Vegetation characteristics and precipitation jointly influence grassland bird abundance beyond the effects of grazing management

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ABSTRACT

Grassland birds have experienced some of the steepest population declines of any guild of birds in North America. The shortgrass steppe contains some of North America's most intact grasslands, which makes the region particularly important for these species. It is well known that grassland birds differentially respond to variation in vegetation structure generated by spatiotemporally varying disturbance like grazing management. However, understanding how species respond to characteristics beyond vegetation structure or grazing could better inform management for these species in the shortgrass steppe. We analyzed point count data for 5 grassland bird species breeding on the Central Plains Experimental Range in northeastern Colorado from 2013 to 2017 to examine the predictive capacity of models representing fine-scale (~5 ha) vegetation attributes (vegetation structure and cover type) and topography, combined with interannual precipitation variability (i.e. vegetation-abiotic models). We then compared these models to models based on grazing management treatments (applied to whole pastures, ~130 ha) and edaphic conditions (ecological sites), which represented information more generally available to rangeland managers. Precipitation, vegetation structure, and vegetation cover type influenced all species in a manner consistent with, but more nuanced than, vegetation structure alone. These models also explained more variation in abundance for species that responded to grazing management. Thus, while grazing management can be applied adaptively to improve habitat for these species, our more detailed vegetation-abiotic models identified species-specific habitat components that could be targeted for management. For example, not grazing pastures with extensive, homogenous stands of mid-height grasses (e.g., *Hesperostipa comata*) for an entire growing season during wet years could be one strategy to enhance Grasshopper Sparrow (*Ammodramus savannarum*) abundance and stockpile residual forage for future utilization by livestock. Our models provide a better understanding of and reveal nuances in the suite of environmental conditions to which grassland birds respond in shortgrass steppe rangelands.

Keywords: Grasshopper Sparrow, habitat, Horned Lark, Lark Bunting, livestock grazing, rangeland management, Thick-billed Longspur, Western Meadowlark

LAY SUMMARY

- We lack clear understanding of which environmental characteristics might support declining bird species breeding in the shortgrass steppe of the United States.
- These bird species often breed on lands managed for cattle grazing and are known to respond to vegetation structure generated by grazing and/or soil conditions. We sought to evaluate how precipitation and different types of vegetation cover (e.g., shrubs, shortgrasses) could explain additional variation in bird abundance in this system.
- We found vegetation cover, vegetation structure, and precipitation could explain more variation in abundance than cattle grazing management and/or ecological sites (i.e. unique soil types with associated plant communities) for most bird species. For bird species that did not respond to grazing management, ecological site and year effects explained more variation in abundance than vegetation characteristics and precipitation.
- Precipitation conditions, types of vegetation cover, and ecological sites often are not considered when developing grazing management plans to support grassland birds; incorporating these factors into management plans may help support populations of these declining species.

Las características de la vegetación y la precipitación influyen conjuntamente en la abundancia de las aves de pastizal más allá de los efectos del tratamiento de pastoreo

RESUMEN

Las aves de pastizal han experimentado algunas de las disminuciones poblacionales más pronunciadas de cualquier gremio de aves en América del Norte. La estepa de pastos cortos contiene algunos de los pastizales más intactos de América del Norte, lo que hace que la región sea particularmente importante para estas especies. Las aves de pastizal responden de manera diferente a la variación en la estructura de la vegetación generada por el manejo del pastoreo que simula alteraciones que varían en espacio y tiempo. Sin embargo, comprender cómo las especies responden a características más allá de la estructura de la vegetación o del pastoreo podría aportar al manejo de estas especies en la estepa de pastos cortos. Analizamos los datos de puntos de conteo para 5 especies de aves de pastizal que se reproducen en el Rango Experimental de las Llanuras Centrales en el noreste de Colorado desde 2013 hasta 2017, para examinar la capacidad predictiva de los modelos que representan los atributos de la vegetación (estructura de la vegetación y tipo de cobertura) a escala fina (~3 ha) y de la topografía, combinados con la variabilidad interanual de las precipitaciones (i.e., modelos abióticos de vegetación). Luego comparamos estos modelos con otros basados en tratamientos de manejo del pastoreo (aplicados a pasturas enteras, ~130 ha) y en condiciones edáficas (sitios ecológicos), que representan la información disponible de manera más general para los gestores de praderas. La precipitación, la estructura de la vegetación y el tipo de cobertura de la vegetación influyeron en todas las especies de una manera consistente, pero con más matices, que la estructura de la vegetación por sí sola. Estos modelos también explicaron una mayor variación en la abundancia de las especies que respondieron al manejo del pastoreo. Por lo tanto, si bien el manejo del pastoreo se puede aplicar de manera adaptativa para mejorar el hábitat de estas especies, nuestros modelos más detallados que combinan vegetación y rasgos abióticos identificaron componentes de hábitat específicos para cada especie que podrían ser objeto de manejo. Por ejemplo, una estrategia para mejorar la abundancia de *Ammodramus savannarum* y acumular forraje residual para su uso futuro por parte del ganado podría ser mantener pasturas con rodales extensos y homogéneos de pastos de altura media (e.g., *Hesperostipa comata*) durante toda una temporada de crecimiento durante los años húmedos. Nuestros modelos proporcionan una mejor comprensión y revelan matices en el conjunto de condiciones ambientales a las que responden las aves de pastizal en las praderas de pastos cortos y estepas.

Palabras clave: Ammodramus savannarum, *Calamospiza melanocorys*, *Eremophila alpestris*, hábitat, manejo de praderas, pastoreo de ganado, *Rhynchophanes mccownii*, *Sturnella neglecta*

INTRODUCTION

Temperate grasslands are one of the most endangered eco-systems worldwide (Hoekstra et al. 2005). Over the last 200 years, 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 United States, to less than 30% of its original extent (Samson et al. 2004). Grassland birds, many species of which breed in the Great Plains, belong to one of the most threatened guilds of birds in North America (Brennan and Kuvlesky 2005, Sauer et al. 2017, Rosenberg et al. 2019). 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 domestic livestock, 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).

As classically described by Knopf (1996), grassland birds breed across a gradient of vegetation height and density (hereafter, vegetation structure) generated by grazing disturbance. Historically, the interaction between fire and grazing by native herbivores (e.g., American bison [*Bison*

bison] and prairie dogs [*Cynomys* spp.]) generated the structural heterogeneity needed to support the full suite of grassland bird species native to North America's grass-lands (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 increase abundance of some grassland bird species (Augustine and Derner 2015, Ahlering and Merkord 2016, Golding and Dreitz 2017, Lipsey and Naugle 2017). How grazing management can best support the full suite of grassland birds, however, remains a conservation challenge (Derner et al. 2009).

