 2007a, 2007b, 2007c).

We fit models to all detections of both sexes for western meadowlark, horned lark and grasshopper sparrow because sexes could rarely be distinguished with certainty. Lark bunting and McCown's longspur males, however, have unique flight displays (skylarking) during the breeding season to attract mates (Shane 2000, With 2010). Skylarking males of these species are substantially more detectable than females, and over 90% of our detections for these species were males. Due to this skew in detection, we fit models for lark bunting and McCown's longspur to male detections only. In addition, there was only one detection of a McCown's longspur on a non-loamy ecological site over the five years of our surveys. Therefore, we fit models for McCown's longspur to detections of longspur males on the loamy ecological site only.

We fit the two models described above using the packages rjags (Plummer 2016) with three MCMC chains for 200,000-550,000 iterations and saved the final 50,000-100,000 iterations per chain. We calculated means and 95% credible intervals (CRI) for all model parameters.

Results

We surveyed 92 point count locations twice per year over 5 years, resulting in 920 surveys. Lark bunting males were detected the most (2,660) and McCown's longspur males were detected the least (287). For both sexes combined of western meadowlark, horned lark and grasshopper sparrow, we had 1,367, 1,327, and 715 detections, respectively.

Different factors influenced species' availability for and probability of detection (i.e., temporary emigration and detection probability; Appendix 1). Models for all species except lark bunting included temporary emigration. Models for horned lark and western meadowlark included a null model on emigration, while models for grasshopper sparrow and McCown's included an effect of VOR on temporary emigration. The average probability that McCown's longspur, horned

lark, and western meadowlark were available to be detected ranged from approximately 17 to 27% (from coefficient estimates calculated from the logit scale; Appendix 1). The average probability grasshopper sparrow was available to be detected was noticeably higher, around 62%. Grasshopper sparrow availability for detection increased while McCown's longspur availability for detection decreased with vegetation structure (VOR); at one standard deviation above average vegetation structure on the site, grasshopper sparrow availability increased to ~ 89% and longspur availability decreased to ~11% (Appendix 1). Given birds were available to be detected, survey and a random term for year influenced detection probability of McCown's longspur and grasshopper sparrow (Appendix 1). A random term for year influenced detection probability of horned lark and a random term for observer influenced detection probability of western meadowlark (Appendix 1). Survey influenced detection probability of lark bunting.

Our model fit with year, treatment, and ecological site on abundance revealed that two of the five focal species responded strongly to grazing management. Resting pastures (i.e., no grazing throughout the previous growing season) positively influenced grasshopper sparrow abundance and negatively influenced McCown's longspur abundance in the subsequent year (Table 1.1, Figure 1.2). In pastures that received rest from grazing, rather than traditional or pulse grazing, grasshopper sparrow density increased by 0.471 – 0.528 birds/ha, respectively, or approximately 2 birds per point count location. In both traditionally and pulse grazed pastures, male McCown's longspur density increased by 0.078 or 0.069 birds/ha, respectively, or approximately 0.4 – 0.5 males per point count location, compared to rested pastures in the loamy plains ecological site. Grazing treatment did not strongly influence western meadowlark, horned lark and lark bunting abundance (Table 1.1, Figure 1.3).

Table 1.1. Coefficient means and 95% credible intervals (CRIs) of year (2013 – 2017), grazing treatment (traditional, pulse grazed, rested) and ecological site (loamy plains, salt flats, sandy plains) modeled on abundance for five grassland birds breeding on the Central Plains Experimental Range, Colorado, from 2013 – 2017. The intercept reported for lark bunting, horned lark, grasshopper sparrow and western meadowlark is the average of the block-specific intercept. The intercept reported for McCown's longspur is the average of the pasture-specific intercept. Estimates for year are in relation to 2013. Estimates for grazing treatment are in relation to the traditional rangeland management treatment (TRM; continuous, season-long grazing). Estimates for ecological site are in reference to the loamy plains ecological site. Bolded values are those for which the 95% credible interval of the coefficient does not include 0. Abundance for lark bunting was modeled using only male detections. Abundance for McCown's longspur was modeled using only male detections on the loamy ecological site. MCLO = McCown's longspur, HOLA = horned lark, LARB = lark bunting, WEME = western meadowlark, GRSP = grasshopper sparrow.

| | MCLO | | HOLA | | LARB | | WEME | | GRSP | |
	Mean	CRI	Mean	CRI	Mean	CRI	Mean	CRI	Mean	CRI
Intercept	-1.170	(-3.385, 0.431)	**2.684**	(2.119, 3.362)	**1.551**	(1.371, 1.732)	**1.571**	(1.000, 2.276)	0.011	(-0.663, 0.718)
2014	0.463	(0.064, 0.992)	**0.320**	(0.051, 0.585)	**0.786**	(0.648, 0.927)	0.184	(-0.111, 0.484)	0.034	(-0.619, 0.717)
2015	**0.515**	(0.044, 0.980)	**0.606**	(0.366, 0.847)	**0.673**	(0.518, 0.829)	**0.928**	(0.667, 1.189)	**1.186**	(0.577, 1.822)
2016	-0.206	(-0.856, 0.407)	**0.709**	(0.458, 0.959)	**-0.697**	(-0.908, -0.489)	**1.680**	(1.429, 1.934)	**1.135**	(0.472, 1.812)
2017	0.395	(-0.248, 1.140)	-0.233	(-0.534, 0.068)	**-0.325**	(-0.514, -0.136)	**1.005**	(0.738, 1.279)	-0.101	(-0.728, 0.557)
Pulse grazing	-0.101	(-0.692, 0.474)	0.112	(-0.052, 0.275)	0.066	(-0.080, 0.210)	0.039	(-0.116, 0.193)	-0.064	(-0.287, 0.155)
Rested	**-1.276**	(-2.588, -0.213)	-0.106	(-0.294, 0.078)	0.022	(-0.165, 0.206)	0.004	(-0.174, 0.180)	**0.344**	(0.091, 0.595)
Salt flats			**-1.499**	(-1.821, -1.192)	**-0.383**	(-0.575, -0.194)	**0.447**	(0.243, 0.646)	**0.931**	(0.591, 1.289)
Sandy plains			**-0.583**	(-0.795, -0.368)	0.015	(-0.125, 0.159)	**0.196**	(0.011, 0.375)	**0.694**	(0.395, 1.003)
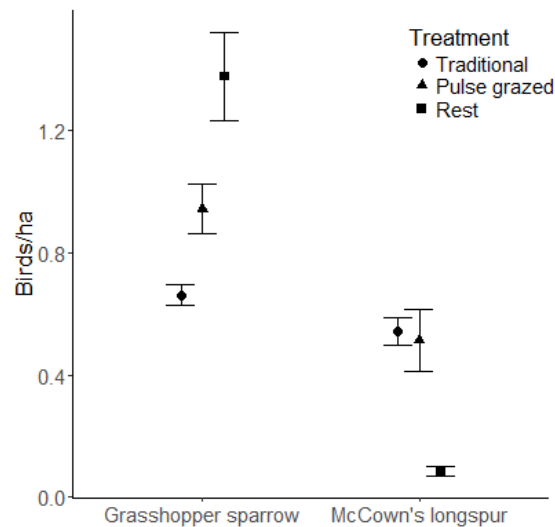
Figure 1.2. Mean densities and standard errors of the two grassland bird species that responded to grazing management in our study – grasshopper sparrow and McCown's longspur – in the traditional, pulse grazed and rested grazing treatments from 2013 – 2017 on the Central Plains Experimental Range, Colorado.
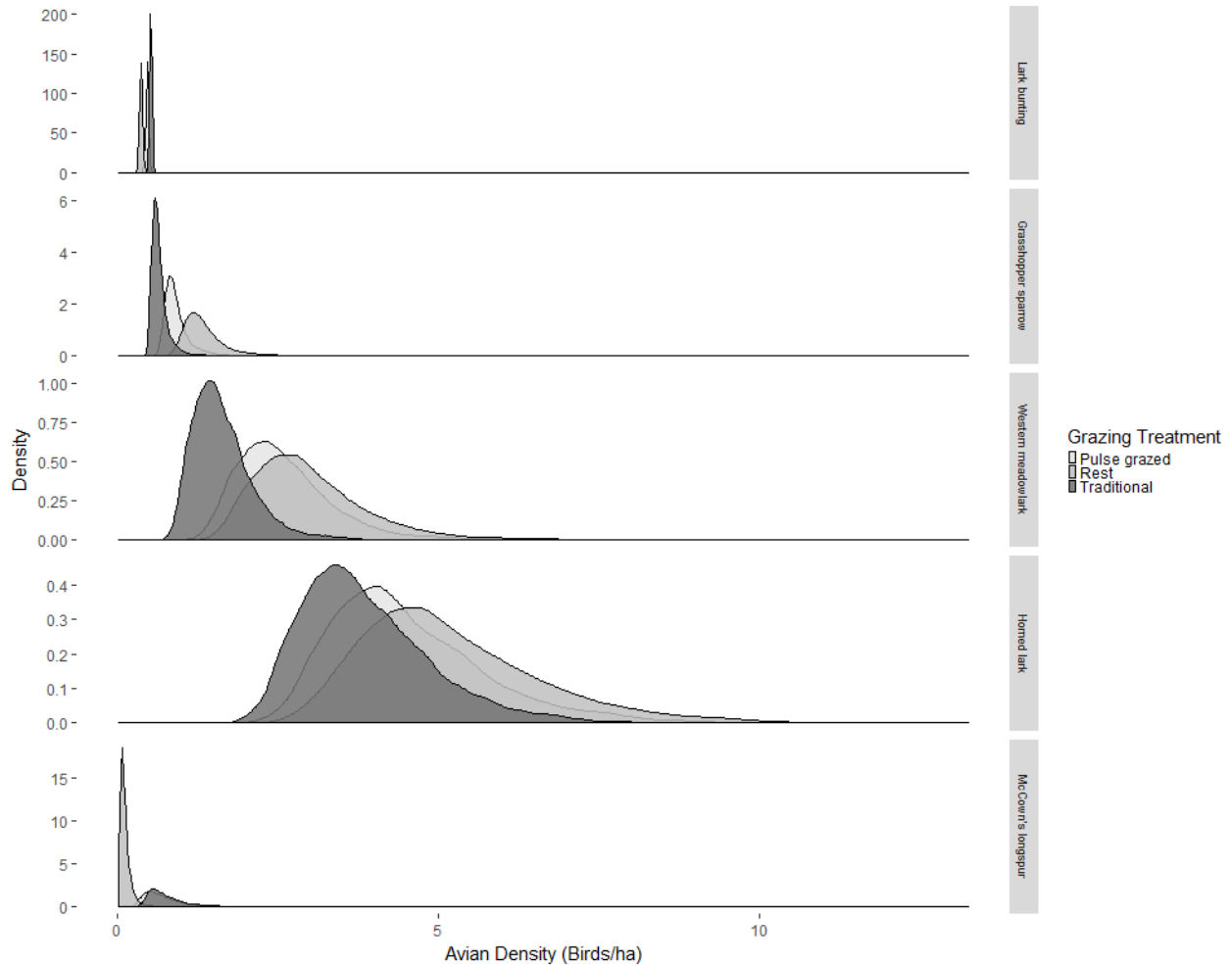
Figure 1.3. Posterior distributions of estimated avian density (birds/ha) of our five focal grassland bird species in the traditional, pulse grazed and rested grazing treatments from 2013 – 2017 on the Central Plains Experimental Range, Colorado.

For all focal species, year and ecological site influenced bird abundance more than grazing management. Abundance for each species differed substantially between 2013 and 2015, and differed in at least one year compared to 2013 (e.g., grasshopper sparrow abundance was greater in 2015 and 2016 compared to 2013; Table 1.1). McCown's longspurs were detected almost exclusively in the loamy plains ecological site, and horned larks were more abundant on the loamy plains ecological site compared to the sandy plains or salt flat ecological sites. Lark buntings were more abundant in the loamy and sandy plains ecological sites than in the salt flat ecological site.

In contrast, grasshopper sparrow and western meadowlarks were more abundant in the salt flat and sandy plains ecological sites than the loamy plains ecological site (Table 1.1).

Interactions between grazing and ecological site were not supported for any species except horned lark. Horned lark abundance was lower in pulse grazed pastures in the sandy plains ecological site compared to the sandy plains ecological site (β=-0.420, CRI: -0.788, -0.64; Figure 1.4). This model, however, was the only model we considered that indicated lack of fit (Bayesian p-value = 0.08).

Discussion

Heterogeneity-based grazing management is posited to maintain avian biodiversity by generating the entire spectrum of vegetation structure utilized by grassland birds on their breeding grounds (Knopf 1996, Fuhlendorf and Engle 2001, Derner et al. 2009, Toombs et al. 2010). In our study, heterogenous grazing management affected the abundance of two grassland bird species
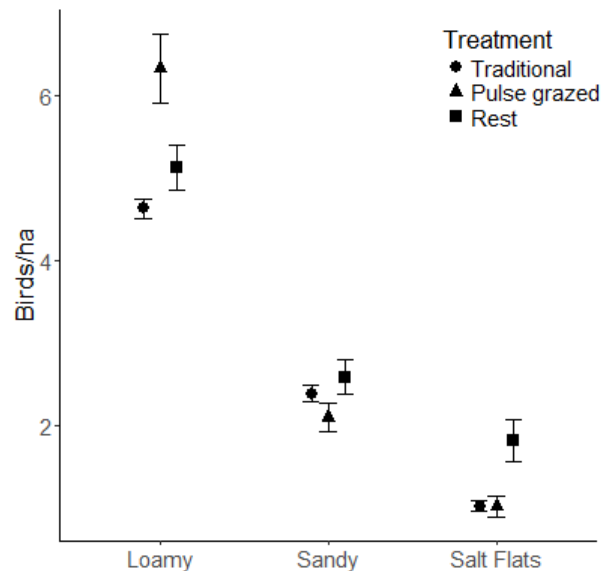
Figure 1.4. Mean density and standard error of horned lark by ecological site and grazing treatment from 2013 – 2017 on the Central Plains Experimental Range, Colorado. Metrics were calculated from the model with an interaction between grazing treatment and ecological site.

that prefer the opposite extremes of grassland vegetation structure in the shortgrass steppe (Knopf 1996, Augustine and Derner 2015a).

