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Adaptive rangeland management benefits grassland birds utilizing opposing vegetation structure in the shortgrass steppe

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Abstract. Rangelands are temporally and spatially complex socioecological 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. While livestock grazing management may benefit certain grassland bird species by generating the vegetation structure and density they prefer, these outcomes are poorly understood for avian species breeding in the shortgrass steppe. We evaluated how two grazing management systems, continuous, season-long grazing and adaptive, rest-rotational grazing, affected grassland bird abundance from 2013 to 2017 in Colorado's shortgrass steppe. We examined grazing impacts in conjunction with ecological sites, which constitute unique soil and plant communities. When grazing management was evaluated in conjunction with spatial variation in ecological sites, we found three of our five focal bird species responded to grazing management. McCown's Longspur abundance decreased in pastures rested from grazing the previous year. The effect of grazing on Horned Lark and Grasshopper Sparrow depended on ecological site: Horned Lark density was highest in pastures that were intensively grazed and Grasshopper Sparrow density was highest in pastures that were rested the previous year in the least productive ecological site. In addition, densities of all species varied across ecological sites. Our results suggest consideration of soil and vegetation characteristics can inform how adaptive management is applied on a landscape to benefit the full suite of breeding grassland birds, including species that have seemingly contrasting habitat needs. For example, a manager could target adaptive drought mitigation practices, such as resting pastures for 1 yr to generate grassbanks, in less productive soils to benefit grassland birds that prefer taller/denser vegetation structure, or could apply intensive, short-duration grazing on less productive soils to benefit species preferring shorter/sparser vegetation. A single year of intensive, short-duration grazing (i.e., one component of our rotational treatment) across the landscape, however, might not create sufficient habitat for species that prefer short/sparse vegetation in our system (e.g., McCown's Longspur). Ultimately, our study indicates how cattle production on rangelands can congruently support grassland bird populations in the shortgrass steppe.

Key words: abundance; adaptive management; grassland birds; hierarchical count models; rotational grazing; shortgrass steppe.

Introduction

Rangelands comprise approximately 40% of the Earth's terrestrial surface and today are managed primarily in ways that allow native or naturalized 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

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the past 200 yr 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 trade-offs for producers, however, rarely have been studied in an experimental framework. Furthermore, evidence suggests current agricultural yield trends, including livestock production, 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 2003), understanding how to balance livestock production needs with biodiversity conservation in grazed systems is increasingly important.

In North America, rangeland management historically emphasized practices that created a more uniform pattern of forage utilization across landscapes to most efficiently consume forage without degrading plant communities (Fuhlendorf et al. 2017, Sayre 2017). However, rangelands are increasingly being recognized as spatially, temporally, and ecologically complex agroecosystems (Fuhlendorf et al. 2012, 2017) and, to the extent that management for uniform utilization leads to structural and compositional homogenization of rangelands, such practices can also potentially decrease 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 and rotational grazing systems that include both intense grazing and rest from grazing, to support native flora and fauna (Fuhlendorf et al. 2006, Toombs and Roberts 2009). Rotational grazing systems also are posited to generate heterogeneity by providing a sufficiently long release from grazing pressure, thereby allowing vegetation to recover and attain structural characteristics that support different wildlife species compared to recently grazed communities (Briske et al. 2011).

Although rotational grazing systems are currently widespread across North America's rangelands, the temporal and spatial pattern of livestock movement varies widely across individual ranches, with unknown implications for sustaining biodiversity (Briske et al. 2008, Roche et al. 2015). Additionally, experimental evidence for benefits of grazing for wildlife is lacking (Briske et al. 2011). A review of grazing experiments 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 in 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 greater spatiotemporal 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 habitat occurred primarily in 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 heterogeneity-based grazing management on biodiversity in semiarid 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, rangeland management, and urban development in the Great Plains likely contributed to 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 heterogeneity in vegetation 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. Prescribed 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 (i.e., in the absence of fire) to promote vegetation heterogeneity 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 ongoing experiment is examining the effects of traditional grazing management (i.e., continuous, season-long grazing) vs. 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*). These five species experienced significant population declines over the past 70 yr (Sauer et al. 2017), and a group of local stakeholders engaged in our project identified these species as management priorities on the site. Additionally, McCown's Longspur and Grasshopper Sparrow are species of conservation concern in multiple states where they breed (Oklahoma Department of Wildlife Conservation 2005, Colorado Parks and Wildlife 2010, Guttery et al. 2017).

Grassland birds differentially use a gradient of vegetation structural heterogeneity generated by disturbance processes such as grazing: some species prefer short, sparse vegetation created by heavy grazing, whereas others prefer tall, dense vegetation under lighter grazing regimes (Wiens 1973, Knopf 1996). We implemented our three grazing treatments in an attempt to create heterogeneous habitat structure and determined if avian density varied by treatment. We predicted our focal 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, Colorado (40°50′ N, 104°43′ W) in the semiarid shortgrass steppe. Mean daily maximum and minimum temperatures range from −12°C to 4°C in January and 15°C to 26°C in July (Skagen et al. 2018). Long-term mean annual precipitation on the CPER is 340 mm (Augustine and Derner 2015), greater than 80% of which occurs during the growing season of April through September (Lauenroth and Burke 2008). 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 Sala 1992). 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 2015).

Experimental design

The collaborative adaptive rangeland management (CARM) experiment began in 2013 to contrast the effects of a collaborative form of rotational, multi-paddock grazing management with continuous, season-long grazing management (traditional rangeland management [TRM]) on multiple ecosystem services, including grassland bird diversity, abundance, and reproductive performance (Wilmer et al. 2018). For this experiment, 20 130-ha pastures were paired into 10 blocks where each block contained two pastures similar in terms of soil and plant characteristics, 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 the CARM treatment (Fig. 1).

While all TRM pastures were grazed (i.e., none were rested) by 10 small herds of approximately equal size that occupied each pasture separately, some of the CARM pastures were grazed by a single large herd of yearling steers managed with an adaptive, rotational grazing