Factors such as cover of vegetation types (e.g., percent cover of grasses, forbs; hereafter, vegetation cover) and weather conditions also affect grassland birds (Niemuth et al. 2008, Fisher and Davis 2010, Gorzo et al. 2016, Lipsey and Naugle 2017). Yet, these factors generally have received less research attention than the influence of vegetation structure or grazing. For example, grassland birds differentially respond to cover of bare ground, litter, grasses, and forbs (Fisher and Davis 2010, Lipsey and Naugle 2017). Precipitation may affect grassland birds via its influence on insect populations (Lenhart et al. 2014), which are grassland birds' primary prey source during the breeding season. Evidence suggests regional abundance of some grassland bird species is correlated with annual variation

in precipitation (Gorzo et al. 2016). Precipitation patterns also can dictate whether or how grazing affects grassland birds—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, Ahlering and Merkord (2016) found year effects explained more variation in annual grassland bird community composition than did grazing management. This likely was due to 2 exceptionally dry years during their study; high temperatures and severe drought have been associated with nest abandonment, the termination of nesting, and lower species richness and diversity of grassland birds (George et al. 1992, Igl and Johnson 1999, Ahlering and Merkord 2016). This suggests the factors influencing grassland bird abundance may be more complex and temporally variable than have been previously considered in conceptual models of grassland bird habitat (Knopf 1996).

While most research investigating drivers of grassland bird abundance in North America has occurred in tallgrass and mixed-grass prairies (Fuhlendorf et al. 2006, Ahlering and Merkord 2016, Lipsey and Naugle 2017), few studies have investigated such drivers in the shortgrass steppe (though see Augustine and Derner 2015 and Skagen et al. 2018). The shortgrass steppe is the warmest and most arid region of North America's Great Plains. It is characterized by dramatically variable precipitation within and across years (Wiens 1973). This variable climate produces a vegetation community that is uniquely drought- and grazing-adapted and contains the shortest vegetation of the Great Plains' grasslands (Lauenroth et al. 1999). The shortgrass steppe also contains some of North America's most intact grasslands (~50% of its historic extent; Samson et al. 2004), which makes the region particularly important for grassland birds.

We conducted our current study within a larger, ongoing grazing experiment occurring at the Central Plains Experimental Range (CPER) in northeastern Colorado's shortgrass steppe. This experiment is examining how season-long grazing vs. adaptive, multi-paddock rotational grazing affect a variety of ecosystem services, including grassland bird abundance (Wilmer et al. 2018, Davis et al. 2020). Davis et al. (2020) evaluated how grazing management within this experiment affected grassland bird abundance and found 3 of 5 grassland bird species breeding on the CPER responded to grazing management. However, the effect of grazing depended on ecological site (n = 3 on the CPER; Davis et al. 2020), which are U.S. Department of Agriculture designations that describe how soil conditions are linked to variation in plant community composition and productivity (USDA-Natural Resources Conservation Service [USDA-NRCS] 2007a, 2007b, 2007c; https://www.nrcs.usda.gov/wps/portal/nrcs/main/national/technical/

ecoscience/desc/). Horned Lark (*Eremophila alpestris*) abundance was highest in pastures that were intensively grazed and Grasshopper Sparrow (*Ammodramus savannarum*) abundance was highest in pastures that were rested (i.e. not grazed) the previous year in the least productive ecological site. Thick-billed Longspur (*Rhynchophanes mccownii*) abundance decreased in pastures rested from grazing the previous year in the least productive ecological site, which was the only ecological site within which it occurred during our study. In addition, abundance of all species varied across ecological sites. However, this analysis did not directly account for annual variation in precipitation (Ahlering and Merkord 2016), nor did it examine how specific aspects of vegetation structure or cover were related to grassland bird abundance (Lipsey and Naugle 2017). Prior research conducted as a part of this grazing experiment found that grazing treatments described above did not affect the relative abundance of C_3 midgrasses vs. C_4 shortgrasses on the CPER (Augustine et al. 2020), but grazing effects on vegetation structure were not evaluated.

Here, we examined how both vegetation structure and cover, precipitation, and topography influenced abundance of Thick-billed Longspur, Horned Lark, Lark Bunting (*Calamospiza melanocorys*), Western Meadowlark (*Sturnella neglecta*), and Grasshopper Sparrow breeding on the CPER during 2013–2017. We then examined whether models including these factors could better explain abundance of our focal species compared to the grazing management models developed in Davis et al. (2020) or models describing abiotic or soil conditions alone. We predicted species would respond to vegetation structure along a gradient of height/density (Knopf 1996; Figure 1); Thick-billed Longspur and Horned Lark abundance would decrease and Western Meadowlark and Grasshopper Sparrow abundance would increase with vegetation structure. We expected Lark Bunting abundance to increase slightly with vegetation structure as they prefer relatively taller vegetation structure in the shortgrass steppe (Figure 1). We predicted all species would respond to vegetation cover, but differentially on the basis of species' nesting preferences. Specifically, we predicted Thick-billed Longspur and Horned Lark abundance would increase with cover of shortgrasses and forbs and decrease with litter and shrub cover (With and Webb 1993); Lark Bunting abundance would increase with cover of subshrubs, shrubs, shortgrasses, and midgrasses; and Western Meadowlark and Grasshopper Sparrow abundance would increase with cover of midgrasses (Figure 1). We also expected species would respond to precipitation conditions that supported their preferred vegetation structure; abundance of species that prefer short, sparse vegetation, like Thick-billed Longspur and Horned Lark, would decrease while those that prefer tall, dense structure, like Western Meadowlark
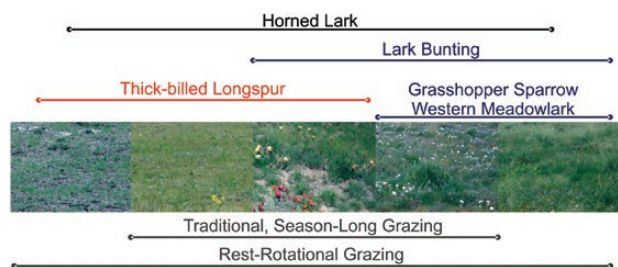
FIGURE 1. Hypothesized influence of grazing management on vegetation heterogeneity and grassland birds in shortgrass steppe rangelands of the western Great Plains. Photographs depict variation in vegetation structure/cover ranging from a blue grama (*Bouteloua gracilis*)/bare soil mosaic (far left) to a closed-canopy sward of perennial forbs and mid-height C_3 grasses (far right). The length of the 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 (i.e. rested). Colors indicate different guilds of species, with listed example species: red represents associates of sparse/prostrate vegetation (e.g., Thick-billed 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 Grasshopper Sparrow, would increase with precipitation. We predicted Lark Bunting abundance might respond most strongly to precipitation of all focal species given this species' abundance can be highly variable across years due to nomadism associated with regional precipitation conditions (Wilson et al. 2018, Green et al. 2019). Although some of our focal species previously responded to grazing management (Davis et al. 2020), we expected our models reflecting environmental conditions (vs. models reflecting grazing management or soil or abiotic conditions) would be better supported for all species because these models may better represent mechanisms by which grassland birds respond to their environment.

