



Research Article

Patch-Burn Grazing Management, Vegetation Heterogeneity, and Avian Responses in a Semi-Arid Grassland

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ABSTRACT Anthropogenic changes to disturbance regimes in grasslands, and associated homogenization of vegetation structure, have been implicated as factors contributing to declines in populations of grassland birds in North America. We examined the influence of patch-burn grazing management, which employs spatiotemporal interactions between fire and livestock grazing guided by historical disturbance patterns, on vegetation structure and bird abundance in shortgrass steppe in northeastern Colorado, USA. All study pastures were grazed by cattle at moderate stocking rates from May to October each year. In the patch-burn treatment, we burned 25% of each pasture in autumn (Oct or Nov) each year during 2007–2010; control pastures were not burned. Patch-burn grazing management increased vegetation heterogeneity by generating short (<4 cm), sparse vegetation on recent burns. Although cattle selectively grazed recent burns, this did not alter vegetation structure in unburned portions of patch-burned pastures relative to controls. Of the 6 grassland bird species we examined, mountain plovers (*Charadrius montanus*) occurred exclusively on recent burns, whereas grasshopper sparrows (*Ammodramus savannarum*) occurred exclusively in grassland not burned for ≥ 3 years. Two species (lark bunting [*Calamospiza melanocorys*] and western meadowlark [*Sturnella neglecta*]) were 2–3 times less abundant on recent burns compared to controls, whereas densities of horned larks (*Eremophila alpestris*) and McCown’s longspur (*Rhynchophanes mccownii*) were unaffected by burning. Lark bunting, western meadowlark, and grasshopper sparrow densities varied substantially among years. In the years when they were abundant, all 3 species increased in density across the time-since-burning gradient. Consistent with this pattern, patch-burn grazing management reduced the abundance of all 3 species at the whole-pasture scale. We found no evidence that unburned patches within the patch-burned pastures differed from unburned pastures in terms of the abundance of any bird species. Patch-burn grazing management was an effective strategy to create breeding habitat for mountain plovers. However, our findings suggest that in the shortgrass steppe, additional strategies that generate taller, more dense vegetation than occurs under moderate cattle grazing need to be considered in combination with patch-burn grazing management to sustain breeding habitat for the full suite of native grassland birds. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS fire-grazing interactions, grasshopper sparrow, horned lark, lark bunting, McCown’s longspur, mountain plover, prescribed fire, pyric herbivory, shortgrass steppe, western meadowlark.

Grassland birds that breed in the North American Great Plains evolved with dynamic disturbances associated with herbivory, fire, and drought that together shaped their habitats, food, and predator communities (Samson et al. 2004, Fuhlendorf et al. 2006, Derner et al. 2009). Heterogeneity in grassland vegetation structure at scales from individual plants to extensive landscapes has long been

recognized as a key factor shaping grassland bird community composition and diversity (Wiens 1973, 1974; Knopf 1996; Davis 2005). More recently grassland birds have been identified as one of the most rapidly declining guilds of bird species in North America, and anthropogenic changes to historical disturbance regimes in grasslands may be contributing to these declines (Brennan and Kuvleskey 2005, Askins et al. 2007). Management of grasslands using spatiotemporal interactions between fire and grazers that are guided by historical disturbance patterns has been advanced as a means to enhance the heterogeneity of vegetation structure present in grassland landscapes, and thereby restore

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habitats for a broad suite of grassland bird species (Fuhlendorf et al. 2006, 2009). Although a significant body of research has examined the direct effects of livestock grazing on grassland birds (Saab et al. 1995), far less is known about the interactive effects of fire and grazing.