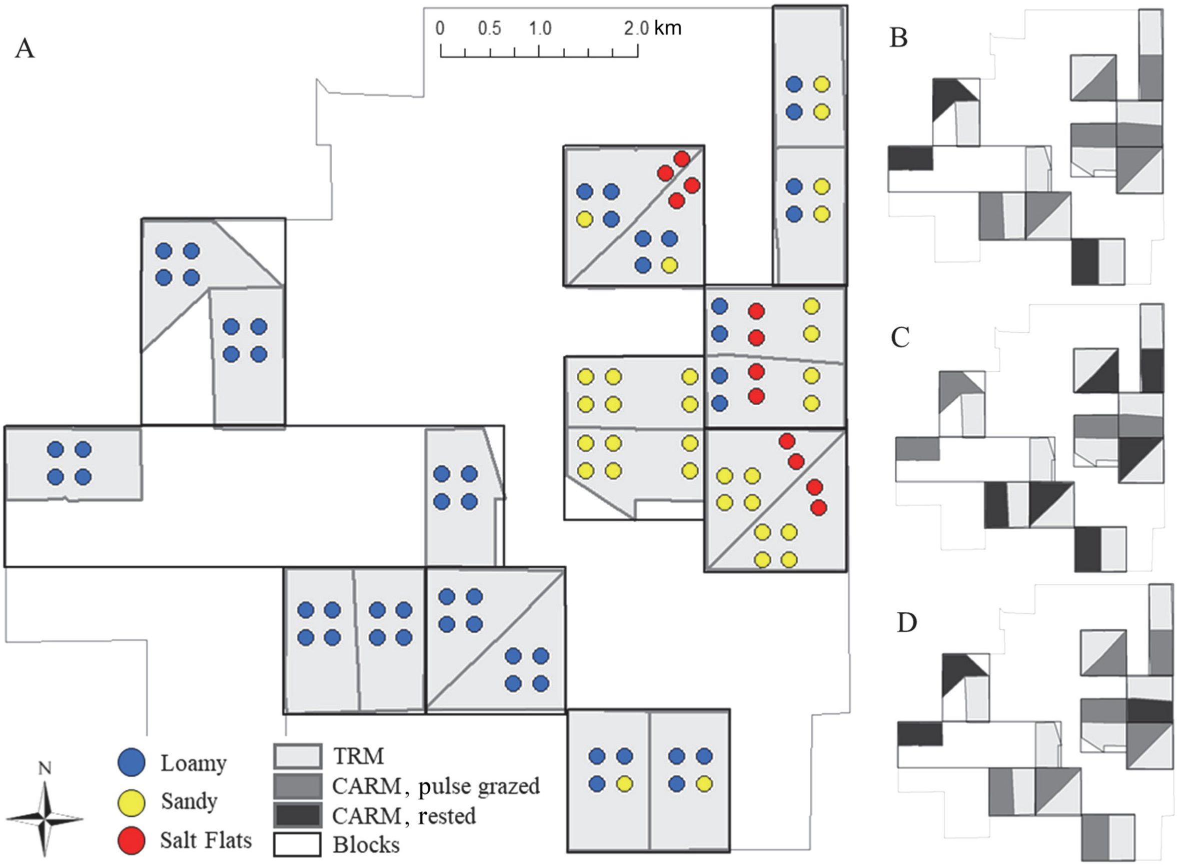

FIG. 1. Monitoring plots within each ecological site among 10 pasture pairs (blocks), where one pasture in each pair received the collaborative adaptive rangeland management (CARM) treatment and one received a traditional rangeland management (TRM) treatment at the Central Plains Experimental Range (CPER) in northeastern Colorado. The light gray line represents the boundary of the CPER. (A) Grazing treatment applications in 2013 and 2014, in relation to the bird surveys; 2013 was a pretreatment year, so the entire site was traditionally grazed (TRM). Because birds were surveyed only a few weeks after grazing treatments were applied each year, we considered grazing treatment to have a lagged effect on abundance (*Abundance models*). Thus, we also considered 2014 as a pretreatment year. (B–D) Grazing treatment applications in 2015–2017, respectively.

system and some were rested each year. 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 eight pastures each year, contingent on weather patterns, with the remaining two pastures planned for year-long rest. The same total number of steers grazed in the CARM and TRM pastures each year, which was initially set at 214 yearlings in 2014 based on the recommended moderate stocking rate for the soil and plant communities present in the study area (equivalent to 0.61 animal unit months [AUM]/ha, where an animal unit month is the amount of forage needed to support one month of grazing by the equivalent of a mature 1,000 pound cow (1 pound = 0.45 kg) with or without a suckling calf; USDA-NRCS 2007*a*, *b*, *c*, Society for Rangeland Management 2017). In subsequent years, the stakeholder group adjusted the stocking rate in April of each year prior to the 15 May grazing start date, depending on past vegetation conditions and weather forecasts for the upcoming grazing season. 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 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. Pretreatment 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 (Fig. 1). The larger number of rested pastures in 2015 was a result of above-average forage production in both 2014 and 2015, which allowed the CARM cattle herd to meet its forage requirements by grazing only four pastures over the growing season.

To evaluate vegetation and avian responses to grazing management, we sought to account for variation within and among pastures in soil types and associated variation in plant communities and habitat potential for birds. To achieve this, we used maps of ecological sites derived from the national soil survey (SSURGO), where an ecological site represents a distinctive kind of land with specific soil processes and properties that determine the land’s ability to support certain kinds and amounts of vegetation (Duniway et al. 2010). Our study pastures encompassed three types of ecological sites: loamy plains, sandy plains, and salt flats (USDA-NRCS 2007*a*, *b*, *c*). On the CPER, the loamy plains ecological site is dominated by C_4 shortgrasses (*B. gracilis*, *B. dactyloides*; USDA-NRCS 2007*a*) and is the most prevalent but least productive ecological site; the sandy plains ecological site is characterized by increased codominance by C_3 midgrasses (*P. smithii*, *H. comata*) and scattered shrubs (*A. canescens*; USDA-NRCS 2007*b*) and is moderately prevalent and productive; and the salt flats ecological site is characterized by the dominance of C_4 saltgrasses (*Sporobolus airoides*, *Distichlis spicata*; USDA-NRCS 2007*c*) and is the least prevalent but most productive ecological site.

Environmental data

Pastures were stratified by ecological site and monitoring plots were placed randomly within strata. Each plot contained a systematic grid of four 25-m transects oriented north-south and spaced 106 m apart where we measured various vegetation metrics. Because vegetation structure is known to influence grassland bird populations (Knopf 1996, Fisher and Davis 2010, Lipsey and Naugle 2017), we used visual obstruction readings (VOR) to quantify vegetation height density. We measured VOR by placing a Robel pole (Robel et al. 1970; modified with 1-cm increments) at eight locations spaced every 3 m along the transects in each monitoring plot and recorded the highest band on the pole that was at least partially obscured by vegetation. We measured VOR annually in June and calculated the mean VOR for each avian point count location per year. Data are provided in Data S1.

Avian data

We collected avian abundance data using a standard 6-minute point count (Hanni et al. 2013; Fig. 1). 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. Point count locations were surveyed between sunrise and ~10:30 twice during the breeding season between 26 May and 17 June. One survey of all points was conducted by the same observer each year, and a second survey of all points was conducted by an observer that changed each year. Surveys were separated by a range of 1–9 d. 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 sex (if determinable) and method of detection (e.g., aural, visual) for each individual. Data are provided in Data S1.