METHODS

Study Area

The CPER, managed by the U.S. Department of Agriculture-Agricultural Research Service, encompasses 6,270 ha and is located ~12 km northeast of Nunn, Colorado (40.8°N, 104.7°W). Mean daily temperatures ranged from −20°C to 11°C in January and from 13°C to 26°C in July from 2008 to 2017. Greater than 80% of annual precipitation occurs during the growing season of April through September (Lauenroth and Sala 1992), and long-term mean annual precipitation (January–December) and mean annual growing season precipitation (April–August) on the CPER were 340 and 242 mm, respectively (Augustine and

Derner 2015). Total growing season precipitation for the years of our study was 406, 370, 380, 256, and 272 mm (2013–2017). 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 consists of gently undulating plains, varying from 1,600 to 1,690 m in elevation. 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 prickly pear 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 2015).

Grazing Experiment

The grazing experiment included 20 treatment pastures, each ~130 ha, paired into 10 blocks (Figure 2). Each block contained one pasture assigned randomly to a traditional rangeland management (TRM; i.e. continuous, season-long grazing) treatment and the other assigned to a collaborative adaptive rangeland management (CARM) treatment. In TRM pastures, single small herds (of approximately similar size in each pasture) of yearling steers grazed continuously throughout the growing season (mid-May to early October). In CARM pastures, a single large herd of yearling steers was rotated through these pastures with at least one pasture left out of rotation, or rested, each year. The CARM herd was 10 times the size of a single TRM herd, but the same total number of steers grazed in the TRM and CARM pastures each year (both treatments used the same moderate stocking rate of 0.61 animal unit months [AUM] ha^{-1}, where an AUM is the amount of forage needed to support one month of grazing by the equivalent of a mature 1,000-pound cow; Society for Rangeland Management 2017). This resulted in a wider range and variance in grazing intensity experienced by individual pastures in the CARM vs. the TRM treatment. Specifically, in any given year, pastures assigned to the CARM treatment could either experience (1) intensive, short-duration grazing by the large herd in the pastures where the CARM herd was rotated through (i.e. pulse grazing), or (2) rest for a full year in the pasture(s) left out of rotation. From 2014 to 2017 (i.e. treatment years), the number of pastures rested ranged from 1 in the driest year to 6 in the wettest year (see Supplementary Material Table S1 for a detailed rotation/rest schedule for the CARM herd). The rotation schedule was decided upon annually by a stakeholder group comprised of federal and state land management
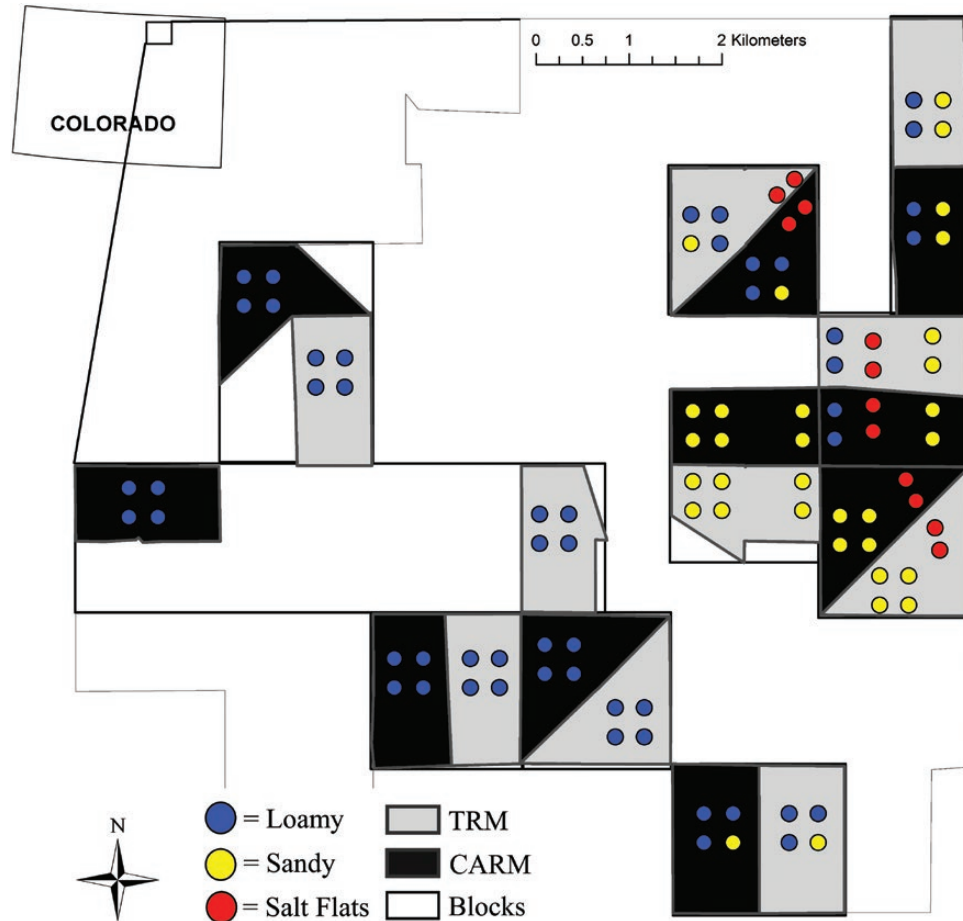
FIGURE 2. A map of the CPER (Colorado, USA) showing grazing treatment pastures (TRM and CARM) and monitoring plots (represented by circles). Colors correspond to the main ecological sites present on the site: loamy plains, sandy plains, and salt flats.

agencies, private ranchers, and non-governmental organizations (hence termed "collaborative adaptive" management; Wilmer et al. 2018).

Each pasture contained 4–6 monitoring plots (125 m radius; 4.9 ha) that were distributed following a stratified random sampling design on the basis of ecological site (Figure 2). The 3 ecological sites on the CPER—loamy plains, sandy plains, and salt flats—vary along a gradient of prevalence and productivity where the loamy plains ecological site is least productive but most prevalent and the salt flats ecological site is most productive but least prevalent (see USDA-NRCS 2007a, 2007b, 2007c for details on soil series and plant communities associated with each ecological site). We established 4 monitoring plots in pastures that only contained loamy plains and/or sandy plains ecological sites. For pastures that additionally contained the salt flats ecological site, we established 4 plots on the loamy and/or sandy plains ecological sites and 2 additional plots on the salt flats ecological site, for a total of 6 plots in the pasture. This resulted in 92 monitoring plots across the 20 study pastures (Davis et al. 2020; Figure 2).