Research in mesic grasslands of North America and Africa has generated 4 important findings that underpin the use of fire-grazer interactions for grassland bird habitat management. First, applying prescribed burns in a spatially and temporally variable mosaic and allowing large herbivores to select among burned and unburned patches in the landscape (referred to as patch-burn grazing management) results in strong herbivore selection for recent burns and associated low grazing intensity in unburned patches (Sensenig et al. 2010, Allred et al. 2011). Second, patch-burn grazing management creates areas in the landscape with both shorter and taller vegetation structure compared to the effects of traditional management approaches that uncouple the distribution of grazers and fire (Fuhlendorf and Engle 2004, McGranahan et al. 2012). Third, increased vegetation structural heterogeneity increases the availability and/or quality of breeding habitat for some grassland birds of conservation concern (Fuhlendorf et al. 2006, Gregory et al. 2010, Holcomb et al. 2014). Fourth, patch-burn grazing management can have neutral to positive effects on cattle weight gains compared to traditional management approaches (Fuhlendorf and Engle 2004, Limb et al. 2011, Allred et al. 2014), indicating patch-burn management may be a viable option in grasslands managed primarily for livestock production.

Over the past decade, quantitative studies have increasingly supported the idea that management for vegetation heterogeneity is important for sustaining grassland bird diversity both in semi-arid grasslands (Davis 2005, Johnson et al. 2011, Lusk and Koper 2013, Henderson and Davis 2014) and mesic grasslands (Fuhlendorf et al. 2006, Gregory et al. 2010, Ranellucci et al. 2012, Holcomb et al. 2014). Although some studies in semiarid regions have examined the direct effects of grazing (e.g., Johnson et al. 2011, Lusk and Koper 2013), the application of the fire-grazing interaction has not been evaluated.

Traditionally, prescribed fire has been viewed as having few management applications in the western, semiarid region of the North American Great Plains, primarily because management of these lands was focused on livestock production (Wright and Bailey 1982). However, studies have shown that prescribed fire can suppress unpalatable plant species (e.g., McDaniel et al. 1997, Augustine and Milchunas 2009) and enhance habitat for swift fox (*Vulpes velox*; Thompson et al. 2008) and pronghorn antelope (*Antilocapra americana*; Augustine and Derner 2015). In addition, the direct effects of prescribed fire creates breeding habitat for the mountain plover (*Charadrius montanus*), which is a species of significant conservation concern in the region (Knopf and Wunder 2006, Augustine and Derner 2012). Although fire and its interaction with large herbivores was a component of the historical disturbance regime in the western Great Plains (Fuhlendorf et al. 2009, Guyette et al. 2012), the lower fuel loads, greater frequency and intensity of

drought, and lower investment in stem tissue by dominant grasses in semi-arid compared to mesic grasslands calls into question the role of fire-grazer interactions in shaping avian communities.

We examined the effects of fire and fire-grazer interactions on a community of grassland bird species in the shortgrass steppe of northeastern Colorado. Seven species dominate the community and collectively exhibit a broad suite of habitat associations varying from short and sparse to tall and dense vegetation (Knopf 1996). Mountain plovers nest almost exclusively in areas with extensive bare soil exposure and vegetation <4 cm tall (Augustine and Derner 2012). McCown's longspur (*Rhynchophanes mccownii*) and horned lark (*Eremophila alpestris*) nest in short, sparse vegetation but also use areas with taller vegetation than mountain plovers (Knopf 1996). Lark buntings (*Calamospiza melanocorys*) and western meadowlarks (*Sturnella neglecta*) nest in taller and more dense vegetation than occurs under average precipitation in shortgrass steppe, with lark buntings sensitive to both vegetation structure and recent precipitation (Skagen and Yackel Adams 2012, Lusk and Koper 2013). Grasshopper sparrows (*Ammodramus savannarum*) and Brewer's sparrows (*Spizella breweri*) generally nest in tall, dense vegetation (relative to typical shortgrass conditions), the former selecting large patches of tall, dense grasses, and the latter nesting in sparse shrubs interspersed with grasses (Knopf 1996). Patch-burn grazing management, which has the potential to increase heterogeneity in vegetation structure across the landscape, could thus be an important way to sustainably enhance habitat for the full suite of grassland birds in this community.