Statistical approach

We fit hierarchical distance sampling models (Kéry and Royle 2016) in a Bayesian framework to examine the effect of grazing management on grassland bird abundance. These models use a joint likelihood to simultaneously estimate parameters associated with the detection process and the biological process (in this case, abundance).

Model structure

We assumed observed counts y at point-year k (with counts summed over the two surveys) were the outcome of a binomial distribution conditioned on abundance N_k and detection probability p_k:

$$y_k \sim \text{binomial}(N_k, p_k).$$

We estimated the detection process using a distance sampling model where p_k was a function of detection distances from each observation (*Detection model*). We then modeled N_k for each species as a Poisson random variable with mean abundance λ_k:

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

We specified covariates to λ_k on the log-scale, and we included an offset for the number surveys at each point-year (log(2)). We therefore estimated the number of individuals present and available per survey (Nichols et al.

2009), and we assumed probabilities of presence and availability were constant or did not vary by treatment or ecological site (Monroe et al. 2019). We then calculated density based on abundance and the maximum detection radius for each species (Kéry and Royle 2016).

We fit models to all detections of both sexes for Western Meadowlark, Horned Lark, and Grasshopper Sparrow because sex could rarely be distinguished in the field 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 (which do not skylark), 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 plains ecological site over the 5 yr of our surveys. Therefore, we fit models for McCown's Longspur to detections of males on the loamy plains ecological site only.

Detection model

To account for potential variation in detection probability, we first truncated the furthest 10% of our distance sampling data as they can be difficult to model (sensu Buckland et al. 2001). We then used distance sampling with a hazard rate detection function to model the shape of the detection function (Buckland et al. 2001). We used the hazard rate instead of the half-normal detection function because preliminary analyses of our data in the program Distance (version 6.3; Thomas et al. 2010) suggested the hazard rate function fit best for our data. We used a log-link function to model covariates on the scale parameter of the detection function (σ; Royle et al. 2004). These covariates included VOR and a random term for year. We specified a vague normal prior with mean 0 and variance 100 for the coefficient for VOR. The random term for year was normally distributed with mean 0. Due to convergence issues in preliminary analyses, we specified a weakly informative half-Cauchy prior for the standard deviation of the random term for year (Gelman 2006).

Abundance models

For each species, we first fit a model on abundance that included effects of year, grazing management, and ecological site (hereafter, our base treatment model). We included an effect of year in these models (with the intercept representing the reference year, 2013) because grassland bird populations vary annually (Green et al. 2019) and preliminary investigations of our raw data revealed that yearly changes in abundance were not linear. We categorized grazing management as three treatments: the two components of the CARM treatment (pulse grazed and rested) and the traditional, season-long grazing treatment (TRM, which was the reference treatment). 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 and CARM where CARM was a single treatment (i.e., combining pulse grazed and rested pastures into one adaptive rotational treatment) 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 (*Experimental design*): loamy plains (which was the reference site), sandy plains, and salt flats.

To account for the experimental design of the CARM experiment, we modeled an effect of experimental block (i.e., pasture pairs, see *Experimental design*; $n = 10$) on the intercept of abundance for all models and species except McCown's Longspur. For McCown's Longspur, we modeled a pasture-specific intercept because the parameters associated with block were unidentifiable. This resulted in the following base treatment model for species-specific abundance:

$$\begin{aligned}\log(\lambda_k) = {} & \beta_{0,\mathrm{block}_k\ \mathrm{or\ pasture}_k} + \beta_1 2014_k + \beta_2 2015_k + \beta_3 2016_k \\ & + \beta_4 2017_k + \beta_5 \mathrm{pulse\ grazed}_k + \beta_6 \mathrm{rested}_k \\ & + \beta_7 \mathrm{salt\ flats}_k + \beta_8 \mathrm{sandy\ plains}_k + \log(2).\end{aligned}$$

In addition to the base treatment model for abundance, we fit an abundance model with covariates from the base treatment model and an interaction between grazing management and ecological site. Our base treatment model represented our interest in how grazing management affected grassland bird abundance while accounting for known sources of variation across years and ecological sites on our study site. We considered interactions between treatment and ecological site because the ecological sites on the CPER differ in productivity (USDA-NRCS 2007*a*, *b*, *c*) and previous research found soil productivity explained grazing effects on grassland birds (Lipsey and Naugle 2017). Because we were interested in specific covariate relationships rather than overall model predictive ability, we did not formally compare models with model selection.

For all abundance models, we specified vague normal priors with mean 0 and variance 100 for all coefficients and the mean of the block or pasture random terms. We specified a uniform prior from 0 to 10 for the standard deviation of the block or pasture random terms.

Computing

We fit all models using JAGS (version 4.2.0, Plummer 2003) and the package jagsUI (version 1.5.0; Kellner 2018) in R (version 3.4.3; R Development Core Team 2017) with 200,000–900,000 iterations from three parallel MCMC chains each and discarded 100,000–850,000 iterations per chain as burn-in. To assess parameter convergence, we visually evaluated traceplots and used the Gelman-Rubin statistic (Gelman et al. 2013). We considered parameters with Gelman-Rubin statistics ≤1.10 as converged (Gelman et al. 2013). To assess model fit, we used posterior predictive checks (Bayesian *P* values) based on chi-square discrepancy test statistics (Kéry and Royle 2016). We considered Bayesian *P* values ≤0.1 or ≥0.9 to indicate a lack of fit. We also calculated means and 95% credible intervals (CRI) for all model parameters. We considered a covariate to have strong support for affecting a focal process (abundance or detection) if the CRI of the covariate did not include zero.

RESULTS

We surveyed 92 point count locations twice per year for 5 yr, resulting in 460 counts by point-year. Lark Bunting males were detected the most (2,660 detections) and McCown's Longspur males were detected the least (287 detections). For both sexes combined of Western Meadowlark, Horned Lark, and Grasshopper Sparrow, we recorded 1,367, 1,327, and 715 detections, respectively.

We first fit the base treatment model for all species (Table 1). We then fit an interaction model that included the same covariates as the base treatment model plus interaction terms for grazing treatments and ecological sites (see *Abundance models*; Table 2). Interactions between grazing treatment and ecological site were supported only for Horned Lark and Grasshopper Sparrow (Table 2). We therefore interpret estimates from the interaction models for these species. For all other species, we interpret estimates from the base treatment models (Table 1). All models we interpret had adequate fit.

Vegetation height–density (i.e., VOR) affected detection probability of most of our focal species (Tables 1, 2). The probability of detecting Western Meadowlark decreased with increasing VOR (Table 1). The probability of detecting Grasshopper Sparrow increased while the probability of detecting Horned Lark decreased with increasing VOR (Table 2).