Data Collection

Vegetation. Vegetation structure and cover data were collected annually in June 2013–2017 from a systematic grid of four 25-m transects oriented north-south and spaced 106 m apart within each monitoring plot ($n = 368$ transects). These 4 transects within each plot were designed to sample vegetation within ~5-ha area of grassland surrounding each point count (i.e. a 125-m radius area surrounding each point count). Vegetation technicians received a week-long training at the start of the field season (mid-May) to identify the plant species present on the CPER. Technicians used the line-point intercept method to quantify canopy and basal vegetation cover by species along each transect. This involved passing a laser vertically down through the vegetation canopy and recording the species identity where the laser intercepted the vegetation canopy or the ground surface at 50 locations per transect spaced at 0.5-m intervals following Herrick et al. (2005), but modified to record all canopy intercepts for each species. We cumulated all vegetation species detected in these surveys into 8 cover groups that we predicted may

influence the abundance of our focal species: shortgrass, midgrass, cactus, forb, shrub, subshrub, standing dead, and litter. We calculated mean absolute cover across all transects for each cover group per plot per year. We calculated absolute cover (which is the sum of foliar cover, and thus 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 used vegetation visual obstruction (VO), which is a combination of vegetation height and density, to quantify vegetation structure. Technicians measured VO by placing a VO pole modeled after Robel et al. (1970; modified with 1-cm increments) at each of 8 locations spaced every 3 m along each transect. They recorded the highest band on the pole that was partially or entirely obscured by vegetation, with 2 readings for each pole placement taken from locations perpendicular to the transect at a distance of 4 m from the pole and 1 m above the ground (Robel et al. 1970). We calculated mean VO for each plot as the average of the 16 readings from each of the 4 transects. We measured VO twice each year, first in June at the same time as vegetation cover measurements, and a second time in early October, after cattle were removed from all pastures. The June measurement coincided with the avian point counts (see Birds section below) and peak nesting period of the bird species. The October measurement provides an index of the structure of dormant vegetation over the winter, as well as the conditions that some bird species experience when establishing territories in April and early May, prior to significant new plant growth.

Topographic indices. We used the topographic ruggedness index (TRI) and topographic wetness index (TWI) to quantify topography on the CPER. The TRI denotes average elevation change between any point on a grid and its surrounding area (Riley et al. 1999). The TWI is a steady-state wetness index where larger values represent drainage depressions, or wetter areas, while smaller values represent crests and ridges, or drier areas (Beven and Kirkby 1979). The TWI and TRI layers for CPER were derived from a 10-m resolution digital elevation model. We calculated average TRI and TWI over a 150-m circular buffer surrounding the point count location to represent the area encompassing the resources surrounding an average territory for our focal species (Beason 2020, Davis and Lanyon 2020, Shane 2020, Vickery 2020, With 2020). This scale also is comparable to that at which our vegetation data were collected. TRI and TWI were calculated in ArcGIS version 10.2.2 (Environmental Systems Research Institute 2014) using a digital elevation model of the CPER developed by the National Ecological Observation Network 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. We considered 5 windows of cumulative precipitation and soil moisture that could influence bird abundance (Supplementary Material Table S2). We calculated all precipitation windows except soil moisture as cumulative precipitation collected at the CPER during our focal temporal windows. Cumulative precipitation was calculated from precipitation data collected from a rain gauge at the headquarters of CPER (located near the center of the site) that was checked daily Monday through Friday. We obtained daily volumetric soil moisture data from the USDA-Soil Climate Analysis Network station 2017, Nunn #1, which is located approximately in the center of the CPER. We calculated average percent soil moisture as the mean daily soil moisture between 10 and 20 cm, as moisture in this soil layer is expected to have the greatest effect on vegetation productivity. We used the same precipitation and soil moisture measurements to characterize all pastures within a given time period.

Birds. Avian point count locations were placed in the center of each monitoring plot (≥250 m apart). Thus, each pasture contained 4- to 6-point count locations (see Grazing Experiment section and Figure 2). Trained observers conducted 6-min, unlimited radius point count surveys on days with appropriate weather conditions (i.e. wind speeds <19 km hr^{-1}, no precipitation) between sunrise and ~10:30 AM. Point counts were conducted twice during the breeding season between late May and the second week of June. Observers used rangefinders to measure the distance to all individual birds detected and recorded the distance and the method of detection (e.g., aural, visual) and sex (if determinable) of each individual. Ninety-six point count locations were surveyed twice per year for 5 years, totaling 920 point counts.

Statistical Analyses

Vegetation structure. We used linear mixed models to examine short-term grazing effects on vegetation structure (i.e. height and density) as measured by VO. We log-transformed the VO data prior to fitting models to remove heteroscedasticity. Our models treated block as a random effect, accounted for repeated measures in each plot over time, and evaluated potential interactions among grazing treatment, ecological site, and year. We used thresholds of $\alpha = 0.05$ to evaluate main effects and $\alpha = 0.1$ to evaluate interaction terms (as per Augustine et al. 2020). We fit models using Proc GLIMMIX in SAS software v9.4 (SAS Institute, Cary, North Carolina, USA). We analyzed whether the grazing treatment applied to each pasture in the current year (traditional, pulse grazing, or rest) affected VO in October, and whether the grazing treatment applied in the previous year affected VO in June of the subsequent year.

Bird abundance. We fit hierarchical distance sampling models in a Bayesian framework using the package *jagsUI*

(Kellner 2018) in R (R Development Core Team 2019) to model grassland bird abundance at the CPER. We summed the 2 counts per point count location each year (hereafter, survey; n = 460) prior to model fitting so that our models would be comparable to those fit in Davis et al. (2020). We assumed counts y at survey k were the outcome of a binomial distribution conditional on true abundance N_k and detection probability p_k,

$$y_k|N_k \sim \text{ Binomial } (N_k, p_k)$$

We modeled detection probability (p) using distance sampling with a hazard rate detection function because preliminary analyses in program DISTANCE (Thomas et al. 2010) suggested this detection function best fit our data (Buckland et al. 2001; see Davis et al. 2020). We truncated the 10% farthest counts sensu Buckland et al. (2001) before fitting models. We used a log-link function to model covariates (which varied by survey k) on the scale parameter of the detection function (σ; Amundson et al. 2014). These included a coefficient for VO and a random term for year. We specified vague normal priors (Normal [0, 10]) on coefficients for the detection model, and either a weakly-informative half-Cauchy (Gelman 2006) or a vague uniform (0, 10) prior for the standard deviation of the random terms.

We modeled abundance of each species at survey k (N_k) as a function of a Poisson distribution with mean abundance λ_k:

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

To account for the design of the grazing experiment, we modeled a random term for block on the intercept for abundance for all species except Thick-billed Longspur. For Thick-billed Longspur, we used a pasture-specific intercept because parameters associated with the block random term were not identifiable in models for this species (Davis et al. 2020). We modeled focal covariates on λ using a log-link function and included a random term for survey to improve model fit and an offset term to account for the 2 counts conducted at each survey (which made our response birds per count). We specified vague normal priors for the intercept and abundance coefficients. We specified vague uniform priors for the standard deviations of the random terms for block and pasture. For Grasshopper Sparrow, Horned Lark, and Lark Bunting, we employed a hierarchical-centering approach to model block and survey random terms to facilitate convergence of these parameters (Ogle and Barber 2020).

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 Thick-billed 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 2 species were males. Due to this, we fit models for Lark Bunting and Thick-billed Longspur using male detections only.