As we predicted, a lack of grazing for an entire growing season negatively affected McCown's longspur and positively affected grasshopper sparrow abundance in the subsequent year. This matches these species' respective breeding preferences for short, sparse vegetation and tall, dense vegetation (Vickery 1996a, With 2010). We found no effect of grazing management on western meadowlark, lark bunting, or horned lark abundance. Western meadowlark prefers taller, denser vegetation while horned lark prefers shorter, sparser vegetation, but both species are more widespread generalists compared to our other focal species (Beason 1995, Davis and Lanyon 2008). Previous research found horned lark abundance did not differ between season-long grazing and rest-rotational grazing systems in a sagebrush system (Golding and Dreitz 2017), and meadowlark abundance was both higher and lower in season-long vs. rotationally grazed pastures in mixed-grass prairie depending on the year (Ranellucci et al. 2012). Lark buntings prefer more moderate structure (Shane 2000) and were more abundant in continuously-grazed pastures in a sagebrush system (Golding and Dreitz 2017), but evidence suggests abundance for this species is driven more by regional precipitation patterns than local habitat conditions (Skagen and Adams 2012). Our results and these previous studies suggest both grazing management systems can generate sufficient habitat for these species in the shortgrass steppe, these species are responding to a resource on the landscape that is not being affected by grazing management (e.g., insect abundance; Newbold et al. 2014), or abundance for these species is driven by processes occurring at scales larger than our site (Skagen and Adams 2012).

We were surprised to find pulse grazing on the sandy plains ecological site negatively affected horned lark abundance. We would expect pulse grazing on the sandy plains ecological

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site to benefit horned larks by generating the shorter structure they prefer (Beason 1995) in a more productive ecological site. However, this result may reflect the complexity of implementing adaptive management to achieve desired outcomes across space and time (Aldridge et al. 2004). Our pulse grazing treatment was designed to create short vegetation through grazing at high stock density, but each grazed pasture in the CARM treatment was only pulse grazed once during a growing season. If the pasture was pulse grazed early in the growing season, vegetation could regrow such that the pulse-grazed pasture could potentially support tall, dense vegetation by the end of a growing season. In contrast, vegetation in pastures pulse grazed at the end of the growing season could remain relatively short until the next growing season. The timing of grazing could be even more important depending on whether it was a wet or dry year (Ahlering and Merkord 2016, Lipsey and Naugle 2017), where a pasture pulse grazed early in the season would be more likely to support tall, dense vegetation by the end of the growing season in a wet year. This could increase variability in our evaluation of a 'static' treatment category, and illustrates the inherent and significant complexity in rangeland systems, the need to explicitly consider and manage for this complexity, and the importance of examining adaptive management in an experimental framework.

Our study supports the emerging paradigm of managing for heterogeneous vegetation structure in rangelands to sustain native biodiversity (Derner et al. 2009, Toombs et al. 2010, Fuhlendorf et al. 2017), but adds additional insight. We found heterogeneous grazing treatments were not always sufficient to achieve desired outcomes. Rather, applying grazing in the right place at the right time was necessary to benefit focal species. For example, McCown's longspur remained restricted to the loamy plains ecological site even though other portions of the CPER were pulse grazed each year to generate the short vegetation structure that longspurs prefer (With

2010). Similarly, while grasshopper sparrows benefitted from rest, grasshopper sparrows were always most abundant in the salt flats and sandy plains ecological sites. Given these results, we hypothesize that targeting more frequent pulse grazing on loamy plains would benefit McCown's longspur and targeting more frequent rest on sandy plains and salt flats would benefit grasshopper sparrow. Adaptive changes to the CARM grazing rotation were made in 2017 and 2018 to test these hypotheses.

Ultimately, we found grazing management on rangelands can enhance habitat for a diverse grassland bird community. Achieving this outcome may require focused and flexible management where grazing is applied to areas with appropriate topo-edaphic conditions to support the habitat needs of focal species. Our study addressed shortcomings of prior rotational grazing research by employing realistic spatial scales and controlling for stocking rate effects (see Briske et al. 2011, Teague and Barnes 2017), and represents one of the first experiments to document effects of livestock movement patterns on wildlife habitat (though see also Golding and Dreitz 2017). Our work suggests the effects of grazing management on grassland birds are more context-specific than suggested by the grazing/vegetation heterogeneity model originally presented by Knopf (1996) and support the view of rangelands as spatially and temporally complex ecological systems (Fuhlendorf et al. 2017). Applying adaptive management in the context of this complexity may allow rangelands to serve as important repositories of biodiversity under future climate and population change, while continuing to support livestock and human livelihoods.

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Chapter 2 – Vegetation Composition, Vegetation Structure and Precipitation Jointly Influence Grassland Bird Abundance in the Shortgrass Steppe

Introduction

Temperate grasslands are one of the most endangered ecosystems worldwide (Hoekstra et al. 2005). Agricultural conversion and urban development have reduced North America's Great Plains, a region of temperate grasslands which used to cover almost half of the continental U.S., to less than 30% of its original extent over the last two hundred years (Samson et al. 2004). Grasslands in the U.S. western Corn Belt continue to be converted to cropland at a rate comparable to deforestation rates in Brazil and the South Pacific (Wright and Wimberly 2013). Concurrent with this loss of native grasslands has been a loss of native wildlife that depends on them. Grassland birds, many species of which breed in the Great Plains, are one of the most threatened guild of birds in North America (Brennan and Kuvlesky 2005, Sauer et al. 2017). Of the 46 species that breed in grasslands, 48% are species of conservation concern and 50% are declining (North American Bird Conservation Initiative U.S. Committee 2009). With grassland conversion still occurring and the global human population projected to grow, it is increasingly important to understand and manage for the factors that influence population viability of grassland species.

More than 80% of remaining grassland bird habitat occurs on private lands that are primarily managed for cattle production (North American Bird Conservation Initiative U.S. Committee 2013). While this creates challenges for conservation and management for grassland birds, there is great potential for cattle, and their associated effects on the structure and function of Great Plains grasslands, to coexist with native fauna (Fuhlendorf et al. 2006, Derner et al. 2009). Grassland birds breed across a gradient of vegetation structure generated by disturbance, ranging from short, sparse vegetation to tall, dense vegetation (Figure 1; Knopf 1996, D. Augustine,

unpublished data). Historically, grazing by native herbivores (e.g., bison and prairie dogs) and fire generated the structural heterogeneity needed to support the full suite of grassland bird species native to North America's grasslands (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006). Today, fire and/or cattle grazing are used to manage most grasslands, and research shows these management practices can enhance habitat for and/or increase abundance of some grassland bird species (Augustine and Derner 2015b, Ahlering and Merkord 2016, Golding and Dreitz 2017, Lipsey and Naugle 2017). Additionally, the cattle production industry supports rural cultures, sustains human livelihoods and provides important food products to local and regional economies (Sayre et al. 2013). If implemented properly, cattle grazing could potentially benefit both the economy and vulnerable grassland bird species.

While it is widely accepted that grassland birds respond to vegetation structure (and thus indirectly to grazing), other factors, such as vegetation composition and fluctuating weather conditions, also affect grassland bird abundance (Samson et al. 2004, Niemuth et al. 2008, Fisher and Davis 2010, Gorzo et al. 2016, Lipsey and Naugle 2017). For example, grassland birds differentially respond to cover of bare ground, litter, grasses and forbs (Fisher and Davis 2010, Lipsey and Naugle 2017). Recent evidence suggests precipitation variability both positively and negatively affects abundance of some grassland bird species at regional scales (Gorzo et al. 2016), and at more local scales, regional precipitation patterns dictate whether or how grazing affects grassland birds (Ahlering and Merkord 2016, Lipsey and Naugle 2017). For example, in wet, productive years, grazing may benefit species that prefer more sparse/short vegetation by reducing vegetation structure, but not affect the abundance of species that prefer taller and denser vegetation (Lipsey and Naugle 2017). Additionally, precipitation in the 12 months preceding the breeding season may drive avian community composition regardless of grazing management (Ahlering and

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Merkord 2016). The factors influencing grassland bird abundance may be more complex and temporally variable than have been previously considered in simple conceptual models of grassland bird habitat (e.g., Knopf 1996; Figure 2.1).

Most research investigating drivers of grassland bird abundance in North America has occurred in tallgrass and mixed-grass prairies (Fuhlendorf et al. 2006, Ranellucci et al. 2012, Ethier and Nudds 2015, Duchardt et al. 2016, Greer et al. 2016, Golding and Dreitz 2017, Lipsey and Naugle 2017) while few studies have investigated such drivers in the shortgrass steppe (though see Augustine and Derner 2015). The shortgrass steppe is the warmest and most arid region of North America's Great Plains, and is characterized by dramatically variable precipitation within
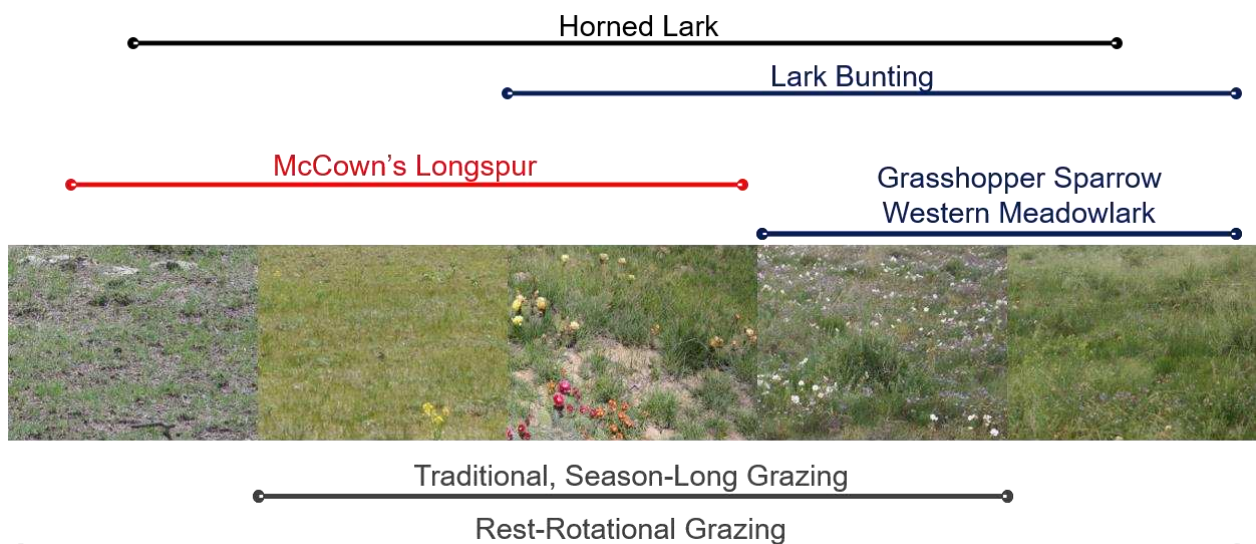
Figure 2.1. Hypothesized influence of grazing management on vegetation heterogeneity and grassland birds in shortgrass rangelands of the western Great Plains (created by D. Augustine, unpublished data). Photographs depict variation in vegetation structure ranging from a blue grama/bare soil mosaic (far left) to a closed-canopy sward of perennial forbs and mid-height, C_3 grasses (far right). The width of bars represents the range of vegetation structure/density over which each bird species occurs and/or that is generated by different grazing management. Traditional, season-long grazing refers to grazing management where cattle are kept in a single pasture for the entirety of the growing season. Rest-rotational grazing refers to grazing management where cattle are rotated through multiple pastures over the course of the growing season, with some pastures left ungrazed, or rested. Colors indicate different guilds of species, with listed example species: red represents associates of sparse/prostrate vegetation (i.e., McCown's longspur), blue represents associates of dense/tall vegetation (e.g., western meadowlark) and black represents a generalist that utilizes a wide range of conditions (e.g., horned lark).

and across years (Wiens 1973). This variable climate produces a vegetation community that is uniquely drought- and grazing-adapted and contains the shortest vegetation structure of the Great Plains' grasslands (Lauenroth et al. 1999). The shortgrass steppe also contains some of North America's most intact grasslands (Samson et al. 2004), which makes the region particularly important for grassland birds. To best manage for these declining species, it is critical to understand factors driving abundance for grassland bird populations breeding in warmer, drier, and more interannually variable grasslands than have been studied previously.

To address the research gaps described above, we examined how environmental characteristics (e.g., precipitation, vegetation composition/structure, topography) influence grassland bird abundance in the shortgrass steppe. We conducted this study within a larger, ongoing grazing experiment comparing how season-long grazing versus adaptive, multi-paddock rotational grazing affect a variety of ecosystem services, including grassland bird abundance. This experiment began in 2013 and is expected to continue until 2023. Using data collected during the first five years of the study, we first fit hierarchical distance sampling models in a Bayesian framework to determine whether grazing management affected grassland bird abundance (described in Chapter 1). We then used the same model structure to determine the degree to which environmental characteristics predict grassland bird abundance in the shortgrass steppe. Finally, we compared the predictive capacity of our grazing models to our environmental models using deviance information criterion (DIC; Spiegelhalter et al. 2002).