We found three of our five focal species responded to adaptive grazing management. For two species, Horned Lark and Grasshopper Sparrow, these responses depended on ecological site. Our interaction models revealed that intensive grazing in the loamy plains ecological site benefited Horned Larks in the subsequent year, whereas grazing had more neutral effects on density in the sandy and salt flats ecological sites (Table 2, Fig. 2). In the loamy plains ecological site, Horned Lark density increased by an average of 0.213 or 0.202 birds/ha in pulse-grazed pastures compared to rested (i.e., no grazing throughout the previous growing season) or traditionally grazed pastures, respectively. In the sandy plains and salt flats ecological sites, however, Horned Lark density ranged from decreasing by 0.202 birds/ha to increasing by 0.086 birds/ha on average in pulse grazed pastures compared to rested or traditionally grazed pastures. This pattern was similar but the opposite for Grasshopper Sparrow—resting pastures in the loamy plains ecological site benefited Sparrows in the subsequent year, whereas grazing had more neutral effects in the sandy and salt flats ecological sites (Table 2, Fig. 3). In the loamy plains ecological site, Grasshopper Sparrow density increased by an average of 0.415 or 0.361 birds/ha in rested pastures compared to pulse or traditionally grazed pastures, respectively. In the sandy plains and salt flats ecological sites, however, Grasshopper Sparrow density ranged from decreasing by 0.022 birds/ha to increasing by 0.164 birds/ha on average, in rested pastures compared to pulse- or traditionally grazed pastures, respectively.

From our base treatment models, we found resting pastures negatively affected McCown's Longspur populations in the subsequent year (Table 1, Fig. 4). In the loamy plains ecological site, male McCown's Longspur density increased by an average of 0.024 or 0.018 birds/ha in traditionally and pulse grazed pastures, respectively, compared to rested pastures. Grazing treatment did not strongly influence densities of Lark Bunting males or Western Meadowlark (Table 1, Figs. 4, 5).

For all focal species, year and ecological site influenced bird density more than grazing management (i.e., the standardized coefficient estimates for years and ecological sites were greater than those of grazing; Tables 1, 2). Density for each species differed between 2013 (i.e., the pretreatment year) and 2016, and differed in at least one year compared to 2013 (e.g., male Lark Bunting density was lower in 2016 compared to 2013; Table 1). McCown's Longspur was detected almost exclusively in the loamy plains (i.e., the least productive) ecological site, and Horned Larks were more abundant on the loamy plains ecological site compared to the sandy plains and salt flats ecological sites (i.e., the moderately and most productive ecological sites, respectively; Fig. 2). Lark Bunting males were more abundant in the loamy and sandy plains ecological sites than in the salt flats ecological site (Table 1). In contrast, Western Meadowlarks and Grasshopper Sparrows were more abundant in the salt flats and sandy plains ecological sites (Tables 1, 2).

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 and non-breeding grounds (Knopf 1996, Fuhlendorf and Engle 2001, Derner et al. 2009, Toombs et al. 2010, Hovick et al. 2014). In our study, heterogeneous grazing management affected the density of three grassland bird species that prefer the opposite extremes of grassland vegetation structure in

Table 1. Coefficient means and 95% credible intervals (CRI) from the base treatment models for effects modeled on focal processes affecting grassland bird abundance by survey point at the Central Plains Experimental Range.

	McCown's Longspur		Horned Lark		Lark Bunting		Western Meadowlark		Grasshopper Sparrow	
Factor	Mean	CRI	Mean	CRI	Mean	CRI	Mean	CRI	Mean	CRI
Abundance										
Intercept	**−1.781**	**−3.822, −0.262**	**0.922**	**0.669, 1.164**	**1.355**	**1.164, 1.543**	−0.275	−0.553, 0.006	**−0.768**	**−1.357, −0.164**
2014	−0.125	−0.569, 0.371	**0.381**	**0.131, 0.631**	**1.205**	**1.039, 1.373**	**0.597**	**0.272, 0.920**	0.277	−0.350, 0.886
2015	0.264	−0.145, 0.697	**0.645**	**0.418, 0.868**	**0.897**	**0.722, 1.072**	**1.161**	**0.886, 1.434**	**1.325**	**0.736, 1.897**
2016	**−0.666**	**−1.232, −0.108**	**0.739**	**0.504, 0.972**	**−0.369**	**−0.608, −0.132**	**2.084**	**1.820, 2.351**	**1.553**	**0.930, 2.180**
2017	−0.207	−0.661, 0.268	**0.323**	**0.091, 0.553**	−0.203	−0.416, 0.009	**1.304**	**1.021, 1.585**	0.084	−0.534, 0.699
Pulse grazed	−0.214	−0.729, 0.291	0.099	−0.034, 0.233	0.110	−0.009, 0.228	−0.048	−0.190, 0.093	−0.023	−0.218, 0.170
Rested	**−1.278**	**−2.314, −0.385**	−0.038	−0.200, 0.120	0.050	−0.103, 0.200	0.021	−0.141, 0.179	**0.378**	**0.143, 0.607**
Sandy plains			**−0.557**	**−0.744, −0.372**	0.032	−0.089, 0.155	**0.215**	**0.037, 0.389**	**0.941**	**0.673, 1.205**
Salt flats			**−1.240**	**−1.523, −0.967**	**−0.412**	**−0.580, −0.245**	**0.521**	**0.316, 0.725**	**1.308**	**1.011, 1.603**
Detection										
Intercept	**0.869**	**0.657, 1.178**	**0.770**	**0.649, 0.938**	**1.194**	**1.003, 1.485**	**1.473**	**1.093, 2.029**	**0.567**	**0.297, 0.996**
VOR	−0.152	−0.332, 0.001	**−0.074**	**−0.114, −0.035**	0.015	−0.008, 0.037	**−0.036**	**−0.064, −0.008**	**0.074**	**0.027, 0.126**
SD year	**0.138**	**0.004, 0.563**	**0.162**	**0.053, 0.461**	**0.170**	**0.061, 0.484**	**0.289**	**0.113, 0.770**	**0.529**	**0.203, 1.395**

Notes: Effects on abundance included year (2013–2017), grazing treatment (traditional, pulse grazed, rested), and ecological site (loamy plains, sandy plains, salt flats; i.e., the base treatment model on abundance). All models were fit with a random term for block (or pasture, in the case of McCown's Longspur) modeled on the intercept for abundance; the intercept reported here represents the traditional grazing treatment in the loamy plains ecological site in 2013, averaged across blocks (or pastures, in the case of McCown's Longspur). Effects on detection probability included visual obstruction reading (VOR) and a random term for year (SD year representing the standard deviation for the random term). Values in boldface type denote those where the credible interval of the coefficient does not include 0. Abundance for Lark Bunting was modeled using male detections only. Abundance for McCown's Longspur was modeled using male detections on the loamy plains ecological site only.