Model fitting and comparisons. Once we identified the most predictive precipitation window for each species (Supplementary Material Table S3), we fit 4 models for each species: (1) an abiotic model, (2) an edaphic-year model, (3) a vegetation-abiotic model, and (4) the grazing model fit in Davis et al. (2020), hereafter the grazing-edaphic-year model. The abiotic models included only TRI, TWI, and the top precipitation window selected for each species (Supplementary Material Table S3) and the edaphic-year model included only ecological site (loamy plains, sandy plains, salt flats) and year. We considered the abiotic and edaphic-year models as "base" models because they served to reveal whether our vegetation-abiotic and/or grazing-edaphic-year models could explain variation in grassland bird abundance beyond baseline edaphic or abiotic conditions alone. The vegetation-abiotic models included our 12 focal vegetation and abiotic covariates: vegetation cover (n = 8), vegetation structure (VO), TRI, TWI, and the top precipitation window selected for each species (Supplementary Material Table S3). The grazing-edaphic-year models for Horned Lark and Grasshopper Sparrow included year and an interaction between grazing treatment (traditional, pulse grazing, rest) and ecological site. The interaction between grazing treatment and ecological site was not supported for Lark Bunting and Western Meadowlark (Davis et al. 2020), so the grazing-edaphic-year models for these species included main effects of year, grazing treatment, and ecological site. The grazing-edaphic-year model for Thick-billed Longspur included grazing treatment and year only because Thick-billed Longspurs were detected almost exclusively on the loamy plains ecological site on the CPER from 2013 to 2017 (Davis et al. 2020). We compared the predictive capacity of our 4 focal models using posterior predictive loss, which is similar to other model selection criteria for models fit in a Bayesian framework but is more appropriate for hierarchical models and correlated data (Gelfand and Ghosh 1998, Hobbs and Hooten 2015). We checked whether focal covariates were highly correlated (i.e. $|r|$ > 0.7; Supplementary Material Table S4) prior to model fitting and did not include correlated covariates in the same model.

We fit all models with 3 parallel MCMC chains for 500,000–1,050,000 iterations and saved 50,000–100,000 iterations per chain. We visually examined trace plots of MCMC chains and considered parameters with Gelman–Rubin statistics <1.1 to have converged (Gelman et al. 2013). We used a chi-squared discrepancy goodness-of-fit

test to evaluate model fit and compared observed and predicted test statistics with posterior predictive checks (i.e. Bayesian *P* values; Amundson et al. 2014, Kéry and Royle 2016). We considered Bayesian *P* values ≤0.1 and ≥0.9 to indicate lack of fit (Amundson et al. 2014). Means and 95% credible intervals (CIs) were calculated for all model parameters. We only interpreted models that had good fit and considered a focal covariate to have strong support for affecting abundance if the CI of the coefficient estimate did not include zero.

RESULTS

Vegetation Structure
The interaction between grazing treatment in the current year, ecological site, and year significantly affected vegetation structure (VO) in October (*P* = 0.008; Supplementary Material Table S5). VO in rested pastures was 25–69% greater than VO in both the pulse grazed and traditionally grazed pastures on the loamy plains ecological site in 2014, 2015, and 2017 (*P* ≤ 0.04), on the sandy plains ecological site in 2014, 2016, and 2017 (*P* ≤ 0.05), and on the salt flats in 2015 and 2016 (*P* < 0.05; Supplementary Material Figure S1).

Grazing treatment in a given year also significantly affected VO in June of the subsequent year and showed a significant interaction by ecological site and year (*P* = 0.06; Supplementary Material Table S6). VO in rested pastures was 20–40% greater than in pulse grazed and traditionally grazed pastures in the loamy plains ecological site in 2015 (*P* = 0.007), and on both the sandy plains (*P* = 0.05) and salt flats (*P* = 0.008) ecological sites in 2017 (Supplementary Material Figure S2).

Bird Abundance
During our study, Lark Bunting males were detected the most (2,660 detections) and Thick-billed Longspur males were detected the least (287 detections). We had 1,367, 1,327, and 715 detections for Western Meadowlark, Horned Lark, and Grasshopper Sparrow, respectively.

Our examination of the most predictive precipitation window for each species revealed that cumulative precipitation the prior year's growing season (i.e. summer lagged) was most predictive for Thick-billed Longspur and Lark Bunting, and late spring soil moisture was most predictive for Horned Lark, Western Meadowlark, and Grasshopper Sparrow (Supplementary Material Table S3).

Our vegetation-abiotic models showed that a combination of precipitation, vegetation structure, and vegetation cover could be used to effectively model abundance of all focal species (Table 1). Cumulative precipitation the previous growing season or late spring soil moisture positively affected abundance for all focal species (Table 1). Only

Grasshopper Sparrow responded to topography (topographic ruggedness); the vegetation-abiotic model for this species showed abundance increased in areas with more variable topography at a 150-m scale (Table 1; Figure 3). However, there was no relationship between Grasshopper Sparrow abundance and topography in the abiotic model (i.e. the base model that included only topography and precipitation; Supplementary Material Table S7).

Vegetation structure (VO) affected abundance of all species except Lark Bunting (Table 1). Both Thick-billed Longspur and Horned Lark, which prefer shorter and more sparse vegetation, declined with increasing structure (Table 1; Figure 3). Abundance of Western Meadowlark and Grasshopper Sparrow, which prefer taller and/or more dense grass cover in the shortgrass steppe, increased with increasing structure (Table 1; Figure 3).

Vegetation cover also affected abundance of all species, though for some species the effect was small (e.g., Lark Bunting; Table 1; Figure 3). Horned Lark responded most to vegetation cover compared to our other focal species; 5 cover covariates were supported for Horned Lark abundance compared to 1–3 for other focal species (Table 1). Absolute percent cover of shortgrass and standing dead vegetation were the most common cover variables explaining variation in abundance across species. Horned Lark and Western Meadowlark abundance increased while Grasshopper Sparrow abundance decreased with increasing shortgrass cover, and Western Meadowlark and Grasshopper Sparrow abundance increased while Horned Lark abundance decreased with increasing cover of standing dead vegetation (Table 1). Cover of litter, midgrasses, forbs, and shrubs each affected abundance for 2 species. For example, Grasshopper Sparrow abundance increased while Horned Lark abundance decreased with cover of midgrasses, and Horned Lark and Lark Bunting abundance increased with forb cover (Table 1; Figure 3).

Our vegetation-abiotic models were the best supported models for predicting abundance for 3 of our 5 focal species: Thick-billed Longspur, Horned Lark, and Grasshopper Sparrow (Table 2). The edaphic-year models (ecological site and year) were best supported for our other 2 focal species: Lark Bunting and Western Meadowlark (Table 2; see Supplementary Material Table S8).