Methods

Study area

      The Central Plains Experimental Range (CPER), managed by the USDA-ARS in Colorado's semiarid shortgrass steppe, encompasses 6,270 hectares located ~12 km northeast of Nunn, CO (40°50´N, 104°43´W). Mean daily max and min temperatures range from -12 to 4°C in January and 15 to 26°C in July (Skagen et al. 2018). Long-term mean annual precipitation and mean annual growing season precipitation (April – August) on the CPER were 340 mm and 242 mm, respectively (Augustine and Derner 2015a). Growing season precipitation for the years of our study were 406 mm, 370 mm, 380 mm, 256 mm, and 272 mm (2013 – 2017). Greater than 80% of annual precipitation occurs during the growing season of April through September (Lauenroth and Sala 1992). Soils on the CPER vary from fine sandy loams on upland plains to alkaline salt flats bordering a large drainage running north-south in the eastern portion of the site. Topography is flat to gently rolling. Blue grama (*Bouteloua gracilis*) and buffalograss (*Bouteloua dactyloides)* comprise over 70% of aboveground net primary productivity on the site (Lauenroth and Burke 2008). C_3 perennial grasses (*Pascopyrum smithii*, *Hesperostipa comata*, and *Elymus elymoides*), C_4 bunchgrasses (*Aristida longiseta*, *Sporobolus cryptandrus*), plains pricklypear cactus (*Opuntia polyacantha*), subshrubs (*Gutierrezia sarothrae*, *Eriogonum effusum*, *Artemisia frigida*), and saltbush (*Atriplex canescens*) are less abundant but widespread and generate taller structure on the landscape (Augustine and Derner 2015a).

Data collection

Vegetation

To evaluate vegetation and avian responses to grazing management, 20 treatment pastures were paired into 10 blocks. Pastures were then stratified by ecological site and monitoring plots were randomly placed within these strata in each pasture. Pastures included 3 types of ecological sites: loamy plains, sandy plains, and salt flats (see USDA-NRCS 2007a, 2007b, 2007c for details on soil series and plant communities associated with each ecological site). The ecological sites on the CPER follow opposing gradients of prevalence and productivity – the loamy ecological site is most prevalent but least productive, while the salt flats ecological site is least prevalent but most productive. Pastures with only sandy and/or loamy ecological sites contained four plots, while pastures with the additional salt flat ecological sites contained six. This resulted in a total of 96 plots across the 20 treatment pastures. Each plot contained a systematic grid of four 25-meter transects oriented north-south and spaced 106 m. Avian point count locations were placed in the center of each plot so that vegetation surrounding the point count location was quantified along with avian abundance. Thus, each pasture contained four to six point count locations.

We collected data on vegetation composition and structure from the four transects within each vegetation plot annually in June from 2013 – 2017. Along each transect, we used the line-point intercept method to quantify canopy and basal vegetation cover by species (50 intercepts per transect, modified to record all canopy intercepts for each species; Herrick et al. 2005). We then cumulated all vegetation species detected in these surveys into eight structural/functional groups: shortgrass, midgrass, cactus, forb, shrub, subshrub, standing dead, and litter. We calculated the mean absolute cover per transect of each of these groups by plot in each year to obtain an absolute cover value for each structural/functional group per plot per year. We calculated absolute cover

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(which can be less than or exceed 100%) rather than relative cover because absolute cover is a measure of both vegetation composition and abundance, while relative cover reflects only composition. We expected that grassland birds may respond not only to species composition on the landscape, but also to the extent and abundance of certain vegetation groups.

We estimated visual obstruction readings (VOR) to quantify vegetation structure (height/density) at each plot. We measured VOR by placing a visual obstruction pole modeled after Robel et al. (1970) but modified with 1-cm increments at each of eight locations spaced every 3 m along the transects established in each plot and recorded the highest band on the pole that was partially or entirely obscured by vegetation (Robel et al. 1970). We calculated mean VOR for each point count location per year.

Topographic indices

We used the topographic ruggedness index (TRI) and topographic wetness index (TWI) to quantify topography on the CPER. The topographic ruggedness index denotes average elevation change between any point on a grid and its surrounding area (Riley et al. 1999). The topographic wetness index (TWI) is a steady-state wetness index where larger TWI values represent drainage depressions, or wetter areas, while smaller TWI values represent crests and ridges, or drier areas (Beven and Kirkby 1979). Because grassland birds exhibit scale-dependent responses to habitat characteristics (Duchardt et al. 2016, Greer et al. 2016, Guttery et al. 2017), we considered TRI and TWI calculated at three scales surrounding the point count location: 50 m, 150 m, and 250 m. These scales were meant to represent an individual bird's territory (50 m; Beason 1995, Vickery 1996a, Shane 2000, Davis and Lanyon 2008, With 2010), the scale immediately surrounding an individual's territory (150 m; also the scale most comparable to that represented by the vegetation

data), and a scale representing the larger landscape surrounding an individual's territory (250 m). TRI and TWI were calculated in ArcGIS version 10.2.2 (ESRI 2014) using a digital elevation model of the CPER developed by the National Ecological Observation Network (NEON) and the "Roughness" tool in the Geomorphometry and Gradient Metrics toolbox for TRI (Evans et al. 2014) and the Landscape Connectivity and Pattern toolbox for TWI (Theobald 2007).

Precipitation

Recent studies have shown current year and previous year's annual precipitation (June-May) to be an important predictor of grassland bird abundance at local and landscape scales (Niemuth et al. 2008, Gorzo et al. 2016, Lipsey and Naugle 2017). Studies examining precipitation on vegetation production on the CPER (i.e., the most likely mechanism by which precipitation would affect birds) found cool-season precipitation (October-April) best explained forage production (Milchunas et al. 1994) while spring precipitation (April-June) best explained annual net primary production (Irisarri et al. 2016). Due to these studies and our own predictions, we considered six precipitation windows that could influence abundance (Table 2.1).

We calculated all precipitation windows using cumulative precipitation collected at the CPER. Cumulative precipitation was recorded daily during the growing season and every few days during the non-growing season from a rain gauge at the headquarters of CPER (located near the center of the site). We calculated averages of our focal precipitation windows for each year.

Table 2.1. Temporal scales of cumulative precipitation considered to potentially influence grassland bird abundance on the Central Plains Experimental Range, Colorado. The Year column refers to whether the focal window was calculated for a period of time within 12 months of the bird survey ("Current") or calculated for a period of time prior to the 12 months preceding a bird survey ("Prior"). The exception to this is summer lagged precipitation – summer precipitation was calculated during a window that fell within 12 months of the bird survey, but was calculated for precipitation that fell the growing season prior to the bird survey. Thus, it is denoted as "Prior". The units for all precipitation windows are centimeters.

Precipitation Window	Time Frame	Year
Annual	June 1 - May 31	Current
Spring	March 1 - May 31	Current
Fall	Sept 1 - May 31	Current
Summer lagged	June 1 - Sept 30	Prior
Spring lagged	March 1 - May 31	Prior
Fall lagged	Sept 1 - May 31	Prior

Birds

We measured avian abundance using six-minute, unfixed-radius point counts (Hanni et al. 2013). Point count locations were surveyed between sunrise and ~10:30 am twice during the breeding season from the end of May to the beginning of June and from the first to second week of June. The same observer conducted one survey at the end of May/beginning of June each year and a second survey was conducted within one to two weeks of the first survey by an observer that varied annually. Observers used a rangefinder to record the distance to all individual birds detected and the method of detection (e.g., aural, visual) and sex (if determinable) of each individual.

Statistical Analyses

Model structure

Our data were collected within the context of an on-going grazing experiment on the CPER that is testing the effects of rest-rotational grazing relative to continuous, season-long grazing. In previous analyses (Chapter 1), we examined the effect of grazing management on grassland bird

abundance using a hierarchical distance sampling model (Amundson et al. 2014). We used repeated counts to estimate temporary emigration for most species to improve model fit (Chandler et al. 2011). We examined covariate influences on detection and temporary emigration in the previous analyses to determine a model structure for each focal species. We then used the same model structure in this analysis so that we could compare our models examining grazing impacts to our models examining environmental influences on grassland bird abundance. This was possible for all species except horned lark. In the horned lark environmental model, the model had difficulty estimating intercepts for temporary emigration and abundance. Thus, we did not include temporary emigration in the horned lark environmental model and we refit the horned lark grazing model without temporary emigration. By retaining the same model structure in both the grazing and environmental models for all species, we could compare the predictive capacity of these models.

For models that included temporary emigration, we assumed observed counts at site k during survey j (y_{kj}) were the outcome of a binomial distribution conditioned on true abundance N, detection probability p_d, and temporary emigration probability p_a,

$y_{kj} \sim$ Binomial(N_k, $p_{d,kj}\, p_{a,k}$),

We modeled detection probability (p_d) using distance sampling with a hazard rate detection function (Buckland et al. 2001). We used a log-link function to model covariates on σ, the scale parameter of the detection function (Amundson et al. 2014). These covariates varied by site k and survey j and included coefficients for survey and random terms for year and observer. Each site was a unique combination of year, pasture, and point count location. We truncated the distance sampling data by 10% per Buckland et al. (2001) before fitting models and specified vague normal priors (Normal(0, 10)) on coefficients for the detection model. We specified either a weakly-

informative half-cauchy (Gelman 2006) or vague uniform(0, 10) prior for the standard deviation of the random terms.

Depending on the species, we included either no temporary emigration, a null model on temporary emigration, or an effect of VOR on temporary emigration with a logit link (p_a; Chandler et al. 2011).

$$\text{logit}(p_{a,k}) = \delta_0, \text{ or}$$

$$\text{logit}(p_{a,k}) = \delta_0 + \delta_{1k}\text{VOR}_k$$

We did not include temporary emigration in models if its inclusion caused parameters to not converge or the model to not fit (see below for goodness-of-fit test). For models with temporary emigration, we specified either vague normal priors on both the coefficients of the temporary emigration model (i.e., δ_0 and δ_1), or a Jeffreys prior on the intercept coefficient (δ_0; Lunn et al. 2012) and a vague normal prior on the coefficient for VOR (δ_1). For models that did not include temporary emigration, we assumed observed counts y_{kj} were the outcome of a binomial distribution conditioned on true abundance N and detection probability $p_{d,kj}$.

We modeled the abundance of each species per site k (N_k) as a function of a Poisson random variable with mean abundance (λ_k) per site:

$$N_k \sim \text{Poisson}(\lambda_k)$$

To account for the experimental design of the grazing experiment within which we conducted our study, we modeled a random term for block on the intercept for abundance ($\beta_{0,\text{block}}$) for all species except McCown's longspur. For McCown's longspur we used a pasture-specific intercept ($\beta_{0,\text{pasture}}$) because the parameters associated with the block random term would not converge after constraining McCown's longspur detections to the loamy plains ecological site (Chapter 1). We modeled one to twelve of our focal covariates (see *Scale selection and final model*) on λ using a

log-link function. We specified vague normal priors for the coefficients for mean abundance per site (λ_k) and for the means of the random terms for block and pasture. We specified vague uniform priors for the standard deviations of the block and pasture random terms.

Scale selection and final model

We used deviance information criterion (DIC) to select a single best TRI scale, TWI scale, and precipitation window to include in our environmental models. Deviance information criterion (DIC) is analogous to Akaike's information criterion (AIC) for frequentist model selection and is calculated most often using the posterior mean of the deviance and a penalty term for the effective number of parameters in the model. The effective number of parameters is influenced by the data, the priors, and the sample space of model parameters (Spiegelhalter et al. 2002).

With the model structure fixed as described above (see *Model*), we fit univariate models with each TRI and TWI spatial scale/extent and temporal precipitation window on abundance for each species and calculated DIC for these models. Unlike AIC, there is no well-established rule of thumb suggesting what magnitude of difference in DIC values distinguishes competing models. Affiliates of the BUGS programming language, a language for fitting Bayesian models in R, suggest differences in DIC values greater than 5 indicate important differences between models (MRC Biostatistics Unit 2004). Thus, we used ΔDIC > 5 as indicating a top scale/window. If ΔDIC < 5 for our topographic scales, we selected the 150-m scale to include in the full environmental model because this scale encompasses the resources surrounding an average territory for our focal species (Beason 1995, Vickery 1996b, Shane 2000, Davis and Lanyon 2008, With 2010) and is comparable to the scale at which our vegetation data were collected.

Once we identified the most predictive TRI and TWI scale and precipitation window for each species, we fit two final models – 1) a model with 12 environmental covariates on abundance: all vegetation covariates (*n*=9), the top TRI scale, the top TWI scale and the top precipitation window selected for each species, and 2) a model with the same vegetation and topographic covariates as 1) but where we replaced the precipitation covariate with a categorical effect of year. We fit this latter model because year could capture important variation in the system beyond that attributed to varying precipitation. We calculated means and 95% credible intervals (CRI) for all model parameters. We calculated DIC for both environmental models for each species and interpreted results from the model with the lower DIC. We also used DIC to compare the predictive power of our two environmental models to our grazing treatment main effects model for each species (Chapter 1).

We fit models to all detections of both sexes for western meadowlark, horned lark and grasshopper sparrow because sexes could rarely be distinguished with certainty. Lark bunting and McCown's longspur males, however, have unique flight displays (skylarking) during the breeding season to attract mates that make them substantially more detectable than females. This skew in detection was reflected in our data – over 90% of our detections for these two species were males. Due to this, we fit models for lark bunting and McCown's longspur using male detections only. In addition, there was only a single detection of a McCown's longspur on a non-loamy ecological site over the five years of our surveys. Thus, we fit models to detections of McCown's longspur males on the loamy plains ecological site only.

We used the R package rjags (Plummer 2016) to fit all models with three MCMC chains for 200,000-800,000 iterations and saved the final 50,000-200,000 iterations per chain. We considered parameters with Gelman-Rubin statistics ≤1.10 to have converged (Gelman et al.

2013). We used a chi-square discrepancy goodness-of-fit test to evaluate model fit and compared observed and predicted test statistics using posterior predictive checks (Bayesian p-values; Amundson et al. 2014, Royle and Kéry 2016). We considered Bayesian p-values ≤0.1 and ≥0.9 to indicate a lack of fit (Amundson et al. 2014).

Results

We surveyed 92 point count locations twice per year for 5 years, resulting in 920 surveys. Lark bunting males were detected the most (2,660) and McCown's longspur males were detected the least (287). We had 1,367, 1,327, and 715 detections for both sexes combined of western meadowlark, horned lark and grasshopper sparrow, respectively.