TABLE 2. Coefficient means and 95% credible intervals (CRI) from the grazing-ecological site interaction models for effects modeled on focal processes affecting grassland bird abundance by survey point at the Central Plains Experimental Range.

	Horned Lark		Lark Bunting		Western Meadowlark		Grasshopper Sparrow	
Factor	Mean	CRI	Mean	CRI	Mean	CRI	Mean	CRI
Abundance								
Intercept	**0.899**	**0.641, 1.141**	**1.343**	**1.150, 1.532**	**−0.298**	**−0.584, −0.009**	**−0.908**	**−1.499, −0.313**
2014	**0.388**	**0.139, 0.641**	**1.207**	**1.040, 1.374**	**0.595**	0.269, 0.923	0.332	−0.253, 0.917
2015	**0.652**	**0.427, 0.879**	**0.892**	**0.716, 1.069**	**1.155**	**0.878, 1.434**	**1.346**	**0.784, 1.899**
2016	**0.737**	**0.507, 0.972**	**−0.346**	**−0.584, −0.108**	**2.086**	**1.818, 2.354**	**1.644**	**1.049, 2.260**
2017	**0.323**	**0.093, 0.554**	−0.201	−0.414, 0.010	**1.303**	**1.021, 1.588**	0.145	−0.438, 0.734
Pulse grazed	**0.183**	**0.031, 0.334**	0.124	−0.031, 0.276	0.006	−0.205, 0.212	−0.201	−0.656, 0.227
Rested	−0.012	−0.186, 0.157	0.114	−0.049, 0.276	0.090	−0.117, 0.293	**0.764**	**0.433, 1.095**
Sandy plains	**−0.445**	**−0.649, −0.243**	0.057	−0.075, 0.190	**0.260**	**0.055, 0.459**	**1.011**	**0.698, 1.327**
Salt flats	**−1.222**	**−1.558, −0.900**	**−0.367**	**−0.553, −0.184**	**0.558**	**0.321, 0.792**	**1.469**	**1.128, 1.809**
Pulse grazed × Sandy plains	**−0.351**	**−0.668, −0.043**	−0.015	−0.230, 0.197	−0.137	−0.435, 0.159	0.334	−0.157, 0.845
Rested × Sandy plains	−0.342	−0.833, 0.117	−0.329	−0.741, 0.057	−0.103	−0.464, 0.250	**−0.624**	**−1.131, −0.122**
Pulse grazed × Salt flats	−0.337	−0.985, 0.267	−0.106	−0.459, 0.236	−0.026	−0.376, 0.319	0.049	−0.475, 0.591
Rested × Salt flats	0.419	−0.299, 1.077	−0.591	−1.465, 0.152	−0.250	−0.676, 0.161	**−0.797**	**−1.350, −0.264**
Detection								
Intercept	**0.765**	**0.647, 0.920**	**1.184**	**1.010, 1.414**	**1.510**	**1.120, 2.408**	**0.590**	**0.353, 1.047**
VOR	**−0.076**	**−0.117, −0.038**	0.016	−0.007, 0.038	**−0.035**	**−0.064, −0.007**	**0.073**	**0.026, 0.123**
SD year	**0.161**	**0.052, 0.454**	**0.163**	**0.062, 0.427**	**0.301**	**0.113, 0.895**	**0.521**	**0.198, 1.472**

Notes: Effects on abundance included year (2013–2017), grazing treatment (traditional, pulse grazed, rested), ecological site (loamy plains, sandy plains, salt flats), and interactions of grazing treatment and ecological site (i.e., the interaction model on abundance). All models were fit with a random term for block modeled on the intercept for abundance; the intercept reported here represents the traditional grazing treatment in the loamy plains ecological site in 2013, averaged across blocks. Effects on detection probability included visual obstruction reading (VOR) and a random term for year (SD year representing the standard deviation for the random term). Values in boldface type denote those where the credible interval of the coefficient does not include 0. Abundance for Lark Bunting was modeled using male detections only. We could not fit a grazing-ecological site interaction model for abundance for McCown's Longspur because this species occurred almost exclusively on the loamy plains ecological site on the CPER.

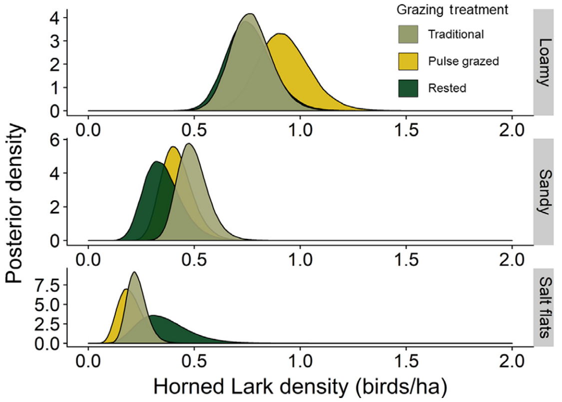

FIG. 2. Predicted posterior distributions of Horned Lark density (birds/ha) by grazing treatment and ecological site in 2017 on the Central Plains Experimental Range. Densities were calculated from the model with an interaction between grazing treatment and ecological site on abundance.

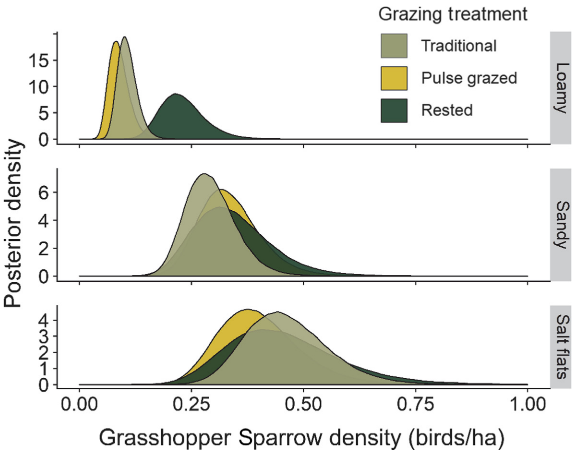

FIG. 3. Predicted posterior distributions of Grasshopper Sparrow density (birds/ha) by grazing treatment and ecological site in 2017 on the Central Plains Experimental Range. Densities were calculated from the model with an interaction between grazing treatment and ecological site on abundance.