We conducted an experiment in the semi-arid, shortgrass steppe of northeastern Colorado comparing patch-burn grazing management to traditional grazing management without fire. During the study, cattle selectively grazed on recently burned patches, but the strength of that selection (31% of grazing time on burns comprising 25% of treatment pastures; Augustine and Derner 2014) was substantially weaker than in tallgrass prairie (approx. 70% of grazing time on burns comprising 25% of pastures; Allred et al. 2011). We examined the consequences of this fire-grazing interaction for vegetation structure and the abundance of 7 grassland bird species. Our previous work showed that mountain plovers breed almost exclusively on recent burns and prairie dog (*Cynomys ludovicianus*) colonies in this region, and are absent from grassland managed only with livestock grazing (Augustine and Derner 2012), but effects on the other bird species have not been evaluated. Based on habitat relationships discussed previously, we hypothesized that McCown's longspur and horned lark would increase in density, whereas lark buntings, western meadowlarks, grasshopper sparrows, and Brewer's sparrows would decline in density on recent patch burns. Conversely, we predicted unburned patches within patch-burned pastures would support higher densities of lark buntings, grasshopper sparrows, and western meadowlarks compared to unburned pastures.

STUDY AREA

We conducted research at the Central Plains Experimental Range (CPER) approximately 12 km northeast of Nunn, Colorado, USA (40°50'N, 104°43'W). Topography was flat to gently rolling, and soils in the study area consisted of very deep, well-drained, fine sandy loams on convex alluvial flats and upland plains. Long-term mean annual precipitation was 340 mm and mean annual precipitation during the growing season (Apr–Aug) was 242 mm. During 2008–2011, annual precipitation was 330, 436, 360, and 356 mm, respectively, and growing season precipitation was 240, 352, 285, and 245 mm, respectively. Two C_4 perennial shortgrasses (blue grama [*Bouteloua gracilis*] and buffalograss [*B. dactyloides*]) dominated the vegetation (>70% of aboveground net primary production; Lauenroth and Burke 2008). Less abundant but widespread plant species that provided taller vertical structure than the dominant shortgrasses included 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*; Lauenroth and Burke 2008).

METHODS

Field Methods

During 2008–2011, we studied 3 replicate 65-ha pastures that each received the patch-burn grazing management treatment, and 3 replicate 65-ha pastures that received no burning treatment. During the last year of the study (2011), we studied 3 additional unburned pastures, for a total of 6 unburned pastures in that year. The pastures were arranged in 3 blocks (eastern, central, and western) with 1 patch-burn pasture and 1 (2008–2010) or 2 (2011) unburned pastures in each block, comprising a randomized complete-block design. All pastures were grazed by crossbred yearling cattle from approximately 15 May–1 October each year at a moderate stocking rate of 0.6 animal unit months (AUM)/ha, which results in approximately 40% forage utilization (Hart and Ashby 1998). Prior to the start of the study, these pastures had been grazed at this moderate stocking rate for >10 years with no burns. In the patch-burn treatment, prescribed burns were applied to 25% of each pasture per year for 4 years such that all areas of a given pasture were burned once over the course of the study. No portion of control pastures were burned during the study. Burned areas were square (16.25 ha), and burns were implemented in autumn (Oct or Nov) of 2007–2010 when vegetation was dormant. Despite low fuel loads (549–1,175 kg/ha), fuels were spatially contiguous and burns were relatively homogenous in all 4 years (see Augustine et al. 2014 for weather conditions, peak fire temperatures, and heat dosages during burns). For details on growing season conditions and cattle responses to the patch-burn treatment, see Augustine and Derner (2014). Our design included recently burned patches within patch-burned pastures and unburned patches within the unburned pastures in all 4 years. The presence of other treatments

within the patch-burned pastures varied across years, and included unburned patches within patch-burn pastures in 2008–2010, 2-year-old burns in 2009–2011, 3-year-old burns in 2010–2011, and 4-year-old burns in 2011.

Each study pasture was divided into 4, 16.25-ha (40 acre) quarters corresponding to the distribution of the patch burns. In patch-burned pastures, we measured vegetation structure and species composition in each of the 4 quarters. In unburned control pastures, we measured vegetation in only 1 randomly selected 16.25-ha quarter of each pasture.