TRI/TWI at the 50-m, 150-m and 250-m scales were equally predictive for all species except McCown's longspur (i.e., ΔDIC < 5; Table 2.2). For McCown's longspur, TWI at the 50-m and 150-m scales were equally predictive (Table 2.2). Because our DIC results suggested equal predictive power of all scales for almost all species, we selected TRI and TWI at the 150-m scale to include in the final environmental models. Using the 150-m scale for TRI/TWI allowed our vegetation and topographic covariates to represent approximately the same scale.

The precipitation scales identified as most predictive for abundance varied by species. For McCown's longspur and horned lark, two precipitation scales had ΔDICs < 5 – fall and lagged summer precipitation for McCown's longspur, and spring lagged and fall lagged precipitation for horned lark (Table 2.2). Although both scales were equally predictive, we fit and interpreted full models for these species using the precipitation scale with the lowest DIC (i.e., fall precipitation for McCown's longspur and fall lagged precipitation for horned lark; Table 2.2). The best precipitation scale for western meadowlark was fall precipitation, but parameters did not converge

Table 2.2. Standardized coefficient effects (means and credible intervals [CRI]) on abundance and DICs (Spiegelhalter et al. 2002) of the scales of topographic indices and precipitation windows fit in univariable models for our five focal grassland bird species breeding on the Central Plains Experimental Range from 2013 – 2017. Topographic Ruggedness Index (TRI) and Topographic Wetness Index (TWI) were calculated using radii of 50 m, 150 m and 250 m around each point count location. Precipitation windows were calculated in centimeters. Bolded values denote the scales and windows selected for inclusion in the final environmental models. In cases for TRI and TWI where ΔDIC was <5, the 150-m scale was retained. For western meadowlark, we fit and interpreted full environmental models with the annual precipitation window because parameters would not converge in models fit with the precipitation window with the lowest DIC (i.e., fall precipitation). MCLO = McCown's longspur, HOLA = horned lark, LARB = lark bunting, WEME = western meadowlark, GRSP = grasshopper sparrow.

	MCLO				HOLA				LARB				WEME				GRSP			
TRI	Mean	CRI	DIC	ΔDIC	Mean	CRI	DIC	ΔDIC	Mean	CRI	DIC	ΔDIC	Mean	CRI	DIC	ΔDIC	Mean	CRI	DIC	ΔDIC
50 m	-0.052	(-0.383, 0.254)	674.70	0.35	-0.046	(-0.124, 0.023)	2850.42	0.00	0.020	(-0.091, 0.128)	3644.118	0.65	-0.003	(-0.067, 0.059)	2313.90	0.88	-0.036	(-0.220, 0.137)	1835.00	0.00
150 m	-0.119	(-0.393, 0.134)	**674.35**	**0.00**	-0.016	(-0.087, 0.054)	**2852.01**	**1.60**	0.002	(-0.018, 0.021)	**3644.084**	**0.61**	-0.014	(-0.086, 0.057)	**2313.32**	**0.30**	0.003	(-0.091, 0.094)	**1835.52**	**0.52**
250 m	-0.145	(-0.419, 0.112)	678.63	4.28	-0.007	(-0.083, 0.067)	2852.16	1.74	0.004	(-0.006, 0.013)	3643.471	0.00	-0.020	(-0.095, 0.054)	2313.02	0.00	0.000	(-0.100, 0.097)	1835.20	0.19
TWI																				
50 m	0.134	(0.007, 0.265)	670.75	5.29	-0.021	(-0.086, 0.045)	2851.78	1.10	-0.016	(-0.066, 0.035)	3643.82	0.40	0.006	(-0.069, 0.080)	2312.98	0.41	-0.006	(-0.107, 0.095)	1836.40	2.35
150 m	0.178	(0.039, 0.320)	**669.12**	**3.66**	-0.015	(-0.088, 0.059)	**2851.80**	**1.12**	-0.017	(-0.073, 0.040)	**3643.85**	**0.43**	0.031	(-0.051, 0.114)	**2312.61**	**0.04**	0.046	(-0.067, 0.159)	**1834.05**	**0.00**
250 m	0.263	(0.106, 0.420)	665.46	0.00	0.041	(-0.038, 0.120)	2850.69	0.00	-0.032	(-0.093, 0.028)	3643.42	0.00	0.024	(-0.064, 0.111)	2312.57	0.00	0.002	(-0.119, 0.120)	1834.60	0.55
Precipitation (in)																				
Annual	0.290	(0.135, 0.444)	740.12	75.50	0.051	(-0.032, 0.131)	2852.71	12.69	0.528	(0.478, 0.579)	3220.34	89.97	-0.277	(-0.359, -0.196)	**2270.24**	**5.90**	0.283	(0.144, 0.414)	1844.19	38.59
Spring	0.146	(-0.019, 0.310)	672.87	8.26	0.042	(-0.046, 0.129)	2849.50	9.48	0.042	(-0.009, 0.094)	3641.94	511.57	-0.016	(-0.093, 0.060)	2312.34	47.99	0.262	(0.137, 0.385)	1838.79	33.19
Fall	0.331	(0.164, 0.503)	**664.62**	**0.00**	0.021	(-0.063, 0.105)	2853.79	13.77	0.589	(0.028, 0.646)	3169.39	39.02	-0.327	(-0.408, -0.246)	2264.34	0.00	0.068	(-0.097, 0.227)	1836.32	30.72
Summer lagged	0.312	(0.139, 0.489)	668.30	3.69	-0.017	(-0.109, 0.073)	2850.38	10.36	0.596	(0.544, 0.649)	**3130.37**	**0.00**	-0.466	(-0.551, -0.382)	2274.95	10.61	0.072	(-0.083, 0.221)	1835.12	29.52
Spring lagged	-0.163	(-0.365, 0.030)	671.25	6.64	0.177	(0.095, 0.259)	2844.83	4.81	-0.148	(-0.201, -0.096)	3612.53	482.16	0.508	(0.433, 0.582)	2652.74	388.40	0.180	(-0.003, 0.365)	1830.24	24.64
Fall lagged	0.028	(-0.149, 0.200)	673.44	8.83	0.255	(0.174, 0.338)	**2840.02**	**0.00**	0.070	(0.019, 0.122)	3637.20	506.83	0.521	(0.436, 0.608)	2348.17	83.83	0.807	(0.648, 0.969)	**1805.60**	**0.00**

in the full environmental model with this scale. We therefore fit and interpreted a full environmental model with the precipitation scale with the next lowest DIC, which fell only slightly outside our threshold as a comparable predictive scale to fall precipitation (ΔDIC = 5.9; Table 2.2).

The results from our environmental-precipitation and environmental-year models were similar (though parameters in the environmental-year model would not converge for western meadowlark; see Appendix 2). Because we were interested in how precipitation affected our focal species, we interpret below results from the environmental-precipitation models.

Our models revealed a combination of vegetation cover, vegetation structure, and precipitation affected the abundance of all focal species (Table 2.3, Figures 2.2-2.4). Cover of shortgrass and standing dead vegetation were the most common composition

Table 2.3. Standardized coefficient effects (means and credible intervals [CRI]) of vegetation composition, vegetation structure, topography and precipitation on abundance from the environmental-precipitation model for each of our five focal grassland bird species breeding on the Central Plains Experimental Range, Colorado from 2013 – 2017 (see results from environmental-year models in Appendix 2). Bolded values denote strong effects on abundance (i.e., the CRI of the coefficient estimate does not include 0). Blank spaces indicate the focal covariate was not included in the environmental model for the listed species. MCLO = McCown's longspur, HOLA = horned lark, LARB = lark bunting, WEME = western meadowlark, GRSP = grasshopper sparrow.

Composition	MCLO Mean	MCLO CRI	HOLA Mean	HOLA CRI	LARB Mean	LARB CRI	WEME Mean	WEME CRI	GRSP Mean	GRSP CRI
Standing dead	0.357	(-0.131, 0.834)	**-0.165**	**(-0.284, -0.047)**	**-0.088**	**(-0.168, -0.009)**	**0.117**	**(0.040, 0.192)**	0.089	(-0.015, 0.190)
Litter	-0.004	(-0.208, 0.201)	0.074	(-0.019, 0.167)	0.023	(-0.048, 0.094)	**0.261**	**(0.168, 0.354)**	-0.070	(-0.200, 0.060)
Shortgrass	-0.027	(-0.328, 0.278)	**0.134**	**(0.034, 0.233)**	-0.029	(-0.091, 0.033)	**0.173**	**(0.079, 0.267)**	**-0.280**	**(-0.413, -0.146)**
Midgrass	-0.476	(-1.073, 0.091)	**-0.131**	**(-0.255, -0.009)**	-0.035	(-0.105, 0.034)	0.038	(-0.037, 0.112)	0.056	(-0.027, 0.138)
Forb	**0.159**	**(0.000, 0.315)**	0.024	(-0.044, 0.091)	0.039	(-0.005, 0.082)	-0.059	(-0.144, 0.021)	**-0.149**	**(-0.262, -0.044)**
Shrub	-0.008	(-0.582, 0.476)	-0.091	(-0.187, 0.001)	0.051	(-0.002, 0.103)	-0.031	(-0.107, 0.042)	-0.043	(-0.153, 0.062)
Subshrub	-0.100	(-0.351, 0.139)	0.035	(-0.041, 0.108)	0.050	(-0.002, 0.101)	0.057	(-0.016, 0.129)	-0.022	(-0.129, 0.083)
Cactus	-0.150	(-0.410, 0.089)	-0.031	(-0.109, 0.046)	0.009	(-0.046, 0.062)	0.009	(-0.068, 0.084)	-0.047	(-0.151, 0.055)
Structure										
VOR	**-1.325**	**(-2.180, -0.514)**	**-0.338**	**(-0.466, -0.211)**	**-0.069**	**(-0.137, -0.003)**	**0.111**	**(0.030, 0.189)**	-0.074	(-0.251, 0.083)
Topography										
TRI at 150 m	0.305	(-0.096, 0.690)	0.033	(-0.056, 0.119)	-0.006	(-0.068, 0.055)	-0.032	(-0.116, 0.052)	0.105	(-0.012, 0.221)
TWI at 150 m	**0.247**	**(0.032, 0.463)**	0.025	(-0.065, 0.114)	0.000	(-0.066, 0.066)	-0.016	(-0.111, 0.080)	0.082	(-0.048, 0.212)
Precipitation										
Summer					0.601	(0.529, 0.673)				
Annual							-0.168	(-0.251, -0.086)		
Fall	**0.404**	**(0.170, 0.637)**								
Fall lagged			0.330	(0.238, 0.422)					0.766	(0.602, 0.931)

Figure 2.2. Predicted means and 95% CRI of the vegetation composition, vegetation structure, topographic and/or precipitation covariates (calculated holding all other covariates at their means) that strongly influenced abundance (i.e., the CRI did not include 0) for McCown's longspur (MCLO) and horned lark (HOLA) on the Central Plains Experimental Range, Colorado from 2013 – 2017. Metrics were calculated from the full environmental-precipitation models.