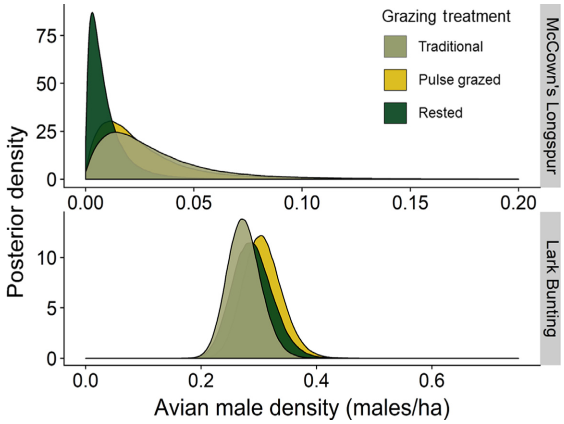

FIG. 4. Predicted posterior distributions of male density (males/ha) of McCown's Longspur and Lark Bunting in the traditional, pulse grazed, and rested treatments in 2017 on the loamy plains ecological site on the Central Plains Experimental Range. Density of male Lark Buntings was calculated from the base treatment model with year, ecological site, and grazing treatment effects on abundance. Density of male McCown's Longspurs was calculated from the model with year and grazing treatment effects on abundance. Note that the *x*- and *y*-axes vary by species.

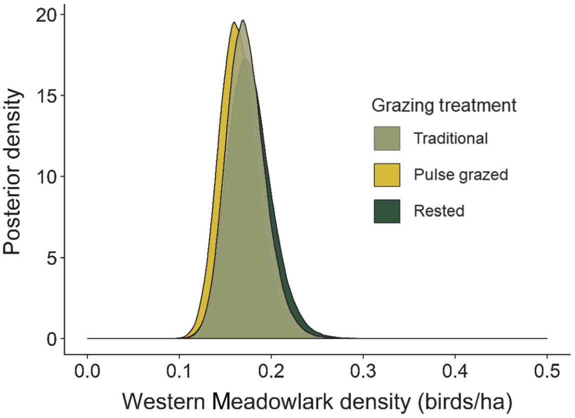

FIG. 5. Predicted posterior distributions of Western Meadowlark density (birds/ha) in the traditional, pulse grazed, and rested treatments in 2017 on the loamy plains ecological site on the Central Plains Experimental Range. Densities were calculated from the base treatment model with year, ecological site and grazing treatment effects on abundance.

the shortgrass steppe (Knopf 1996, Augustine and Derner 2015). For two of these three species, effects of grazing depended on ecological site: intensive grazing and rest from grazing, respectively, positively affected density of Horned Lark and Grasshopper Sparrow on the least productive ecological site. Ecological site and year irrespective of grazing were also important drivers of density for all focal species. This suggests grassland bird responses to grazing are nuanced and depend on sources of landscape variation beyond just vegetation structure.

As we predicted, a lack of grazing for an entire growing season negatively affected male McCown's Longspur density in the subsequent year. This matches with this species' breeding preference for short, sparse vegetation (With 2010). We also predicted Horned Larks would respond to intensive, short-duration grazing and Grasshopper Sparrows would respond to rest (Beason 1995), so our results for these species were expected. It was interesting, however, that these species' responses were associated only with the least productive ecological site. For Grasshopper Sparrows, this suggests resting pastures in the least productive ecological site may generate structure tall enough for them to utilize the following breeding season. For Horned Larks, this supports their preference for short, sparse vegetation, as intensive grazing in the least productive ecological site would generate the shortest, most sparse vegetation on the site. We were surprised to find that intensive grazing in the more productive ecological sites (i.e., the sandy plains or salt flats ecological sites) had more neutral effects on Horned Lark density. We would expect pulse grazing on the sandy plains ecological site, for example, to benefit Horned Larks by generating the shorter structure they prefer (Beason 1995) in a more productive ecological site. However, preliminary analyses of vegetation data collected over the course of our study on the CPER suggest average vegetation structure (i.e., VOR) in the pulse grazed treatment was taller than in the traditional treatment across all ecological sites (D. Augustine, *unpublished data*). This 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, and this structure would carry over to the following breeding season. In contrast, vegetation in pastures pulse grazed at the end of the growing season could remain relatively short until the next growing season (i.e., when we conducted our surveys). 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 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. Explicitly testing the role of timing of adaptive rotational grazing on vegetation and avian responses would be a useful future study.

We found no effect of grazing management on Western Meadowlark or male Lark Bunting density. Previous research found Western 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), suggesting ambiguity in how grazing affects meadowlark populations. Lark Buntings prefer moderate structure (Shane 2000) and were more abundant in continuously grazed pastures in a sagebrush system (Golding and Dreitz 2017), but evidence suggests that the distribution and abundance of this species is driven more by current and trends in annual and regional precipitation patterns than local habitat conditions (Skagen and Adams 2012, Wilson et al. 2018). We observed this pattern anecdotally on our site; in the above-average precipitation years during our study on the CPER (2014 and 2015), the Lark Bunting population appeared to be substantially higher across the entire site, while their population was noticeably lower in the average precipitation years (2013, 2016 and 2017). Our findings for Lark Bunting support these observations, as male bunting density varied more by year than by treatment in our models (Table 1). Overall, our results and these previous studies suggest that (1) both grazing management systems can generate sufficient habitat for male Lark Buntings and Western Meadowlarks in the shortgrass steppe, (2) that these species are responding to a resource on the landscape that is not affected by grazing management (e.g., insect abundance; Newbold et al. 2014), and/or (3) that abundance is driven by processes occurring at scales larger than our site (Skagen and Adams 2012, Wilson et al. 2018, Green et al. 2019).

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 critical 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, rest affected density only when it was applied in the least productive ecological site, and this species was always most abundant in the salt flats and sandy plains ecological sites regardless of grazing management. This leads to an important conclusion: by taking into account specific soil and vegetation characteristics, grazing can be implemented to simultaneously manage for species that have seemingly conflicting habitat needs in the shortgrass steppe. In other words, ignoring small-scale ecological context would suggest an intractable conflict between managing for species that prefer short and tall vegetation structure. Our study suggests that managing ecological sites independently can promote both short- and tall-grass species concurrently. Given these results, adaptive changes to the CARM grazing rotation were made in 2017 and 2018 to test whether targeting more frequent pulse grazing on the loamy plains ecological site would benefit McCown's Longspur and targeting more frequent rest on sandy plains and salt flats would benefit Grasshopper Sparrow. The effects of these changes will be evaluated in subsequent years.

We believe our findings are directly applicable to management for grassland birds across the Great Plains and in other semiarid rangelands. Recent studies in North America's grasslands have found similar context dependency of rangeland management for benefiting grassland birds. For example, in tallgrass prairie, Ahlering and

Merkord (2016) found precipitation conditions could influence avian community composition regardless of grazing management. In Montana's northern steppe, Lipsey and Naugle (2017) suggested grazing management that did not consider edaphic or precipitation conditions could be insufficient to generate grassland bird habitat. Our results add to this growing body of evidence that grazing management for grassland birds across North America's grasslands should consider more sources of annual and landscape variation than just vegetation structure (Knopf 1996, Ahlering and Merkord 2016, Lipsey and Naugle 2017). We also believe our results are relevant to wildlife management in other semiarid rangelands, where vegetation productivity is sensitive to variable precipitation and disturbance processes (i.e., grazing and/or drought) are integral parts of evolutionary history. Our findings may not be as relevant to areas without regular disturbance or with less variable climates, as resources utilized by wildlife in these systems may be more predictable or reliable.