In each pasture quarter, we established 36 sampling locations distributed in a 6×6 grid with 60 m between each sampling location and 50 m between the pasture edge and the outermost sampling locations in the grid (Appendix A, available in Supplemental Materials online). We permanently marked each location with a nail and a 3-cm-diameter washer. We placed the corner of a 50×20 -cm quadrat at each nail, marked the opposite corner of the quadrat with a second nail and washer, and recorded the global positioning system (GPS) location to facilitate measuring the same location each year. In June of each year during 2008–2011, we visually estimated plant canopy cover by species in each 50×20 -cm quadrat. We also measured vegetation visual obstruction (VO) by placing a visual obstruction pole (Robel 1970) at the center of the quadrat and recording observations of the pole from each cardinal direction. The pole followed the design of Robel et al. (1970) except that we used 1-cm intervals. We recorded the lowest interval on the pole that was not completely obscured by vegetation (e.g., if the first 3 intervals were completely obscured and a portion of the fourth interval was partially visible, we recorded a 4), and the plant species that was most responsible for the visual obstruction.

We conducted bird point counts at 4 points within each pasture quarter where we measured vegetation. Bird survey points were separated by 200 m and were 100 m from the pasture boundary or the adjacent pasture quarter (Appendix A). At each point, we conducted a 5-minute count on 3 different mornings in June each year during 2008–2011. Each year, 1 observer conducted 1 round of point counts in all study pastures and a second observer conducted 2 rounds; the same 2 observers conducted counts in all 4 years. Using a laser rangefinder, we measured and recorded the distance to each bird detected, the species, and the bird's sex if sex could be determined.

Data Analyses

For vegetation attributes, we calculated means for the 36 plots in each 16-ha site (pasture quarters), and then analyzed univariate responses based on a repeated-measures analysis of variance (ANOVA) that assumed a randomized, complete-block design with site treated as the subject, year as a random effect, and burn treatment and the year \times treatment interaction as fixed effects. We also conducted a multivariate analysis of plant community composition using a non-metric multi-dimensional scaling ordination of variation among sites (McCune and Grace 2002). We used the Sorensen distance measure as implemented in PC-ORD (v6.0;

McCune and Mefford 2011), and examined variation among sites and treatments along the first 2 axes of the ordination.

To estimate bird densities, we first used Program Distance (v6.2; Thomas et al. 2010) to fit detection functions that described the probability of detection as a function of distance from each point for the 7 most common bird species. We analyzed only birds detected within 100 m of the point, and did not include birds that flew across the plot without stopping within a 100-m radius. For McCown's longspurs and lark buntings, most detections were of singing or skylarking males, so for these 2 species, we calculated density based only on detections of males. For each species, we considered a suite of detection function models that included 1) global detection functions based on conventional distance sampling (CDS) and 2) multiple-covariate distance sampling (MCDS) models with year and vegetation height as covariates. For each point, we calculated vegetation height as the mean of the VO readings from the 9 vegetation sampling locations nearest the bird survey point (Appendix A). We considered CDS models fitted with a half-normal key with hermite polynomial expansion, hazard-rate key with cosine expansion, uniform key with cosine expansion, and uniform key with simple polynomial expansion (Buckland et al. 2001) and MCDS models fitted with half-normal and hazard-rate key functions (Marques and Buckland 2004). For grasshopper and Brewer's sparrows, most detections were of birds calling from perches on shrubs, tall forbs, or tall bunchgrasses, so we modeled the detection function for these 2 species combined (and tested for species as a covariate in MCDS). All models were based on >80 bird detections as recommended by Buckland et al. (2001), and for each model set, we selected the model with the lowest Akaike's Information Criterion (AIC) value. For a seventh species, the mountain plover, we lacked a sufficient number of detections to estimate the detection function. For this species, we used the detection function from a concurrent study that included point counts on a larger set of burns surveyed across Pawnee National Grassland during 2008–2012 (Augustine and Skagen 2014), and was based on >80 mountain plover detections. The suite of detection function models considered for mountain plovers did not include VO as a covariate, but >95% of the plover detections analyzed by Augustine and Skagen (2014), including all detections in this study, were in short (<4 cm), sparse vegetation on recent burns and prairie dog colonies.