covariates to affect abundance; horned lark and western meadowlark abundance increased while grasshopper sparrow abundance decreased with increasing shortgrass cover. Only McCown's longspur responded to topography; longspur abundance increased with increasing TWI at the 150-m scale (Table 2.3, Figure 2.4).
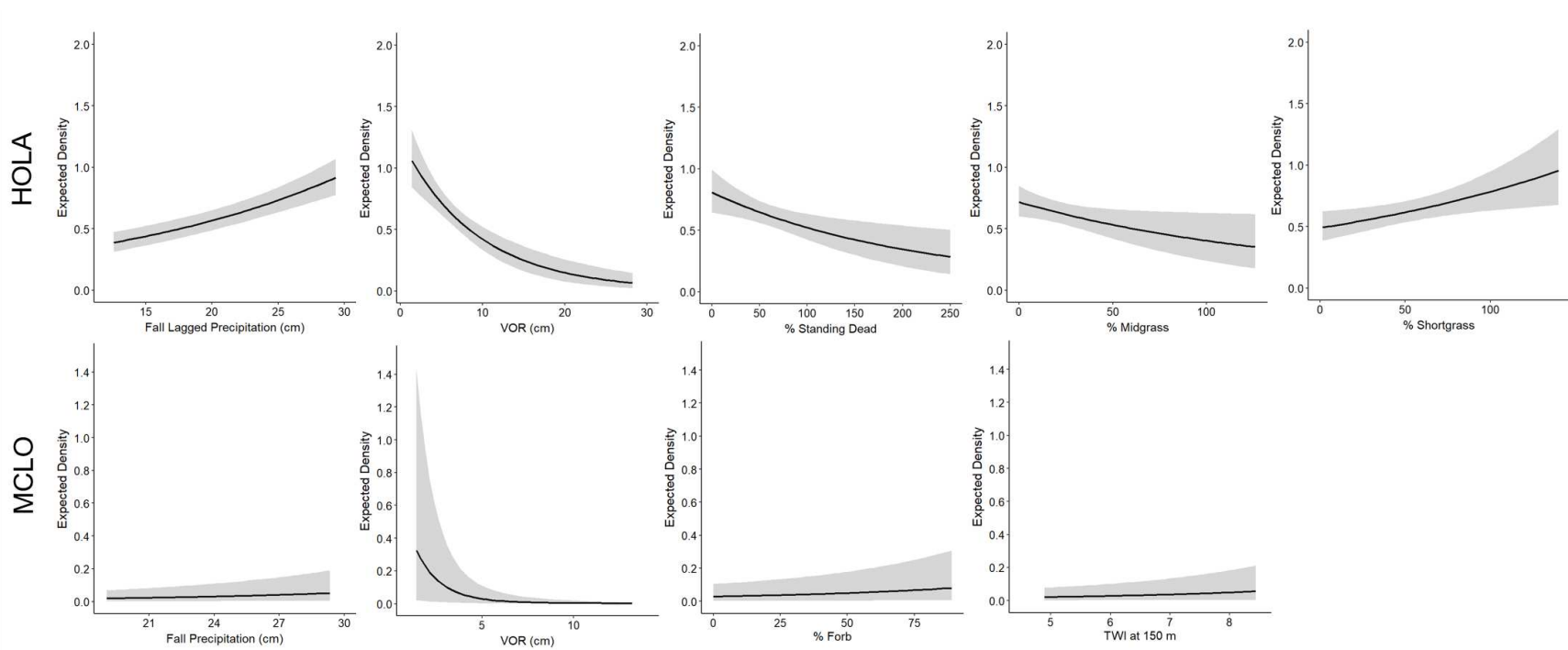
Figure 2.3. Predicted means and 95% CRI of the vegetation composition, vegetation structure, topographic and/or precipitation covariates (calculated holding all other covariates at their means) that strongly influenced abundance (i.e., the CRI did not include 0) for lark bunting (LARB) and grasshopper sparrow (GRSP) on the Central Plains Experimental Range, Colorado from 2013 – 2017. Metrics were calculated from the full environmental-precipitation models.
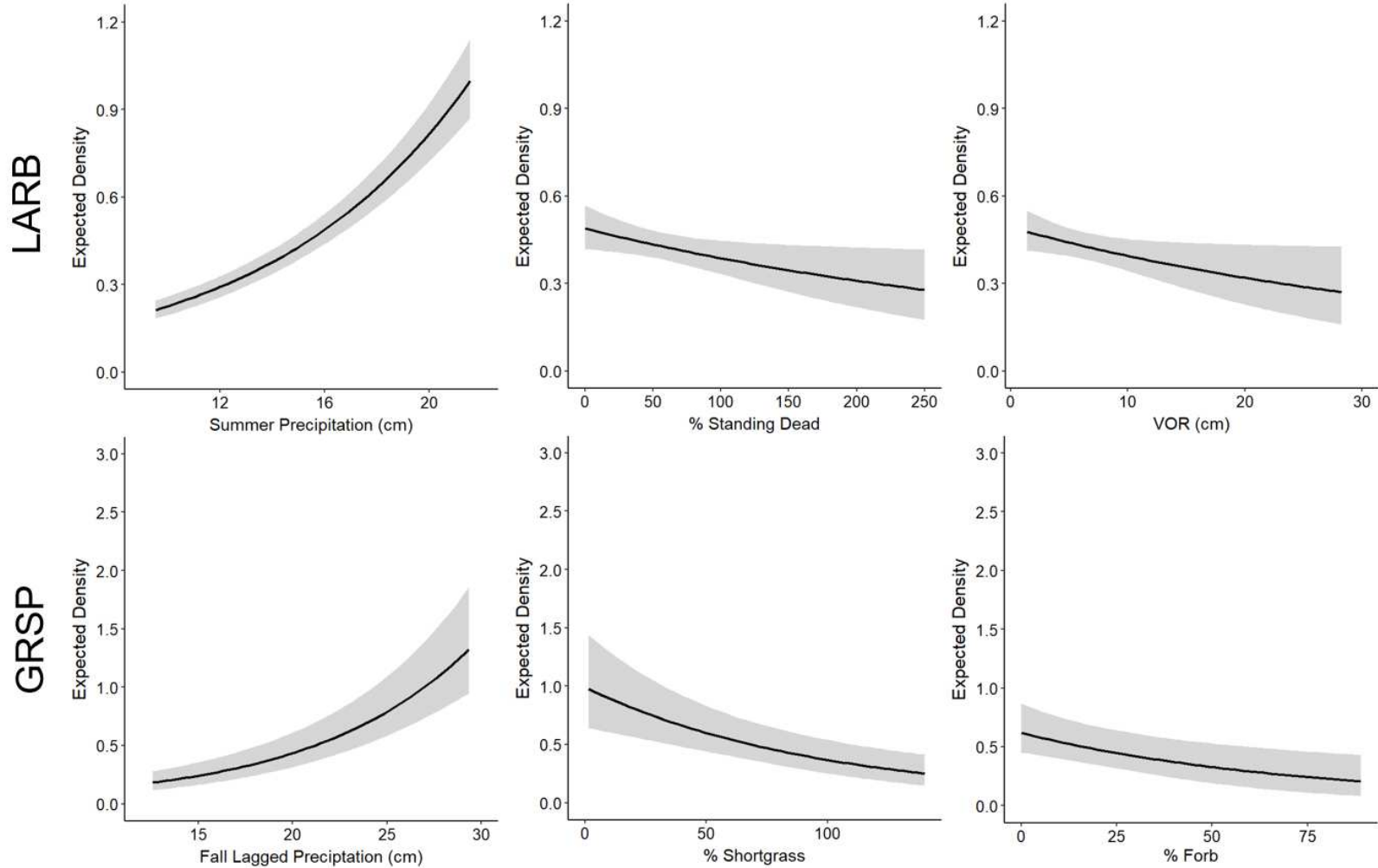
Figure 2.4. Predicted means and 95% CRIs of the vegetation composition, vegetation structure, topographic and/or precipitation covariates (calculated holding all other covariates at their means) that strongly influenced abundance (i.e., the CRI did not include 0) for western meadowlark (WEME) on the Central Plains Experimental Range, Colorado from 2013 – 2017. Metrics were calculated from the full environmental-precipitation models.
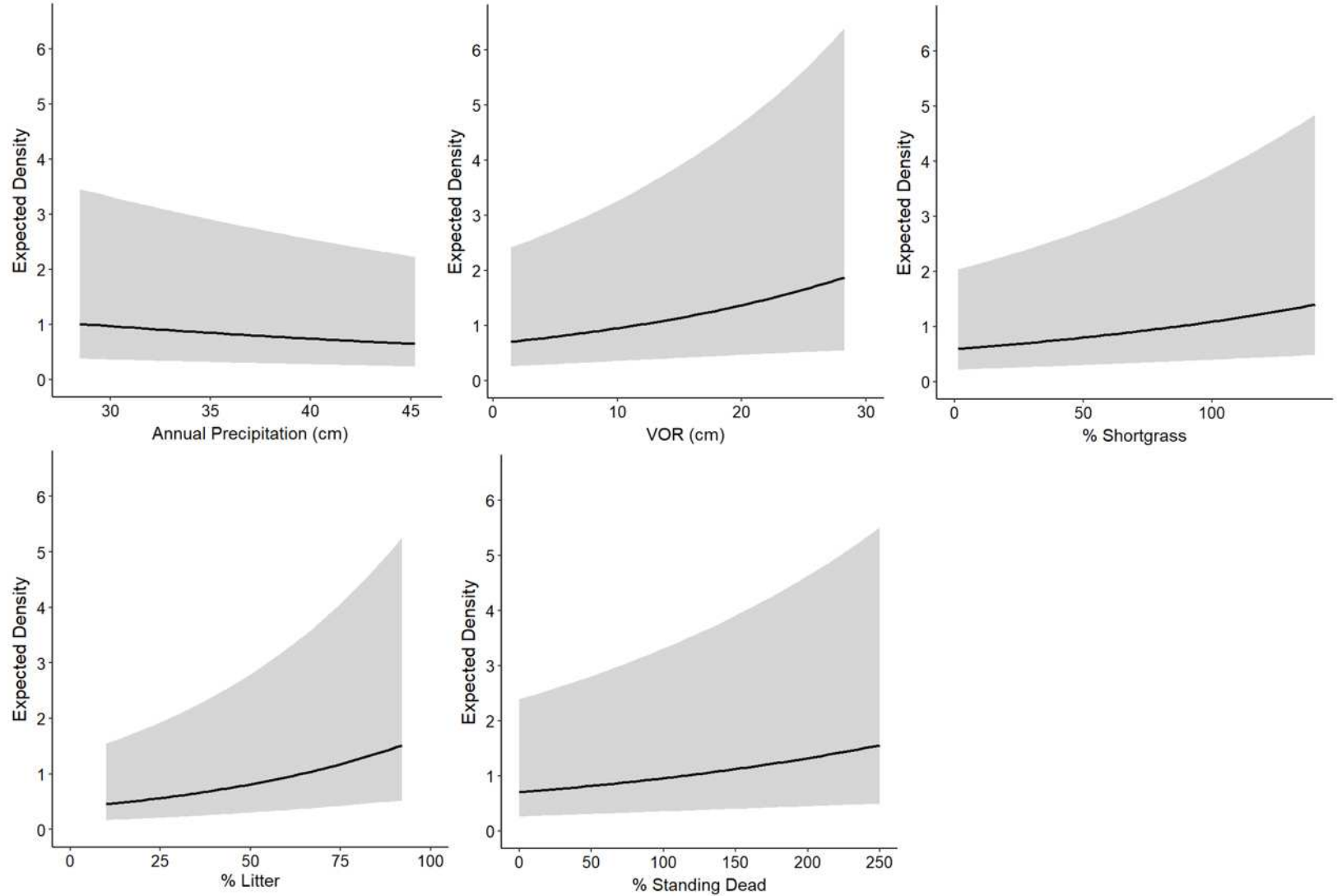
Precipitation strongly affected abundance for all focal species (Table 2.3), and the abundance of all species increased with increasing precipitation except western meadowlark. Precipitation had the largest average magnitude of effect on lark bunting and grasshopper sparrow abundance (Table 2.3, Figures 2.2-2.4). For our species that prefer shorter/sparser vegetation, McCown's longspur abundance increased with cumulative precipitation from the prior fall through the current spring of the bird survey (i.e., October-May) and horned lark abundance increased over that same window but lagged one year (Table 2.3, Figure 2.2). For our species that prefers more moderate vegetation structure and density, lark bunting abundance increased with cumulative precipitation in the prior year's growing season (Table 2.3, Figure 2.3). For our species that prefer taller/denser vegetation, grasshopper sparrow abundance increased with cumulative precipitation the previous fall through spring of the prior years' growing season and western meadowlark abundance decreased with cumulative precipitation over the 12 months preceding the current year's growing season (Table 2.3, Figure 2.3 & 2.4).

Vegetation structure strongly affected the abundance of all species except grasshopper sparrow (Table 2.3, Figures 2.2-2.4). Structure had the greatest average magnitude of effect on McCown's longspur and horned lark abundance, which declined with increasing structure (Figure 2.2). Lark bunting abundance also declined with increasing structure (Figure 2.3). Western meadowlark abundance increased with increasing structure (Figures 2.4, Table 2.3).

Vegetation composition strongly affected abundance of all species (Table 2.3, Figures 2.2-2.4). Composition (specifically litter cover) had the greatest magnitude of effect on western meadowlark abundance (Figure 2.4), and this species responded most to vegetation composition compared to our other focal species (i.e., three composition covariates affected meadowlark abundance compared to one or two composition covariates for our other focal species; Table 2.3).

Lark bunting and western meadowlark abundance increased with increasing cover of standing dead vegetation, while horned lark abundance decreased with standing dead vegetation (Table 2.3, Figures 2.2-2.4). Western meadowlark and horned lark abundance increased with increasing cover of shortgrass, while grasshopper sparrow abundance decreased with shortgrass cover (Figures 2.2 & 2.4). Grasshopper sparrow abundance decreased and McCown's longspur abundance increased with increasing cover of forbs (Figure 2.2 & 2.3, Table 2.3). Meadowlark abundance increased with increasing cover of litter (Figure 2.4).

While each of our focal species responded individually or to a combination of precipitation, vegetation composition and structure, or topography, our grazing model from previous analyses (Chapter 1) was identified by DIC as best predicting abundance for lark bunting and western meadowlark (Table 2.4). In contrast, the environmental-precipitation model was better supported for McCown's longspur. The environmental-precipitation and environmental-year models were equally supported for horned lark. All models were equally supported for grasshopper sparrow. ΔDIC was largest between the grazing and environmental models for western meadowlark and smallest between those models for grasshopper sparrow. We could not calculate DIC for the environmental-year models for western meadowlark or McCown's longspur due to unidentifiable parameters in these models; thus, we could not compare the DICs of these species' grazing and environmental-year models (Table 2.4).

Discussion

All our focal species exhibited varied responses to both vegetation characteristics and precipitation. Precipitation and vegetation composition strongly influenced abundance for all focal species, while vegetation structure strongly influenced abundance for all species except

Table 2.4. DIC values for the grazing model (from previous analyses) and environmental models for each of our five focal grassland bird species breeding on the Central Plains Experimental Range, Colorado from 2013 – 2017. Bolded values indicate the model(s) with ΔDIC < 5. The DICs for the McCown's longspur and western meadowlark environmental-year models could not be calculated due to identifiability issues with parameters in these models. MCLO = McCown's longspur, LARB = lark bunting, WEME = western meadowlark, GRSP = grasshopper sparrow.

Model	MCLO	MCLO ΔDIC	HOLA	HOLA ΔDIC	LARB	LARB ΔDIC	WEME	WEME ΔDIC	GRSP	GRSP ΔDIC
Grazing	663.629	8.167	2767.813	26.187	**3116.135**	**0**	**3393.186**	**0**	**1794.845**	**0**
Environmental-Precip	**655.462**	**0**	**2742.646**	**1.02**	3127.917	11.782	3613.001	219.815	**1797.533**	**2.688**
Environmental-Year	NA	NA	**2741.626**	**0**	3126.185	10.05	NA	NA	**1796.000**	**1.155**

grasshopper sparrow. These results support previous research showing that vegetation composition, structure and precipitation independently affect grassland bird abundance (Knopf 1996, Niemuth et al. 2008, Fisher and Davis 2010, Ahlering and Merkord 2016, Gorzo et al. 2016, Lipsey and Naugle 2017). Our study is one of the first to show these factors, when considered together, jointly influence abundance for grassland birds breeding in the shortgrass steppe.