DISCUSSION

Here, we provide one of the first empirical assessments of Knopf's (1996) classic diagram of grassland bird niche partitioning for the shortgrass steppe. Our analysis of the best vegetation-abiotic model for each species showed all species responded to fine-scale (~5 ha) vegetation characteristics and abiotic factors in more nuanced ways than strictly along a gradient of vegetation structure (i.e. height/

TABLE 1. Standardized coefficient estimates of vegetation cover, vegetation structure, topography, and precipitation from the vegetation-abiotic models for abundance for 5 focal grassland bird species breeding on the CPER (Colorado, USA) from 2013 to 2017. Bolded values denote strong support for the focal covariate affecting abundance (i.e. the credible interval [CI] of the coefficient estimate does not include zero). Blank cells indicate the focal covariate was not included in the model for the listed species

	Thick-billed Longspur		Horned Lark		Lark Bunting	
	(*Rhynchophanes mccownii*)		(*Eremophila alpestris*)		(*Calamospiza melanocorys*)	
	Mean	CI	Mean	CI	Mean	CI
Standing dead	0.328	(–0.105, 0.757)	**–0.190**	**(–0.296, –0.087)**	–0.061	(–0.133, 0.010)
Litter	0.134	(–0.069, 0.340)	**0.118**	**(0.031, 0.207)**	0.039	(–0.029, 0.107)
Shortgrass	–0.028	(–0.290, 0.239)	**0.205**	**(0.113, 0.297)**	0.025	(–0.035, 0.085)
Midgrass	–0.482	(–1.026, 0.041)	**–0.114**	**(–0.224, –0.006)**	–0.043	(–0.104, 0.017)
Forb	**0.145**	**(0.003, 0.282)**	0.015	(–0.048, 0.077)	**0.042**	**(0.003, 0.082)**
Shrub	0.049	(–0.462, 0.489)	**–0.134**	**(–0.222, –0.050)**	**0.054**	**(0.008, 0.100)**
Subshrub	–0.121	(–0.337, 0.086)	0.002	(–0.066, 0.070)	**0.058**	**(0.012, 0.104)**
Cactus	–0.037	(–0.238, 0.153)	–0.004	(–0.071, 0.062)	0.004	(–0.044, 0.051)
VO (cm)	**–0.977**	**(–1.396, –0.560)**	**–0.273**	**(–0.396, –0.151)**	–0.028	(–0.101, 0.045)
TRI at 150 m	0.139	(–0.136, 0.412)	0.010	(–0.070, 0.089)	–0.011	(–0.068, 0.046)
TWI at 150 m	0.172	(–0.011, 0.357)	0.016	(–0.066, 0.097)	–0.017	(–0.078, 0.043)
Summer lagged (cm)	**0.545**	**(0.250, 0.839)**			**0.696**	**(0.615, 0.777)**
Soil moisture (%)			**0.425**	**(0.291, 0.559)**		

	Western Meadowlark		Grasshopper Sparrow	
	(*Sturnella neglecta*)		(*Ammodramus savannarum*)	
	Mean	CI	Mean	CI
Standing dead	**0.141**	**(0.074, 0.208)**	**0.215**	**(0.106, 0.330)**
Litter	**0.182**	**(0.095, 0.268)**	–0.027	(–0.168, 0.111)
Shortgrass	**0.109**	**(0.019, 0.198)**	**–0.153**	**(–0.294, –0.011)**
Midgrass	0.007	(–0.060, 0.073)	**0.099**	**(0.008, 0.191)**
Forb	–0.059	(–0.134, 0.011)	–0.028	(–0.135, 0.075)
Shrub	–0.022	(–0.090, 0.043)	0.009	(–0.100, 0.114)
Subshrub	0.052	(–0.010, 0.113)	0.039	(–0.068, 0.144)
Cactus	–0.019	(–0.083, 0.043)	–0.059	(–0.165, 0.045)
VO (cm)	**0.258**	**(0.164, 0.352)**	**0.157**	**(0.026, 0.289)**
TRI at 150 m	–0.017	(–0.093, 0.057)	**0.140**	**(0.018, 0.261)**
TWI at 150 m	0.019	(–0.064, 0.102)	0.113	(–0.026, 0.252)
Summer lagged (cm)				
Soil moisture (%)	**0.517**	**(0.367, 0.667)**	**0.949**	**(0.715, 1.181)**

density) alone. Vegetation structure had the largest magnitude of effect for our focal species that prefers the shortest structure (Thick-billed Longspur), but metrics of vegetation cover and structure were important predictors for Horned Larks, Western Meadowlarks, and Grasshopper Sparrows. Lark Bunting abundance increased slightly with metrics of vegetation cover but had no relationship with vegetation structure. Annual variation in precipitation and soil moisture also had strong effects on abundance for all species. Moreover, the vegetation-abiotic and edaphic-year models were better supported for explaining variation in abundance than the grazing-edaphic-year model for all focal species. These results suggest grazing management applied without consideration of environmental factors beyond vegetation structure may not be sufficient for supporting the full suite of these declining species in the shortgrass steppe.

The Thick-billed Longspur prefers the shortest vegetation structure of our focal species (With 2020) and is experiencing among the most rapid rates of population decline and range contraction of all grassland-breeding birds in North America (Rosenberg et al. 2016). Our finding that year-long rest from grazing significantly increased vegetation structure (Supplementary Material Tables S5 and S6; Supplementary Material Figures S1 and S2) is consistent both with findings that rest negatively affected Thick-billed Longspur abundance (Davis et al. 2020) and that this species' abundance could be modeled more effectively using a model that included vegetation height-density (Table 2). Vegetation structure had the largest effect on Thick-billed Longspur abundance, with abundance rapidly approaching 0 where mean VO exceeded 5 cm (Figure 3). This is consistent with previous work in the shortgrass steppe showing this species preferentially nests in areas dominated by C_4 shortgrasses (mean VO of ~3–4 cm; Skagen et al. 2018), and that in mixed-grass prairie, their abundance increased with grazing intensity by livestock (Lipsey and Naugle 2017).
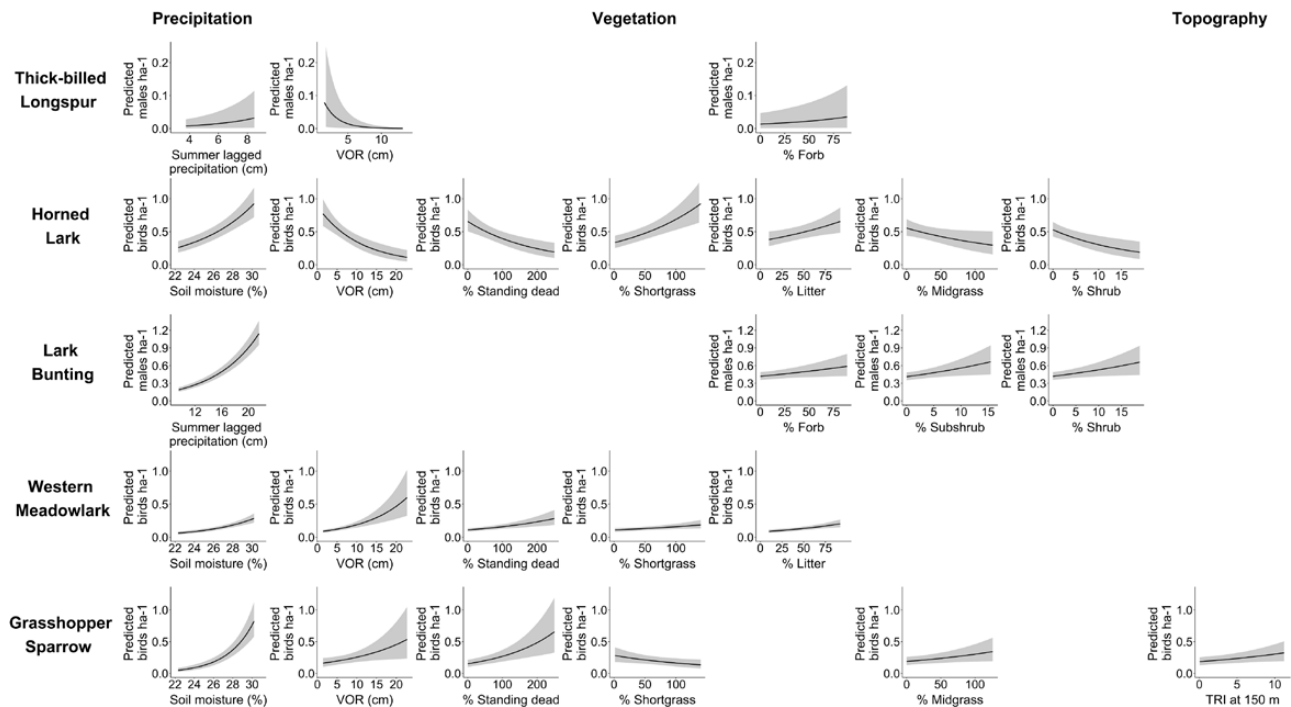
FIGURE 3. Predicted mean responses (± 95% CIs) to precipitation, vegetation structure, vegetation cover, and topography that had the strongest support for affecting abundance from the vegetation-abiotic models for 5 focal grassland bird species breeding on the CPER (Colorado, USA) from 2013 to 2017. Predicted relationships were calculated holding all other covariates in the models at their sample means.