After selecting the best-fitting detection function for a given species, we used Program Distance to estimate density at each point in each year. We then calculated the mean density of each bird species per pasture quarter per year based on the 4 points in each quarter. We analyzed resulting pasture-quarter densities with a repeated-measures ANOVA that assumed a randomized, complete-block design with pasture quarters treated as the subject, year as a random effect, and burn treatment and the year \times treatment interaction as fixed effects using the GLIMMIX procedure in SAS 9.4 (SAS Institute, Inc., Cary, NC). We also analyzed whole-pasture densities for each bird species (averaging across all of the different patch types within

the patch-burned pastures), and analyzed differences between the unburned versus patch-burned pastures using the same repeated-measures ANOVA as above. We examined ANOVA residuals and log-transformed the pasture quarter densities as necessary. For 1 species (Brewer's sparrow, see below), most detections occurred in only 1 block of the experiment so results for this species could not be analyzed statistically relative to patch burning. Thus, our graphical presentations focus on the 6 species that could be analyzed statistically.

We present results for 3 sets of contrasts. First, we compared densities on recent burns versus unburned pastures, which was the only pair of treatments present in all 4 years of the study. In addition, we note that when birds are establishing territories in May each year, current-year grazing by cattle has not yet affected vegetation structure (cattle entering the pastures 15 May each year), whereas vegetation had been affected by recent burns. Thus, in the first year of bird point counts (2008) there was not yet sufficient time for a burn \times grazing interaction to affect vegetation structure or bird habitat selection (i.e., not yet sufficient time for differential grazing intensity on burned vs. unburned patches); hence, we could only examine direct effects of burns in the first year. During the latter 3 years of the study (2009–2011), burn \times grazing interactions in the prior year could carry over to affect vegetation structure and bird habitat selection in the subsequent breeding season. Therefore, during the latter 3 years of the study we tested for differences among all treatments for each year individually (e.g., in the second year, treatments consisted of recent burns, 2-year-old burns, unburned patches in patch-burned pastures, and unburned pastures). For this second set of contrasts among treatments within each year, we used the Tukey's studentized range test to account for multiple comparisons when calculating *P* values; we could not test the year \times treatment interaction (or present treatment main effects) because the same treatments were not present in all years. Finally, we analyzed the contrast between mean bird densities in the patch-burned versus unburned pastures, including a test for interactions between year and pasture type.

RESULTS

Vegetation Structure and Composition

Visual obstruction measured in June each year during 2008–2011 in unburned pastures averaged 3.7, 5.6, 6.6, and 3.6 cm, respectively, which reflects average precipitation received in 2008, above-average precipitation during 2009, which carried over into the slightly above-average precipitation year of 2010, and a return to average precipitation and VO in 2011. Vegetation VO on recent burns was consistently reduced by 50% relative to unburned pastures across all years (mean = 2.4 cm on recent burns vs. 4.8 cm in unburned pastures; treatment \times year interaction, $F_{7,45} = 0.57$, $P = 0.78$; recent burns vs. unburned, $t_{2,45} = 8.27$, $P < 0.001$; Fig. 1). In 2009, VO was significantly lower on recent burns and 2-year-old burns relative to unburned patches in patch burns and