Precipitation was an important predictor of abundance for all focal species and often has not been considered in grazing studies on grassland birds (though see Ahlering and Merkord 2016 and Lipsey and Naugle 2017). Climatic variability is an important evolutionary force in grasslands, particularly in the shortgrass steppe, which receives highly variable inter- and intra-annual precipitation. This variation results in high herbaceous cover and structure produced on the landscape during wet years and significantly reduced herbaceous cover and structure on the landscape in dry years. Given this, we expected species to respond to precipitation based on their vegetation cover/structure preferences – abundance of species that prefer sparse/short grass, such as horned lark and McCown's

longspur, would decline with precipitation, and abundance of species that prefer tall/dense grass, such as grasshopper sparrow and western meadowlark, would increase with precipitation.

Precipitation positively influenced abundance for all species except western meadowlark. The first five years of our study were historically average to wet precipitation years; average growing season precipitation during our study ranged from 272 to 406 mm, with the long-term mean for the site being 242 mm. The negative relationship we found between meadowlark abundance and precipitation may suggest this species prefers a more moderate amount of precipitation, though the negative response was modest (see Figure 2.4). The positive relationship we found between precipitation and horned lark and McCown's longspur abundance (two species that prefer more bare ground and sparse/short vegetation) suggests precipitation may influence grassland birds via a mechanism other than vegetation productivity/structure, and that these effects may be lagged. For example, increased precipitation in the previous growing season may benefit insect populations, which are the primary food source of grassland birds during the breeding season. This may carry over to result in higher insect populations the following breeding season. Furthermore, this region is predicted to experience more extreme climatic events over the next century (Skagen and Adams 2012) and precipitation has been shown to mitigate or accentuate grazing impacts depending on whether conditions are wet or dry (Lipsey and Naugle 2017). Managers should consider precipitation patterns when determining grazing management for grassland birds to ensure sufficient heterogeneity exists on the landscape to support short/sparse grass-preferring species in wet years and tall/dense grass-preferring species in dry years (Lipsey and Naugle 2017).

Our focal avian species responded in relatively predictable ways to vegetation composition and structure, where the abundance of sparse-grass species decreased and the abundance of dense-

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grass species increased with taller structure and denser cover on the CPER. We did observe a few exceptions, however. One exception was that lark bunting abundance decreased slightly with increasing vegetation structure. This species is known to prefer more moderate levels of vegetation structure/density (i.e., it does not occur in tallgrass prairie; Shane 2000). Lark buntings seem to exhibit boom-bust population cycles on the CPER, where they are widespread and numerous during wet years, but almost completely absent during drought years (D. Augustine, pers. obs.). In our environmental models, precipitation over the previous growing season (rather than current-year precipitation or vegetation structure/composition) had the strongest magnitude of effect on bunting abundance. In our grazing model, however, bunting abundance was higher in traditionally-managed pastures than in pastures pulse grazed or rested the year before. This supports the species' preference for more moderate amounts of vegetation structure and cover, and suggests precipitation is affecting this species' abundance via a mechanism other than vegetation productivity (e.g., perhaps through food resources, as described above regarding lagged precipitation and horned lark/McCown's longspur abundance). Another exception was that vegetation structure did not strongly affect grasshopper sparrow abundance. This finding was surprising given that we found sparrow abundance was significantly higher on the ecological sites with the most productive (i.e., tallest, most dense) vegetation in our grazing model (Chapter 1). Grasshopper sparrow was the only species, however, where we included an effect of vegetation structure on temporary emigration. Vegetation structure may have influenced sparrow abundance more strongly if we had not modeled an effect of structure on emigration. Ultimately, our results suggest vegetation structure and composition alone may not predict patterns of grassland bird abundance. Arranging grassland bird species along a gradient of vegetation structure/density is

conceptually simple but may not clearly illustrate all the environmental conditions that affect grassland bird populations.

The abundance of only one of our five focal species was affected by topography – McCown's longspur abundance increased slightly with increasing TWI at the 150-m scale (Figure 2.2, Table 2.3). Higher TWI values denote wetter, more flat areas with poor drainage, such as drainage depressions (Beven and Kirkby 1979). We would expect longspurs to avoid wetter areas given their preference for shorter, sparser vegetation (With 2010), but the magnitude of effect of TWI on longspur abundance was small and anecdotal evidence suggests longspurs select nesting sites on flat, upland tables on the CPER (D. Augustine, pers. obs.). The slight positive relationship between TWI and longspur abundance lends quantitative support to the observation of longspurs nesting in flatter areas, though clarifying this relationship merits further attention and exploration.

We were able to use DIC to select a temporal scale of precipitation to include in our environmental models but not to distinguish between spatial scales of our remotely-sensed topographic indices. Preliminary analyses revealed our topographic indices were correlated between scales. Because these covariates did not vary across the extents over which we evaluated them, it is not surprising we were unable to distinguish their relative predictive capacity using DIC. It was slightly surprising, however, that our grazing model had a lower/comparable DIC compared to our environmental models for two of our focal species. This may be because our environmental models had more covariates on abundance than the grazing models (12-15 covariates on abundance in the environmental models versus 8 in the grazing models), and thus could have had larger penalty terms in the DIC calculation due to a lack of parsimony compared to the grazing models (though not necessarily, as the penalty term for DIC is the <u>effective</u> rather than actual number of parameters; Spiegelhalter et al. 2002). Alternatively, this result suggests our grazing covariates

captured some important habitat attributes for some species not revealed by our environmental covariates. We did not include soil characteristics in our environmental models, but the ecological site covariate in our treatment model encompassed soil and plant characteristics (ecological sites are defined by soil conditions and plant community characteristics; USDA Natural Resources Conservation Service). Soil productivity has been found to explain grazing effects on grassland bird abundance in Montana (Lipsey and Naugle 2017), so perhaps including ecological site in our treatment models explained more variation in grassland bird abundance than fine-scale vegetation data alone. However, our environmental models provide a more mechanistic understanding of what environmental metrics grassland birds may be responding to across grazing treatments and utilizing on their breeding grounds.

Our study revealed important environmental relationships affecting grassland bird abundance in the shortgrass steppe. That our grazing models were better supported than our environmental models for some of our focal species suggests there were some unmodeled relationships contained in our grazing models that were absent from our environmental models. While this necessitates further research, it may be encouraging that grazing management can explain patterns in grassland bird abundance given many managers do not have access to fine-scale vegetation/environmental data. Additionally, while grazing management explained patterns in grassland bird abundance, all our focal species also responded to specific components of vegetation composition, vegetation structure, and precipitation. Managers can use the results of our study to ensure grazing management is generating the vegetation composition and structure preferred by the full suite of breeding grassland birds in the shortgrass steppe. Our study also suggests management for grassland birds should consider recent precipitation conditions. Based on whether recent years were historically wet, average, or dry, grazing should be applied in a way

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that ensures each end of the vegetation spectrum is available on the landscape (i.e., implement intensive grazing in some areas during wet years and a lack of grazing, or rest, in some areas in dry years). Finally, our findings highlight the importance of long-term ecological studies. The first five years of our experiment occurred in historically wet and average precipitation years. Repeating our analyses over the next 5 years of data collection, with the potential for some drought years, will add essential insight into what drives grassland bird abundance in the shortgrass steppe.

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Conclusion

Both grazing management and environmental characteristics affected the abundance of my focal grassland bird species in the shortgrass steppe. Grazing management affected two species that utilize opposite ends of the spectrum of vegetation structure – rest, or a lack of grazing, increased grasshopper sparrow abundance and decreased McCown's longspur abundance the subsequent year. When considered with grazing, however, ecological site and yearly effects influenced abundance for all species more strongly than grazing management. Additionally, all species responded to some combination of the environmental characteristics considered in this study – vegetation composition, vegetation structure, precipitation and topography. Different factors drove abundance for different species; precipitation most strongly affected the abundance of lark bunting and grasshopper sparrow, vegetation composition most strongly affected the abundance of western meadowlark, and vegetation structure most strongly affected the abundance of McCown's longspur. Both precipitation and vegetation structure most strongly affected the abundance of horned lark. Interestingly, precipitation was the only environmental characteristic that had a strong influence on the abundance of all focal species. Precipitation is rarely considered in grazing studies on grassland birds (though see Ahlering and Merkord 2016 and Lipsey and Naugle 2017).

Species responded to grazing management and environmental characteristics in relatively predictable ways, though there were some surprising relationships. For example, western meadowlark abundance decreased with increasing precipitation 12 months before the growing season (Table 2.3). This finding was unexpected given meadowlark abundance increased with cover of standing dead vegetation, litter, and taller vegetation structure (Table 2.3), and this species

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is known to prefer taller, denser vegetation (Davis and Lanyon 2008). In contrast, the abundance of the two sparse-grass preferring species on the site, McCown's longspur and horned lark, increased with increasing and lagged precipitation. This was surprising given these species prefer more sparse/short vegetation and bare ground (Beason 1995, With 2010), and barring major disturbance, larger amounts of precipitation would produce taller and denser vegetation on the landscape that would carry over to the following year. These results suggest precipitation is affecting these species through a mechanism other than vegetation production. For instance, insects are these species' primary food source during the breeding season (Beason 1995, With 2010). Insects may be more abundant in wet years (Horton and Capinera 1989), and population increases may carry over to the following year. However, horned lark abundance decreased with taller vegetation structure, McCown's longspur abundance was lower in rested pastures and in areas with taller vegetation structure, and western meadowlark abundance increased with cover of standing dead vegetation, litter, and taller vegetation (Table 2.3). These results support these species' vegetation structure/density preferences (Beason 1995, Davis and Lanyon 2008, With 2010) despite their observed responses to precipitation in this study.

To my knowledge, this study is the first to use hierarchical models fit in a Bayesian framework to analyze avian data collected from a grazing experiment in the shortgrass steppe. These models are used most often to analyze data collected from observational studies without an experimental framework (Chandler et al. 2011, Sillett et al. 2012, Amundson et al. 2014, Sollmann et al. 2016). The benefits of using these models for observational studies easily extend to experiments – these models allow one to elucidate treatment effects while properly accounting for variation across ecological processes (e.g., detection, emigration, abundance), to borrow strength across data, and to estimate true abundance of a population (Royle and Kéry 2016). Fitting these

models in a Bayesian framework can be more difficult than in a frequentist framework; doing so requires experience with Bayesian statistics, sufficient computing power, and time (e.g., fitting one of our models took an average of 1.5 hours using three cores on an Intel Xeon processor with 48 GB of RAM). There is great value, however, in using these models to analyze population data. As an increasing human population will likely continue to threaten wildlife populations, having a probabilistic framework to estimate the true abundance of a species (rather than an index of abundance) will allow for a more informed balance of natural resource utilization and conservation planning in rangelands.

Model selection is well-established in ecology (Johnson and Omland 2004), but few studies have used model selection for hierarchical distance sampling models fit in a Bayesian framework. I attempted to use DIC to determine the spatial scale of topography and temporal scale of precipitation most predictive for grassland bird abundance, and to determine whether grazing treatments or environmental characteristics better predicted grassland bird abundance. I considered more temporal scales of precipitation than have been considered in studies to-date; most studies that have considered precipitation in models for grassland bird abundance have considered only cumulative precipitation in the 12 and/or 24 months prior to the birds' breeding season (often called annual precipitation; Ahlering and Merkord 2016, Gorzo et al. 2016, Lipsey and Naugle 2017). DIC distinguished the best temporal scales of precipitation for all species except McCown's longspur and horned lark. McCown's longspur had the fewest detections of all focal species, and with more data one might be able to use DIC to identify the predictive capacity of various temporal precipitation scales for the longspur. The DIC for annual precipitation (i.e., the most commonly used precipitation scale in previous local-scale grassland bird studies) did not have the lowest DIC for any of my focal species. I could not use DIC to identify the most predictive spatial scales for

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the topography covariates I considered because all model comparisons had ΔDICs less than our selected threshold, though the abundance of one species (McCown's longspur) was strongly affected by topography. I am unaware of other studies that have investigated how topography influences grassland birds. Using DIC to select the most predictive model of abundance between my grazing models, my environmental models with precipitation, and my environmental models with year produced mixed results. For the species for which I could calculate the DIC of the environmental-year model, either the grazing model was most predictive (lark bunting), the environmental models were most predictive (horned lark), or the environmental-year and grazing models had comparable predictive capacity (grasshopper sparrow). For the two species for which I could not calculate the DIC of the environmental-year model (McCown's longspur and western meadowlark), the grazing model had more predictive power than the environmental model for western meadowlark, but the opposite was true for McCown's longspur. This suggests there are unmodeled relationships in my environmental models that are captured by the grazing model for some species. For other species, however, the grazing and environmental models are capturing relatively comparable relationships. Future studies could benefit from further exploring the utility of model selection for hierarchical count models fit in a Bayesian framework, as well as from considering more spatial and temporal scales of precipitation and topography as potential predictors of grassland bird abundance.

Ultimately, my results suggest the factors that influence grassland bird abundance in the shortgrass steppe are complex and context-dependent. While delineating grassland birds along a spectrum of vegetation structure/density is conceptually simple, my results show grassland birds do not always respond in predictable ways to vegetation structure and cover, and other factors may influence their abundance more than vegetation characteristics (e.g., precipitation for lark bunting

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and grasshopper sparrow). In addition, grazing management can benefit grassland birds in the shortgrass steppe, but grazing alone may not be enough to create habitat for certain species. For example, McCown's longspur abundance predictably declined with a lack of grazing in our study, but the species did not expand to pulse grazed pastures in the sandy or salt flats ecological sites on the CPER, even though these areas were pulse grazed with partial intent of creating McCown's longspur habitat to expand the species' distribution on the site. Recent research also has highlighted the need to consider broader environmental context when developing grazing management for grassland birds (Lipsey and Naugle 2017). Resting pastures in wet years in the core of McCown's longspur distribution on the CPER could be particularly detrimental to the species' population the following year. However, resting pastures benefited grasshopper sparrows, which have a different core area on the CPER than McCown's longspur (grasshopper sparrows being most abundant in the productive ecological sites, and McCown's longspur being present only in the least productive ecological site). This suggests a path for synergistic management, where applying pulse grazing in the pastures where McCown's longspur are most abundant inherently results in more frequent rest in the pastures where grasshopper sparrows are most abundant. With the additional insight provided by my fine-scale vegetation analysis, land managers in the shortgrass steppe have more detailed information about what vegetation components should be monitored and enhanced to ensure the landscape contains the diversity of resources to best support populations for these species. It is important to note, however, that my study occurred during historically wet and average precipitation years. Examining how grazing management and environmental characteristics impact grassland birds in the shortgrass steppe in drought conditions would provide critical insight into the ecology of these species. As grasslands continue to be threatened by climate change and agricultural conversion, studying these species in

other portions of the shortgrass steppe will only benefit the ability to manage for and conserve grassland birds across the Great Plains.