Our second shortgrass-associated species, Horned Lark, exhibits similar habitat relationships to Thick-billed Longspur where they coexist, but occurs across a wider range of vegetation conditions and are more broadly distributed across North America (Wiens 1974, Skagen et al. 2018, Beason 2020). Consistent with prior work, our vegetation-abiotic model identified vegetation structure as a strong predictor of Horned Lark abundance. However, it revealed 2 novel patterns: (1) Horned Larks declined less rapidly with increasing vegetation structure compared to Thick-billed Longspur, and (2) Horned Lark can still persist at notable densities even in grasslands with VO exceeding 10 cm (Figure 3), which typically lack Thick-billed Longspurs (With 2020). Additionally, Horned Lark abundance increased with cover of shortgrasses and litter, and decreased with cover of standing dead vegetation, midgrasses, and shrubs. Previous studies found a negative relationship with litter and a preference for bare ground for this species in mixed-grass prairie and the alpine (Lipsey and Naugle 2017, Beason 2020). However, given that the species is widely distributed and that shortgrass steppe vegetation is inherently more sparse and shorter than other grassland types, it may be that local litter cover (e.g., vs. litter cover across the landscape) was a less restricting habitat requirement in this system (Morris 1992).

The results of our vegetation-abiotic models supported our expectation that Grasshopper Sparrows would prefer the tallest and most dense grassland patches available within this shortgrass landscape (Vickery 2020; Figure 1). These models additionally showed that cover of midgrasses, standing dead, and shortgrass vegetation explained more variation in abundance than the simple metric of vegetation structure. Thus, we hypothesize that Grasshopper Sparrows are associated with specific types of tall-structured vegetation in the shortgrass steppe that cannot be adequately characterized by vegetation height/density alone. In particular, our field observations suggest Grasshopper Sparrows may be selecting for tall, single-layered, and homogeneous canopies that are primarily produced by one midgrass species, needle-and-thread (*H. comata*), on our site. We did not fit models that included species-specific effects of vegetation but suggest this as a further research need.

For Lark Buntings, our vegetation-abiotic models suggested vegetation cover is more important for this species than vegetation structure. Lark Buntings are associated with an intermediate range of vegetation structure in the shortgrass steppe (Figure 1) because they often nest in microsites with tall, dense cover provided by midgrasses, subshrubs, and shrubs, but territories include a mosaic of such microsites interspersed with dominant shortgrasses (Skagen et al. 2018). Over our 5-year study period that included average to above-average precipitation, Lark

TABLE 2. Predictive capacity (i.e. posterior predictive loss; [Gelfand and Ghosh 1998](#)) of the abiotic, edaphic-year, vegetation-abiotic, and grazing-edaphic-year models for abundance of 5 focal grassland bird species breeding on the CPER (Colorado, USA) from 2013 to 2017. *k* is the number of covariates on the abundance portion of each model. Bolded values indicate the model with the lowest value of posterior predictive loss (i.e. the model with the highest predictive capacity).

Species	Model	Posterior predictive loss	*k*
Thick-billed Longspur	**Vegetation-abiotic**	**222.894**	12
	Grazing-edaphic-year	256.401	6 [a]
	Edaphic-year	259.386	4 [a]
	Abiotic	269.107	3
Horned Lark	**Vegetation-abiotic**	**1417.934**	12
	Grazing-edaphic-year	1440.740	12
	Edaphic-year	1442.900	6
	Abiotic	1477.579	3
Lark Bunting	**Edaphic-year**	**2775.682**	6
	Grazing-edaphic-year	2777.816	8
	Vegetation-abiotic	2801.981	12
	Abiotic	2806.353	3
Western Meadowlark	**Edaphic-year**	**1303.667**	6
	Grazing-edaphic-year	1305.569	8
	Vegetation-abiotic	1420.987	12
	Abiotic	1494.655	3
Grasshopper Sparrow	**Vegetation-abiotic**	**853.617**	12
	Abiotic	854.375	3
	Grazing-edaphic-year	856.196	12
	Edaphic-year	863.188	6

[a] The grazing-edaphic-year and edaphic-year models for Thick-billed Longspur have fewer parameters in the abundance portion of the models compared to the same models for the other focal species because abundance for Thick-billed Longspur was modeled for the loamy plains ecological site only (the species was detected only once outside of this ecological site during the duration of our study; [Davis et al. 2020](#)).

Bunting abundance increased slightly with forb, shrub, and subshrub cover, but was unaffected by vegetation structure. We note, however, that Lark Buntings are abundant and widespread on the CPER in wet years, but in years when vegetation structure is short due to drought and senescent vegetation, Lark Buntings may abandon the locality entirely for the breeding season or only occur in patches with particularly high vegetation structure ([Skagen et al. 2018](#), [Shane 2020](#)).