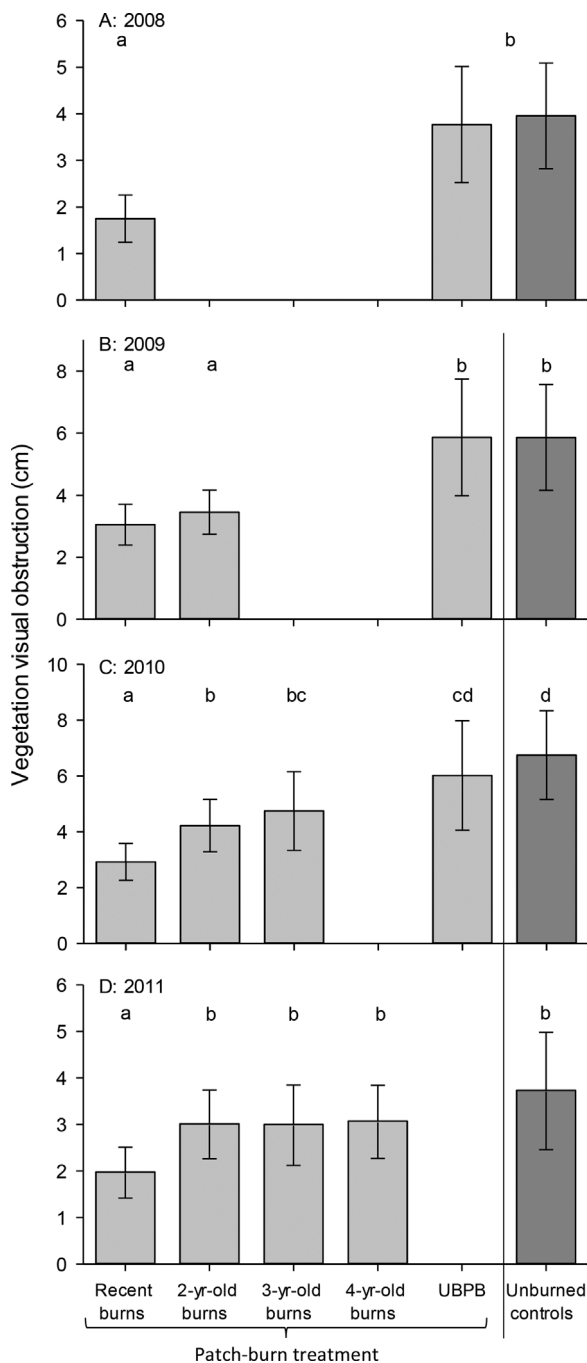


Figure 1. Effects of patch-burn grazing management on vegetation visual obstruction (VO) in shortgrass steppe at the Central Plains Experimental Range in northeastern Colorado during 2008–2011. Light gray bars show treatments within patch-burned pastures (25% of area burned each year) and dark gray bars show unburned control pastures; both sets of pastures received the same moderate cattle-stocking rate each year. UBPB = unburned patches within patch-burned pastures. Measurements in 2008 examined the direct effect of burning, whereas measurements in 2009–2011 examined both the direct effect of recent burns and the spatially variable response of cattle grazing to burn distribution in the previous year. Bars with different letters above them indicate significant differences ($P \leq 0.05$) based on Tukey's studentized range test; error bars show ± 1 standard error.

unburned pastures (Fig. 1B). In 2010, VO increased linearly with time since burning; VO on 3-year-old burns was significantly greater than recent burns and significantly lower

than unburned pastures (Fig. 1C). In 2011, VO on 2-, 3-, and 4-year-old burns was intermediate between recent burns and unburned pastures but not significantly different from unburned pastures. For all 3 years in which we examined the fire-grazing interaction (2009–2011), we found no evidence that unburned patches in the patch-burned pastures or 4-year-old burns differed from unburned pastures in terms of VO (Fig. 1B–D).

Although patch burning significantly reduced vegetation structure, we found few effects on plant species composition. Univariate analyses showed that patch burning did not affect foliar cover of the dominant C_4 grass (*B. gracilis*; treatment \times year interaction, $F_{7,45} = 0.87$, $P = 0.54$; treatment, $F_{5,45} = 1.69$, $P = 0.15$), the dominant C_3 grass (*H. comata*; treatment \times year interaction, $F_{7,45} = 1.16$, $P = 0.34$; treatment, $F_{5,45} = 0.92$, $P = 0.47$), or the dominant forb species (*Sphaeralcea coccinea*; treatment \times year interaction, $F_{7,45} = 1.82$, $P = 0.11$; treatment, $F_{5,45} = 0.42$, $P = 0.83$). The 1 notable effect was a reduction in combined cover of cactus and subshrubs (*O. polyacantha*, *G. sarothrae*, *E. effusum*, *A. frigida*) from 3.4% in unburned pastures to 0.9% in recent burns (treatment \times year interaction, $F_{7,45} = 1.11$, $P = 0.37$; treatment, $F_{5,45} = 7.66$, $P < 0.001$). For a more detailed description of patch burn effects on cactus, and associated interactions with herbivory by pronghorn antelope, see Augustine and Derner (2015). Multivariate analysis of the plant community based on a non-metric multidimensional scaling ordination also showed that compositional variation among unburned pastures was just as great as variation among and within patch burned pastures, indicating that patch burning had minimal effects on plant community composition (Appendix B, available in Supplemental Materials online). Thus, effects of patch burning on vegetation structure and composition involved a significant reduction in vegetation height and density, followed by recovery over the next 3 years back to similar vegetation height and density levels as found in unburned pastures. Reduced vegetation structure was primarily associated with removal of standing dead vegetation from the prior growing season combined with reduced structure provided by cactus and subshrubs but without changes in the composition of the herbaceous plant community.