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Appendix 1

Table A1.1. Coefficient means and 95% credible intervals (CRIs) of temporary emigration (i.e., probability of availability) parameters from our grazing main effects models for our focal grassland bird species breeding on the Central Plains Experimental Range, Colorado from 2013 – 2017. Bolded values are those where the credible interval of the coefficient does not include 0. VOR = vegetation obstruction reading. MCLO = McCown's longspur, HOLA = horned lark, LARB = lark bunting, WEME = western meadowlark, GRSP = grasshopper sparrow.

	MCLO		HOLA		WEME		GRSP	
	Mean	CRI	Mean	CRI	Mean	CRI	Mean	CRI
Intercept	**-1.293**	**(-2.287, -0.425)**	**-1.629**	**(-2.400, -0.992)**	**-1.281**	**(-2.090, -0.553)**	0.495	(-0.916, 1.910)
VOR	**-0.774**	**(-1.205, -0.323)**					**1.647**	**(0.331, 3.236)**

Table A1.2. Coefficient means and 95% credible intervals (CRIs) of detection probability parameters from our grazing main effects models for our focal grassland bird species breeding on the Central Plains Experimental Range, Colorado from 2013 – 2017. Bolded values are those where the credible interval of the coefficient does not include 0. MCLO = McCown's longspur, HOLA = horned lark, LARB = lark bunting, WEME = western meadowlark, GRSP = grasshopper sparrow.

	MCLO		HOLA		LARB		WEME		GRSP	
	Mean	CRI	Mean	CRI	Mean	CRI	Mean	CRI	Mean	CRI
Survey 1	**6.823**	**(2.446, 9.866)**			**1.015**	**(0.971, 1.059)**			**0.669**	**(0.438, 1.195)**
Survey 2	**0.863**	**(0.186, 1.939)**			**1.265**	**(1.217, 1.312)**			**0.625**	**(0.418, 1.106)**
Intercept			**2.684**	**(2.120, 3.362)**			**1.373**	**(1.056, 1.747)**		
2013	1.515	(-0.011, 5.311)	**0.163**	**(0.001, 0.351)**					-0.262	(-0.904, 0.148)
2014	-0.039	(-1.039, 1.366)	-0.084	(-0.269, 0.078)					0.054	(-0.543, 0.431)
2015	0.456	(-0.559, 2.125)	-0.007	(-0.178, 0.158)					-0.034	(-0.635, 0.338)
2016	0.265	(-0.833, 2.177)	-0.060	(-0.238, 0.104)					**-0.456**	**(-1.072, -0.073)**
2017	**-1.585**	**(-2.393, -0.454)**	-0.035	(-0.223, 0.137)					0.210	(-0.376, 0.590)
Observer 1							**-0.329**	**-0.576, -0.084)**		
Observer 2							-0.280	(-0.711, 0.096)		
Observer 3							**0.416**	**(0.145, 0.753)**		
Observer 4							0.103	(-0.159, 0.372)		
Observer 5							-0.031	(-0.286, 0.223)		
Observer 6							0.227	(-0.026, 0.486)		
Observer 7							0.042	(-0.241, 0.327)		
Observer 8							-0.226	(-0.477, 0.024)		

Table A2.1. Standardized coefficient effects (means and credible intervals [CRI]) of vegetation composition, vegetation structure, topography and precipitation on abundance from the environmental-year model for each of our focal grassland bird species breeding on the Central Plains Experimental Range, Colorado from 2013 – 2017. Bolded values denote strong effects on abundance (i.e., the CRI of the coefficient did not include 0). Western meadowlark is not listed because model parameters would not converge in the model for this species. Blank spaces indicate the focal covariate was not included in the environmental model for the listed species. MCLO = McCown's longspur, HOLA = horned lark,

|	MCLO		HOLA		LARB		GRSP	
Composition	Mean	CRI	Mean	CRI	Mean	CRI	Mean	CRI
Standing dead	**0.606**	**(0.062, 1.135)**	**-0.196**	**(-0.322, -0.071)**	-0.079	(-0.162, 0.003)	0.055	(-0.052, 0.160)
Litter	0.155	(-0.151, 0.462)	0.027	(-0.083, 0.136)	0.005	(-0.078, 0.087)	-0.021	(-0.174. 0.130)
Shortgrass	0.012	(-0.294, 0.319)	0.107	(-0.002, 0.215)	0.001	(-0.070, 0.072)	**-0.242**	**(-0.378, -0.104)**
Midgrass	-0.427	(-0.427, 0.191)	-0.108	(-0.234, 0.016)	-0.033	(-0.103, 0.037)	0.062	(-0.020, 0.144)
Forb	**0.211**	**(0.032, 0.386)**	0.040	(-0.032, 0.109)	0.039	(-0.004, 0.082)	**-0.160**	**(-0.274, -0.054)**
Shrub	-0.034	(-0.632, 0.472)	-0.085	(-0.182, 0.007)	0.048	(-0.007, 0.100)	-0.052	(-0.161, 0.053)
Subshrub	-0.125	(-0.373, 0.112)	0.027	(-0.051, 0.102)	0.046	(-0.006, 0.097)	-0.015	(-0.123, 0.091)
Cactus	-0.185	(-0.444, 0.057)	-0.027	(-0.106, 0.050)	0.004	(-0.050, 0.058)	-0.039	(-0.144, 0.063)
Structure								
VOR	-1.458	(-2.372, -0.513)	**-0.360**	**(-0.500, -0.223)**	-0.034	(-0.109, 0.039)	-0.047	(-0.224, 0.109)
Topography								
TRI at 150 m	0.296	(-0.095, 0.685)	0.044	(-0.046, 0.132)	-0.009	(-0.072, 0.053)	0.093	(-0.023, 0.207)
TWI at 150 m	**0.237**	**(0.020, 0.456)**	0.037	(-0.055, 0.127)	-0.004	(-0.070, 0.063)	0.076	(-0.053, 0.205)
Year								
2014	**1.054**	**(0.290, 1.313)**	**0.433**	**(0.095, 0.771)**	**0.770**	**(0.579, 0.962)**	0.148	(-0.480, 0.788)
2015	**0.496**	**(0.496, 0.683)**	**0.700**	**(0.439, 0.960)**	**0.683**	**(0.520, 0.848)**	**1.185**	**(0.619, 1.778)**
2016	-0.802	(-1.770, 0.154)	**1.033**	**(0.720, 1.347)**	**-0.601**	**(-0.847, -0.356)**	**1.098**	**(0.451, 1.781)**
2017	0.453	(-0.369, 1.334)	**0.420**	**(0.084, 0.763)**	**-0.303**	**(-0.526, -0.082)**	-0.184	(-0.802, 0.467)
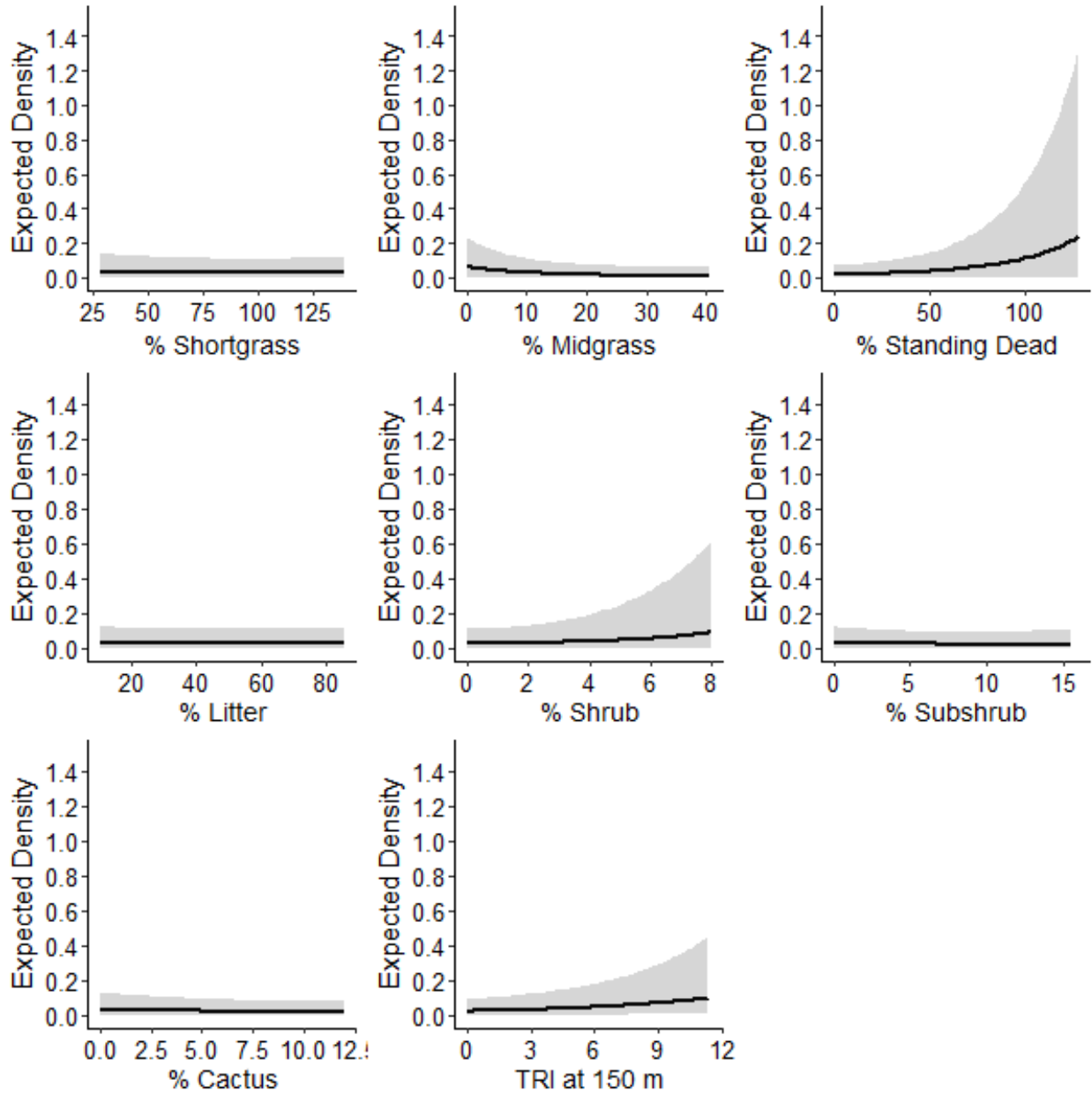
Figure A2.1. Predicted means and 95% CRIs from the environmental-precipitation model of the vegetation composition and topographic covariates that did not strongly influence McCown's longspur abundance (i.e., their credible intervals overlapped 0; calculated holding all other covariates at their means) on the Central Plains Experimental Range, Colorado from 2013 – 2017.
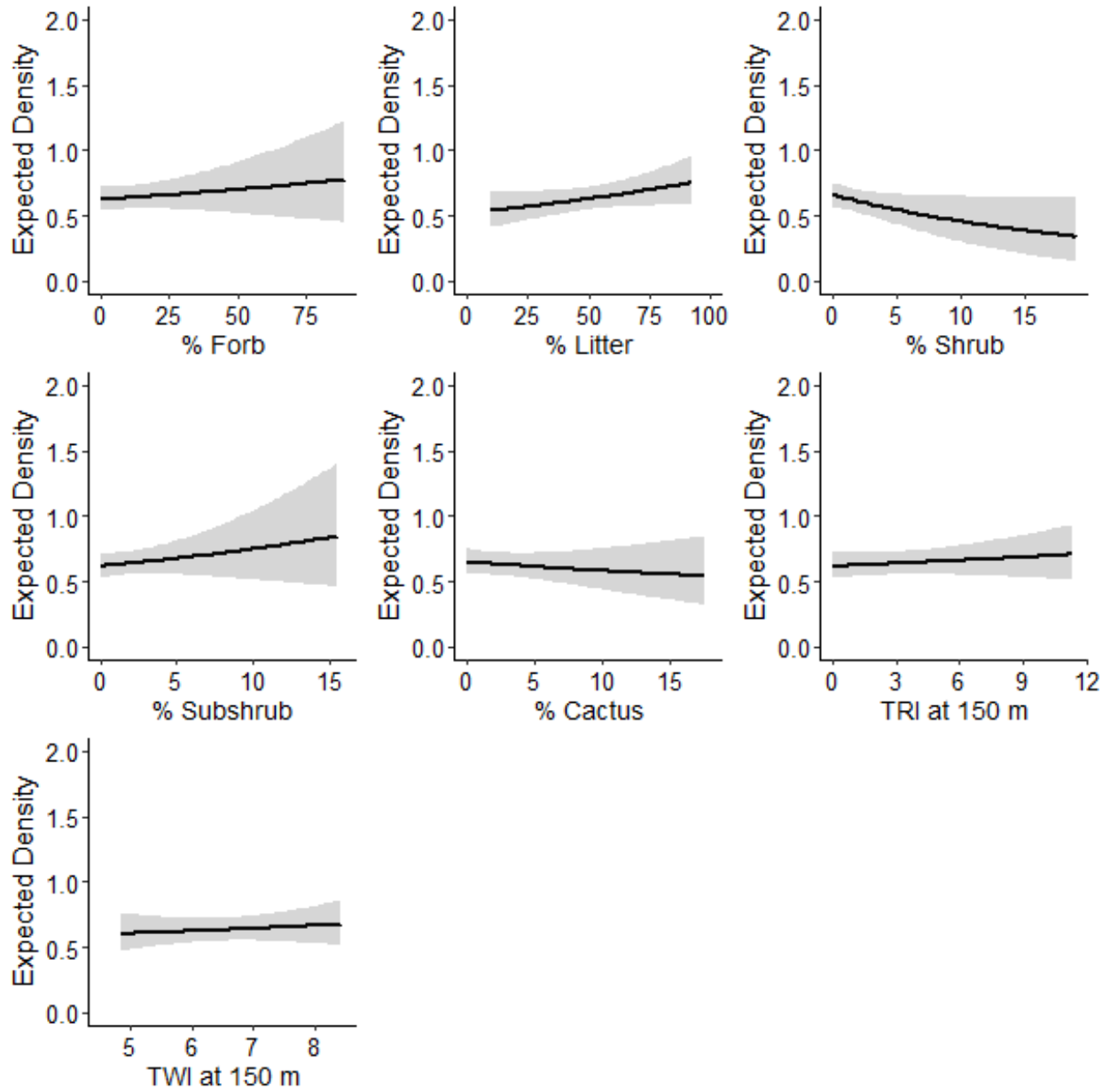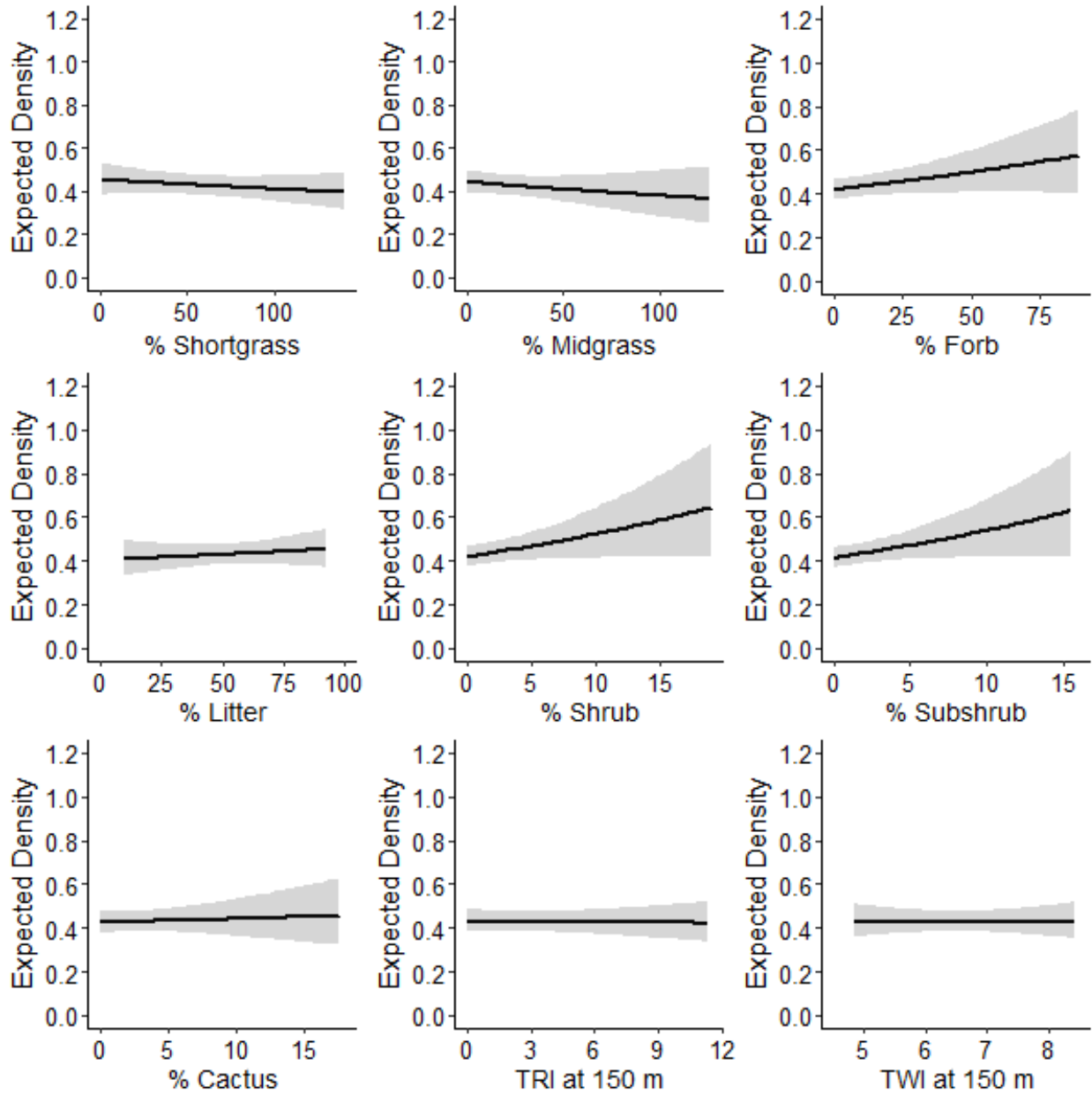
Figure A2.2. Predicted means and 95% CRIs from the environmental-precipitation model of the vegetation composition and topographic covariates that did not strongly influence horned lark abundance (i.e., their credible intervals overlapped 0; calculated holding all other covariates at their means) on the Central Plains Experimental Range, Colorado from 2013 – 2017.