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 topoedaphic conditions to support the habitat needs of focal species. The application of collaborative approaches to adaptive management can build trust among stakeholders, and thereby enhance understanding of such context dependency (Wilmer et al. 2018). Our study addressed shortcomings of prior rotational grazing research by employing realistic spatial scales and controlling for stocking rate effects (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 (see also Golding and Dreitz 2017). Our work suggests the effects of grazing management on grassland birds are more context specific than suggested by previous grazing/vegetation heterogeneity models (e.g, 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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LITERATURE CITED

Ahlering, M. A., and C. L. Merkord. 2016. Cattle grazing and grassland birds in the northern tallgrass prairie. Journal of Wildlife Management 80:643–654.

Aldridge, C. L., M. S. Boyce, and R. K. Baydack. 2004. Adaptive management of prairie grouse: How do we get there? Wildlife Society Bulletin 32:92–103.

Allred, B. W., S. D. Fuhlendorf, and R. G. Hamilton. 2011. The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. Ecosphere 2:1–17.

Augustine, D. J., and J. D. Derner. 2015. Patch-burn grazing management, vegetation heterogeneity, and avian responses in a semi-arid grassland. Journal of Wildlife Management 79:927–936.

Beason, R. C. 1995. Horned lark (*Eremophila alpestris*). *In* A. F. Poole and F. B. Gill, editors. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Beven, K. J., and M. J. Kirkby. 1979. A physically based, variable contributing area model of basin hydrology. Hydrological Sciences Bulletin 24:43–69.

Brennan, L. A., and W. P. Kuvlesky. 2005. Invited paper: North American grassland birds: an unfolding conservation crisis? Journal of Wildlife Management 69:1–13.

Briske, D. D., J. D. Derner, J. R. Brown, S. D. Fuhlendorf, W. R. Teague, K. M. Havstad, R. L. Gillen, A. J. Ash, and W. D. Willms. 2008. Rotational grazing on rangelands: reconciliation of perception and experimental evidence. Journal of Rangeland Ecology and Management 61:3–17.

Briske, D. D., J. D. Derner, D. G. Milchunas, and K. W. Tate. 2011. An evidence-based assessment of prescribed grazing practices. Pages 21–74 *in* D. D. Briske, editor. Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps. United States Department of Agriculture, Natural Resources Research Service, Fort Collins, Colorado, USA.

Briske, D. D., L. A. Joyce, H. W. Polley, J. R. Brown, K. Wolter, J. A. Morgan, B. A. McCarl, and D. W. Bailey. 2015. Climate-change adaptation on rangelands: linking regional exposure with diverse adaptive capacity. Frontiers in Ecology and the Environment 13:249–256.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, UK.

Cohen, J. E. 2003. Human population: the next half century. Science 302:1172–1175.

Colorado Parks and Wildlife. 2010. State wildlife action plan. Colorado Parks and Wildlife, Denver, Colorado, USA.

Commonwealth of Australia. 2016. National recovery plan for the plains-wanderer (*Pedionomus torquatus*). Commonwealth of Australia, Canberra, Australia.

Davis, S. K., and W. E. Lanyon. 2008. Western meadowlark (*Sturnella neglecta*). *In* A. F. Poole, editor. The Birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Derner, J. D., R. H. Hart, M. A. Smith, and J. W. Waggoner. 2008. Long-term cattle gain responses to stocking rate and grazing systems in northern mixed-grass prairie. Livestock Science 117:60–69.

Derner, J. D., W. K. Lauenroth, P. Stapp, and D. J. Augustine. 2009. Livestock as ecosystem engineers for grassland bird habitat in the western Great Plains of North America. Rangeland Ecology & Management 62:111–118.

Duniway, M. C., B. T. Bestelmeyer, and A. Tugel. 2010. Soil processes and properties that distinguish ecological sites and states. Rangelands 32:9–15.

Fisher, R. J., and S. K. Davis. 2010. From Wiens to Robel: a review of grassland-bird habitat selection. Journal of Wildlife Management 74:265–273.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience 51:625.

Fuhlendorf, S. D., D. M. Engle, R. D. Elmore, R. F. Limb, and T. G. Bidwell. 2012. Conservation of pattern and process: developing an alternative paradigm of rangeland management. Rangeland Ecology and Management 65:579–589.

Fuhlendorf, S. D., R. W. S. Fynn, D. A. McGranahan, and D. Twidwell. 2017. Heterogeneity as the basis for rangeland management. Pages 169–196 *in* D. D. Briske, editor. Rangeland systems: processes, management and challenges. Springer International Publishing, Cham, Switzerland.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.

Gelman, A. 2006. Prior distribution for variance parameters in hierarchical models. Bayesian Analysis 1:515–533.

Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2013. Bayesian data analysis. Third edition. CRC Press, Boca Raton, Florida, USA.

Golding, J. D., and V. J. Dreitz. 2017. Songbird response to rest-rotation and season-long cattle grazing in a grassland sagebrush ecosystem. Journal of Environmental Management 204:605–612.

Green, A. W., D. C. Pavlacky Jr., and T. L. George. 2019. A dynamic multi-scale occupancy model to estimate temporal dynamics and hierarchical habitat use for nomadic species. Ecology and Evolution 9:793–803.

Guttery, M. R., C. A. Ribic, D. W. Sample, A. Paulios, C. Trosen, J. Dadisman, D. Schneider, and J. A. Horton. 2017. Scale-specific habitat relationships influence patch occupancy: defining neighborhoods to optimize the effectiveness of landscape-scale grassland bird conservation. Landscape Ecology 32:515–529.

Hanni, D. J., C. M. White, N. J. Van Lanen, J. J. Birek, J. M. Berven, and M. A. McLaren. 2013. Integrated Monitoring in Bird Conservation Regions (IMBCR): Field protocol for spatially balanced sampling of landbird populations. Rocky Mountain Bird Observatory, Brighton, Colorado, USA.

Holechek, J. L., R. D. Pieper, and C. H. Herbel. 2011. Range management principles and practices. Sixth edition. Pearson/Prentice Hall, Upper Saddle River, New Jersey, USA.

Hovick, T. J., R. D. Elmore, S. D. Fuhlendorf, D. M. Engle, and R. G. Hamilton. 2014. Spatial heterogeneity increases diversity and stability in grassland bird communities. Ecological Applications 25:662–672.

Hovick, T. J., J. R. Miller, S. J. Dinsmore, D. M. Engle, D. M. Debinski, and S. D. Fuhlendorf. 2012. Effects of fire and grazing on grasshopper sparrow nest survival. Journal of Wildlife Management 76:19–27.