Grassland Birds

The 7 most common species that we detected collectively comprised 98.2% of all bird detections during the study. For horned larks, McCown's longspur males, and lark bunting males (1,624, 1,204, and 902 detections, respectively), the selected detection functions were based on a hazard-rate key function, included VO as a covariate, and generated varying estimates of detection probabilities and estimated detection radii (Table 1). The ΔAIC for the selected detection function was ≥ 2.69 compared to all other models considered for these 3 species. The selected detection function for western meadowlarks was based on a uniform key with no covariates (Table 1) with $\Delta AIC \geq 5.90$ compared to all other models considered. The selected detection function for grasshopper and Brewer's sparrows was based on the half-normal key function with no covariates (Table 1) with $\Delta AIC \geq 1.59$ compared to all other models considered. Our estimates for

Table 1. The number of detections used to estimate the detection function, and the associated key function (HR = hazard-rate; U = uniform, HN = half-normal) and covariates selected (none, visual obstruction [VO]), for bird species studied in the shortgrass steppe of northeastern Colorado, USA, during 2008–2011. For each selected detection function, we report the associated detection probability and estimated detection radius (EDR) with 95% confidence intervals, along with the coefficient of variation associated with point-level density estimates averaged across all treatments within the experiment.

Species	Sex counted	Detections	Key function	Covariates	Detection probability	95% CI	EDR	95% CI	Density (no./km ²)	CV
Horned lark	Both	1,624	HR	VO	0.47	0.45–0.48	68.2	66.9–69.5	128.1	0.022
McCown's longspur	Males	1,204	HR	VO	0.60	0.55–0.62	77.2	75.8–78.7	68.4	0.020
Lark bunting	Males	902	HR	VO	0.79	0.77–0.82	89.0	87.6–90.3	39.9	0.020
Western meadowlark	Both	225	U	None	1.00	1.00	100	100	7.5	0.080
Grasshopper & Brewer's sparrow	Both	86	HN	None	0.54	0.40–0.72	73.4	63.0–85.4	5.4	0.156

the detection probabilities and detection radii for each species were relatively precise (small 95% CIs) and the point-level density estimates involved low coefficients of variation (Table 1), but we note that ANOVAs testing for effects of patch burning do not consider this source of variation.

For the 6 bird species we analyzed with respect to the patch-burn grazing treatment, we found no evidence of year \times treatment interactions for 5 species ($F_{7,45} < 1.82$, $P > 0.1$). The exception was the mountain plover, for which we detected a year \times treatment interaction ($F_{7,45} = 4.18$, $P = 0.001$) because mountain plovers were detected on all 3 replicate recent burns in 2008 and 2011 but only on 1 of 3 burns in 2009 and 2010. Comparisons of bird density between recent burns versus unburned grassland averaged across all 4 years for each species showed that 1) McCown's longspur and horned lark densities were unaffected by recent burns, 2) lark bunting and western meadowlark densities were reduced significantly on recent burns compared to unburned grassland, 3) grasshopper sparrows occurred only in unburned grassland, and 4) mountain plovers occurred only on recent burns (Table 2; Fig. 2). These responses were consistent with hypothesized relationships based on prior understanding of species-specific habitat relationships for 4 of the 6 species (lark bunting, western meadowlark, grasshopper sparrow, and mountain plover). Two species predicted to increase in response to patch burning (McCown's longspur and horned lark) showed no response. Furthermore, for both of these species, pairwise comparisons among all treatments for 2009, 2010, and 2011 revealed no treatment effects on their abundance (Tukey's honestly significant difference, $P > 0.1$ for all comparisons) McCown's longspurs were patchily distributed in the study area (large standard errors in Fig. 2), whereas horned larks were widely distributed at relatively constant density across the study area (small standard errors in Fig. 2). Brewer's sparrows could not be analyzed statistically because nearly all detections were in the 1 experimental block where pastures included sparsely distributed four-winged saltbush (*Atriplex canescens*); in these pastures, Brewer's sparrow density (mean + 1 SE) was $10.4 + 2.0$ birds/km².