Figure A2.3. Predicted means and 95% CRIs from the environmental-precipitation model of the vegetation composition and topographic covariates that did not strongly influence lark bunting abundance (i.e., their credible intervals overlapped 0; calculated holding all other covariates at their means) on the Central Plains Experimental Range, Colorado from 2013 – 2017.
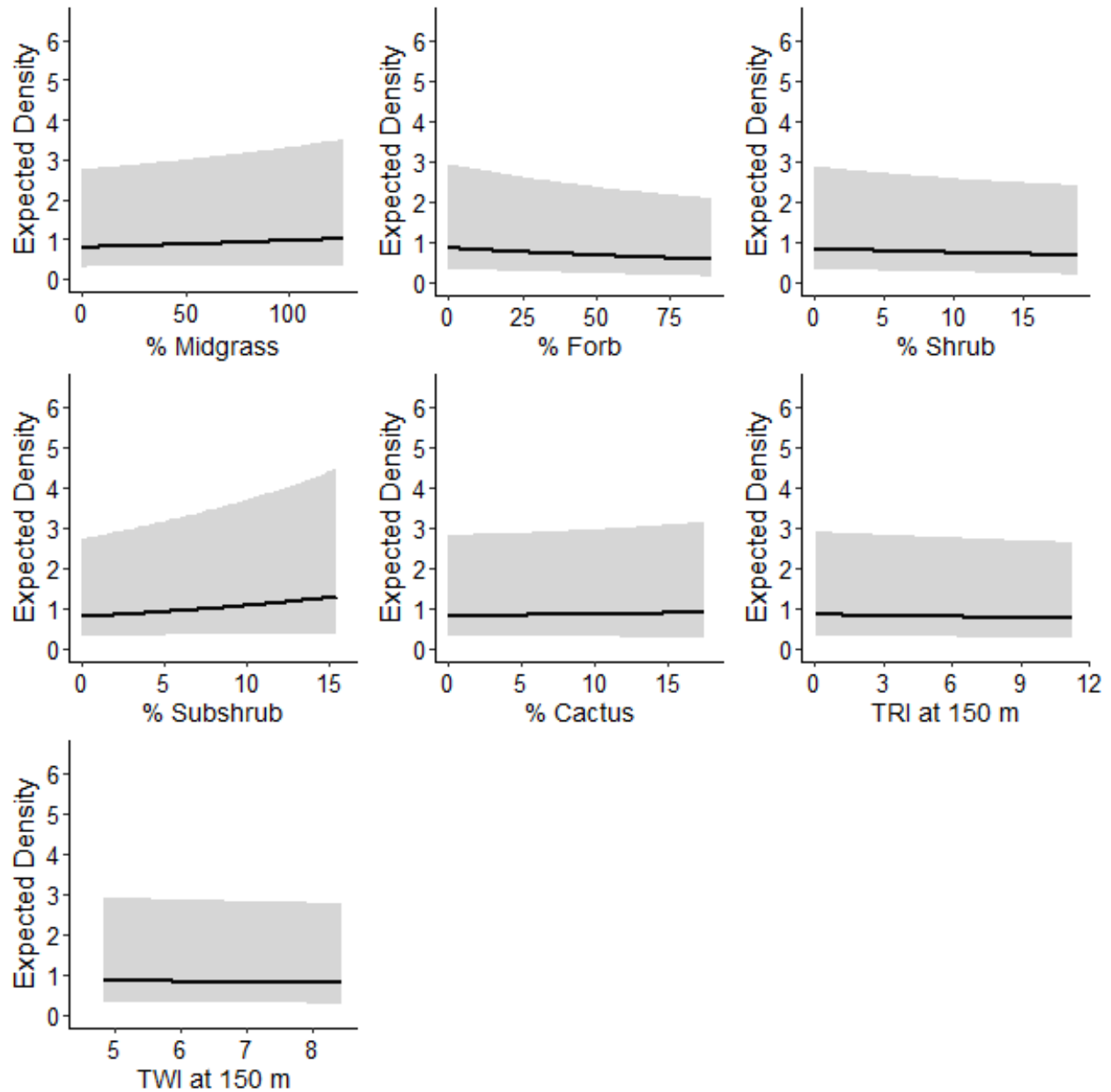
Figure A2.4. Predicted means and 95% CRIs from the environmental-precipitation model of the vegetation composition and topographic covariates that did not strongly influence western meadowlark abundance (i.e., their credible intervals overlapped 0; calculated holding all other covariates at their means) on the Central Plains Experimental Range, Colorado from 2013 – 2017.
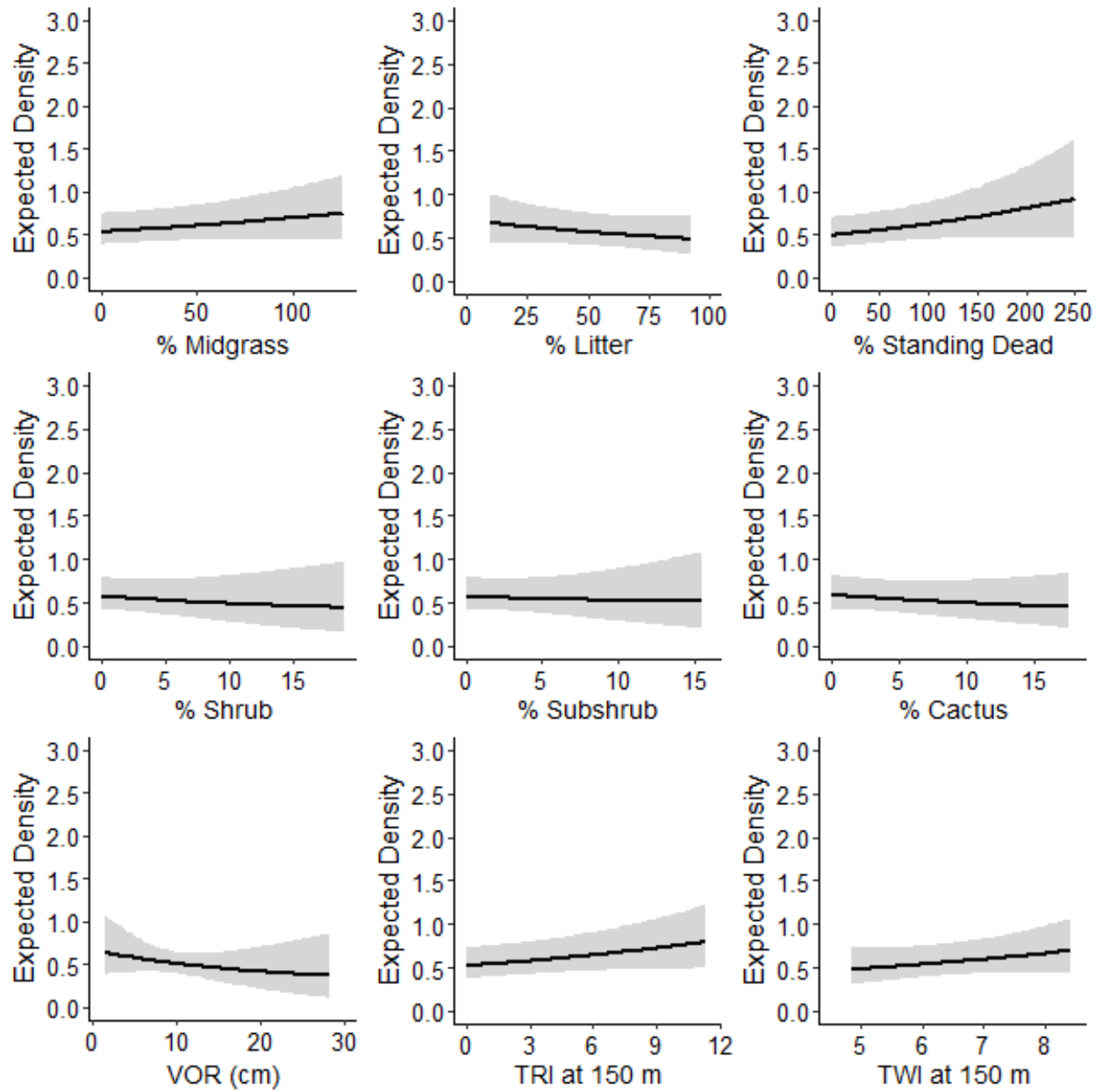
Figure A2.5. Predicted means and 95% CRIs from the environmental-precipitation model of the vegetation composition, vegetation structure and topographic that did not strongly influence grasshopper sparrow abundance (i.e., their credible intervals overlapped 0; calculated holding all other covariates at their means) on the Central Plains Experimental Range, Colorado from 2013 – 2017.