Kellner, K. 2018. Package jagsUI. https://cran.r-project.org/package=jagsUI

Kéry, M., and J. A. Royle. 2016. Applied hierarchical modeling in ecology. First edition. Academic Press, San Diego, California, USA.

Knopf, F. L. 1996. Prairie legacies—birds. Pages 135–148 *in* F. B. Samson and F. L. Knopf, editors. Prairie conservation: preserving North America's most endangered ecosystem. Island Press, Washington, D.C., USA.

Lauenroth, W. K., and I. C. Burke, editors. 2008. Ecology of the shortgrass steppe: a long-term perspective. Oxford University Press, New York, New York, USA.

Lauenroth, W. K., I. C. Burke, and M. P. Gutmann. 1999. The structure and function of ecosystems in the central North American grassland region. Great Plains Research 9:223–259.

Lauenroth, W. K., and O. E. Sala. 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2:397–403.

Lipsey, M. K., and D. E. Naugle. 2017. Precipitation and soil productivity explain effects of grazing on grassland songbirds. Rangeland Ecology and Management 70:331–340.

Monroe, A. P., G. T. Wann, C. L. Aldridge, and P. S. Coates. 2019. The importance of simulation assumptions when evaluating detectability in population models. Ecosphere 10: e02791.

Newbold, T. A. S., P. Stapp, K. E. Levensailor, J. D. Derner, and W. K. Lauenroth. 2014. Community responses of arthropods to a range of traditional and manipulated grazing in shortgrass steppe. Environmental Entomology 43:556–568.

Nichols, J. D., L. Thomas, and P. B. Conn. 2009. Inferences about landbird abundance from count data: recent advances and future directions. Pages 201–236 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer Science+Business Media, New York, New York, USA.

Odadi, W. O., J. Fargione, and D. I. Rubenstein. 2017. Vegetation, wildlife, and livestock responses to planned grazing management in an African pastoral landscape. Land Degradation and Development 28:2030–2038.

Oklahoma Department of Wildlife Conservation. 2005. Oklahoma comprehensive wildlife conservation strategy. Oklahoma Department of Wildlife Conservation, Oklahoma City, Oklahoma, USA.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. https://www.r-project.org/conferences/DSC-2003/Proceedings/Plummer.pdf

R Core Team. 2017. R: a language and environment for statistical computing. R Project for Statistical Computing, Vienna, Austria. www.R-project.org

Ranellucci, C. L., N. Koper, and D. C. Henderson. 2012. Twice-over rotational grazing and its impacts on grassland songbird abundance and habitat structure. Rangeland Ecology and Management 65:109–118.

Ray, D. K., N. D. Mueller, P. C. West, and J. A. Foley. 2013. Yield trends are insufficient to double global crop production by 2050. PLoS ONE 8:e66428.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–297.

Roche, L. M., B. B. Cutts, J. D. Derner, M. N. Lubell, K. W. Tate, L. M. Roche, and B. B. Cutts. 2015. On-ranch grazing strategies: context for the rotational grazing dilemma. Rangeland Ecology & Management 68:248–256.

Royle, J. A., D. K. Dawson, and S. Bates. 2004. Modeling abundance effects in distance sampling. Ecology 85:1591–1597.

Russell, S., P. Tyrrell, and D. Western. 2018. Seasonal interactions of pastoralists and wildlife in relation to pasture in an African savanna ecosystem. Journal of Arid Environments 154:70–81.

Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. Wildlife Society Bulletin 27:571–581.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, K. L. Pardieck, J. E. Fallon, and W. A. Link. 2017. The North American

Breeding Bird Survey, results and analysis 1966–2015. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Sayre, N. F. 2017. The politics of scale: a history of rangeland science. University of Chicago Press, Chicago, Illinois, USA.

Sayre, N. F., R. R. McAllister, B. T. Bestelmeyer, M. Moritz, and M. D. Turner. 2013. Earth Stewardship of rangelands: coping with ecological, economic, and political marginality. Frontiers in Ecology and the Environment 11:348–354.

Shane, T. G. 2000. Lark bunting (*Calamospiza melanocorys*). *In* A. F. Poole and F. B. Gill, editors. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Skagen, S. K., and A. A. Y. Adams. 2012. Weather effects on avian breeding performance and implications of climate change. Ecological Applications 22:1131–1145.

Skagen, S. K., D. J. Augustine, and J. D. Derner. 2018. Semi-arid grassland bird responses to patch-burn grazing and drought. Journal of Wildlife Management 82:445–456.

Society for Rangeland Management. 2017. Does size matter? Animal units and animal unit months. Rangelands 39:17–19.

Teague, R., and M. Barnes. 2017. Grazing management that regenerates ecosystem function and grazingland livelihoods. African Journal of Range and Forage Science 34:77–86.

Teague, R., F. Provenza, U. Kreuter, T. Steffens, and M. Barnes. 2013. Multi-paddock grazing on rangelands: Why the perceptual dichotomy between research results and rancher experience? Journal of Environmental Management 128:699–717.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. Hedley, J. Bishop, T. Marques, and K. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Toombs, T. P., J. D. Derner, D. J. Augustine, B. Krueger, and S. Gallagher. 2010. Managing for biodiversity and livestock: a scale-dependent approach for promoting vegetation heterogeneity in western Great Plains grasslands. Rangelands 32:10–15.

Toombs, T. P., and M. G. Roberts. 2009. Are Natural Resources Conservation Service range management investments working at cross-purposes with wildlife habitat goals on western United States rangelands? Rangeland Ecology & Management 62:351–355.

USDA-NRCS. 2007*a*. Loamy plains ecological site description. https://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R067BY002CO&rptLevel=all&approved=yes&repType=regular&scrns=&comm=

USDA-NRCS. 2007*b*. Sandy plains ecological site description. https://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R067BY024CO&rptLevel=all&approved=yes&repType=regular&scrns=&comm=

USDA-NRCS. 2007*c*. Salt flat ecological site description. https://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R067BY033CO

Vickery, P. D. 1996. Grasshopper sparrow (*Ammodramus savannarum*). *In* A. F. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Wiens, J. A. 1973. Pattern and process in grassland bird communities. Ecological Monographs 43:237–270.

Wilmer, H., J. D. Derner, M. E. Fernández-Giménez, D. D. Briske, D. J. Augustine, and L. M. Porensky. 2018. Collaborative adaptive rangeland management fosters management-science partnerships. Rangeland Ecology and Management 71:646–657.

Wilson, S., A. C. Smith, and I. Naujokaitis-Lewis. 2018. Opposing responses to drought shape spatial population dynamics of declining grassland birds. Diversity and Distributions 24:1687–1698.

With, K. A. 2010. McCown's longspur (*Rhynchophanes mccownii*). *In* A. F. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA.

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