For Western Meadowlarks, variation in abundance was positively related to vegetation structure, as expected, but also was strongly associated with cover of standing dead vegetation, litter, and shortgrasses. These latter relationships suggest maximal Western Meadowlark abundance occurs in grassland with a multilayered canopy containing a fine-scale mixture of C_3 midgrasses that provide tall vegetation structure, abundant standing residual vegetation from the prior growing season, and a shortgrass "understory." This differentiates potential Western Meadowlark habitat from that of Grasshopper Sparrow, as our findings

suggest Grasshopper Sparrow prefers a uniform, homogenous canopy of midgrass.

Contrary to our predictions that species' responses to precipitation would align directly with their preferences for vegetation structure (i.e. abundance of species that prefer short structure would decrease while those that prefer taller structure would increase with precipitation), our vegetation-abiotic models showed that amount of precipitation positively correlated with abundance for all species. This suggests factors influencing variation in bird abundance *among* years may differ from factors driving spatial variation in bird abundance across the landscape *within* a year. For example, annual variation in Lark Bunting abundance at CPER was positively correlated with the amount of precipitation the previous growing season, whereas variation in abundance within years was correlated spatially with vegetation cover. The relationship with precipitation in the preceding growing season may simply reflect an increase in the number of Lark Buntings with high reproductive success the previous breeding season and that shift their breeding locality to CPER in years of favorable precipitation ([Skagen and Yackel Adams 2012](#), [Wilson et al. 2018](#), [Green et al. 2019](#)). Once on site, however, most of those breeding birds selected patches with higher cover of forbs, shrubs, and subshrubs. Although we did not include measures of precipitation across species' ranges in our models, it is well known that landscape-level processes can affect local populations of many species, including grassland birds ([Cunningham and Johnson 2006](#), [Winter et al. 2010](#), [Guttery et al. 2017](#), [Lipsey and Naugle 2017](#)). Future efforts to model grassland bird abundance at a given study site might consider the relative importance of precipitation at multiple spatial scales. Moreover, our findings suggest it is important to consider how cattle grazing strategies for grassland bird management can be flexibly employed in the context of regional precipitation conditions while also recognizing that factors occurring beyond the scale of an individual ranch may influence local populations of breeding grassland birds.

The predictive capacity of our grazing-edaphic-year or vegetation-abiotic models to explain avian abundance compared to base edaphic-year or abiotic models largely aligned with patterns of species' responses to grazing management ([Davis et al. 2020](#); Table 2). The vegetation-abiotic model was best supported for our focal species that responded to grazing management—Thick-billed Longspur, Horned Lark, and Grasshopper Sparrow—while the base model including ecological site and year was best supported for 2 species that did not respond to grazing management—Lark Bunting and Western Meadowlark—in [Davis et al. (2020)](#). [Davis et al. (2020)](#) also revealed that the abundances of these latter 2 species varied across ecological sites on the CPER—Lark Buntings were least abundant in the most productive ecological site, while Western

Meadowlarks were most abundant in the moderately and most productive ecological sites. Although we did not model specific soil attributes, the ecological site variable in our base edaphic-year and grazing-edaphic-year models provided a broad characterization of the soil conditions and plant communities that could occur on a site (USDA-NRCS 2007a, 2007b, 2007c). Thus, Lark Buntings and Western Meadowlarks may be selecting for features resulting from an interaction between soil conditions and plant communities, or for unknown factors correlated with ecological site. Alternatively (or in addition), abundances for these species may be driven by annual variation beyond that explained by precipitation at our site (e.g., the interannual nomadic behavior of Lark Bunting associated with broad-scale precipitation patterns; Wilson et al. 2018, Green et al. 2019). Ultimately, our findings suggest grassland birds are cuing into vegetation conditions both generated by and independent from grazing management (e.g., vegetation structure affected by grazing [Supplementary Material Figures S1 and 2] vs. ecological site categorizations, vegetation cover, and/or other correlated factors unaffected by grazing [Augustine et al. 2020]), emphasizing that models based on vegetation structure and/or grazing management alone may not sufficiently predict all species' habitat needs in the shortgrass steppe.

We note that the vegetation attributes we considered are labor-intensive (and thus costly) to measure and often not readily known by rangeland managers. They also are not available via remote sensing products, which limits the ability of our models to generate spatially explicit predictions of grassland bird abundance over large spatial extents (sensu Monroe et al. 2021). Using management and/or edaphic conditions as a proxy for vegetation attributes may be appealing given the former are readily available (i.e. ecological site maps from the USDA's Soil Survey Geographic database [https://websoilsurvey.nrcs.usda.gov/] combined with a manager's knowledge of grazing intensity in each pasture). Yet, there is little evidence that proxy measures adequately capture ecological processes of interest (Stephens et al. 2015), and our vegetation-abiotic models had greater predictive capacity for most of the species breeding on our site.

Compared to conceptualizations based on vegetation structure/grazing management alone, our models provide a more mechanistic understanding of and reveal nuances in the suite of environmental conditions to which grassland birds are responding in shortgrass steppe rangelands. Our results both confirm and challenge classic knowledge of how vegetation patterns shape grassland bird communities (Knopf 1996; Figure 1): spatial heterogeneity is key, but management for vegetation structure alone may not be sufficient to support the full breeding grassland bird community. Rather, our results suggest managers could refine grazing management on the basis of recent precipitation conditions to facilitate generating the spatial heterogeneity

in vegetation on which the grassland bird community depends. For example, managers could apply intensive grazing in some pastures during wet years for Thick-billed Longspur and Horned Lark, and a lack of grazing in some pastures in dry years for Grasshopper Sparrows and Western Meadowlark (Lipsey and Naugle 2017). Such targeted grazing applications for grassland birds also could support livestock production. For instance, resting pastures with extensive stands of needle-and-thread for an entire growing season during productive years could be one strategy to both enhance Grasshopper Sparrow abundance and stockpile residual forage (i.e. grassbanking) for future utilization by livestock. It is important to note, however, that the first 5 years of our experiment occurred during years of average to above-average precipitation. The shortgrass steppe is predicted to become drier and experience more extreme precipitation events as a result of climate change (Reeves et al. 2014). Data collected from long-term experiments, like those collected during our study, are critical for informing simulation work that could evaluate potential effects of climate change on shortgrass steppe grassland bird communities. In particular, analyses that encompass drought years could add essential insight into drivers of grassland bird abundance in the shortgrass steppe.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement: This study was observational in nature and involved no handling of animals. Due to this, we were not required to follow any formal ethics protocols related to animal care or handling.

Author contributions: K.P.D., D.J.A., and C.L.A. formulated the questions; D.J.A. and K.P.D. collected data and supervised field research; K.P.D., A.P.M., C.L.A., and D.J.A. developed methods; K.P.D. analyzed the data and wrote the paper; K.P.D., D.J.A., A.P.M., and C.L.A. substantially edited the paper; D.J.A. and C.L.A. contributed substantial materials, resources, and/or funding.

Data availability: Analyses reported in this article can be reproduced using the data provided by Davis et al. (2021).

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