Three species (lark bunting, western meadowlark, and grasshopper sparrow) occurred in more than 1 treatment and were significantly affected by patch-burn grazing management. Lark buntings were most abundant in 2009 and 2010 (years with above-average precipitation). In these 2 years,

lark buntings were significantly less abundant on recent burns and 2-year-old burns compared to unburned grassland (both for unburned patches in the patch-burned pastures and unburned pastures; Fig. 3A,D). In 2011, lark bunting density was low and did not vary significantly across the time-since-burn gradient (Fig. 3G). Western meadowlarks were consistently less abundant in recent burns compared to unburned pastures (Fig. 2), but their abundance in older burns was variable (Fig. 3B,E,H). Significant differences across the time-since-burn gradient were observed in 2011, when substantially lower meadowlark densities occurred on recent burns and 2-year-old burns as compared with 4-year-old burns and unburned pastures (Fig. 3H). Grasshopper sparrows were roughly 5 times more abundant in unburned pastures in 2010 (the year when VO was greatest) compared to 2009 and 2011. In 2010, grasshopper sparrows primarily occurred in unburned portions of patch-burned pastures and in unburned pastures, with small numbers occurring in 3-year-old burns (Fig. 3F). In all years, we did not detect grasshopper sparrows in recent burns or 2-year-old burns (Fig. 3C,F,J).

Comparisons of mean densities for each species at the whole-pasture level (i.e., patch-burned vs. unburned pastures) were largely the same as the results for the recent-burn versus unburned contrasts (i.e., Fig. 2). Patch-burning did not affect abundance of McCown's longspurs or horned larks (year \times pasture type interactions, $P > 0.1$, treatment main effect, $P > 0.1$). Results for mountain plovers were the same for both analyses, except that mean densities at the whole-pasture level were 25% of the values for the recent-burn versus unburned contrasts (because mountain plovers only occurred in the quarter of the pasture that was recently burned). Densities were lower in patch-burned compared to unburned pastures for lark buntings (year \times treatment: $F_{3,53} = 20.9$, $P = 0.11$; treatment main effect: $F_{1,53} = 16.39$, $P < 0.001$) and western meadowlarks (year \times treatment: $F_{3,53} = 0.17$, $P = 0.92$; treatment main effect: $F_{1,53} = 4.20$, $P = 0.045$). Densities of grasshopper sparrows were lower in patch-burned compared to unburned pastures in 2010 (treatment \times year interaction: $F_{3,18} = 4.65$, $P = 0.014$; 2010 contrast: $P = 0.006$) but not in the other years ($P > 0.90$), consistent with the results of the patch-specific contrasts (Fig. 3).

At the community level, these results showed that patch-burned pastures supported the full suite of grassland bird

Table 2. Results of repeated-measures analyses of variance (ANOVAs) examining the effect of patch-burn grazing management on densities of 6 bird species in the shortgrass steppe of northeastern Colorado during 2008–2011. Tests for year \times treatment interactions were not significant ($P > 0.1$) for all species except mountain plover (see results). F -tests are based on 5 and 45 degrees of freedom in the numerator and denominator, respectively; t -tests are 2-tailed with 45 degrees of freedom.

	F -test for overall treatment effect		t -test for recent burns vs. unburned	
	F	P	t	P
Lark bunting	11.9	<0.001	-5.92	<0.001
Western meadowlark	4.9	0.0012	-3.28	0.002
Grasshopper sparrow	3.44	0.010	-2.85	0.007
Horned lark	1.77	0.139	-1.59	0.119
McCown's longspur	2.21	0.069	1.6	0.116
Mountain plover	10.78	<0.001	6.6	<0.001

species we studied, because they included mountain plovers on recent burns and grasshopper sparrows on unburned patches or 3–4-year-old burns. In contrast, unburned pastures supported 5 of the 6 species (lacking mountain plovers; Fig. 2) but supported greater densities of lark buntings, grasshopper sparrows, and western meadowlarks than patch-burned pastures.

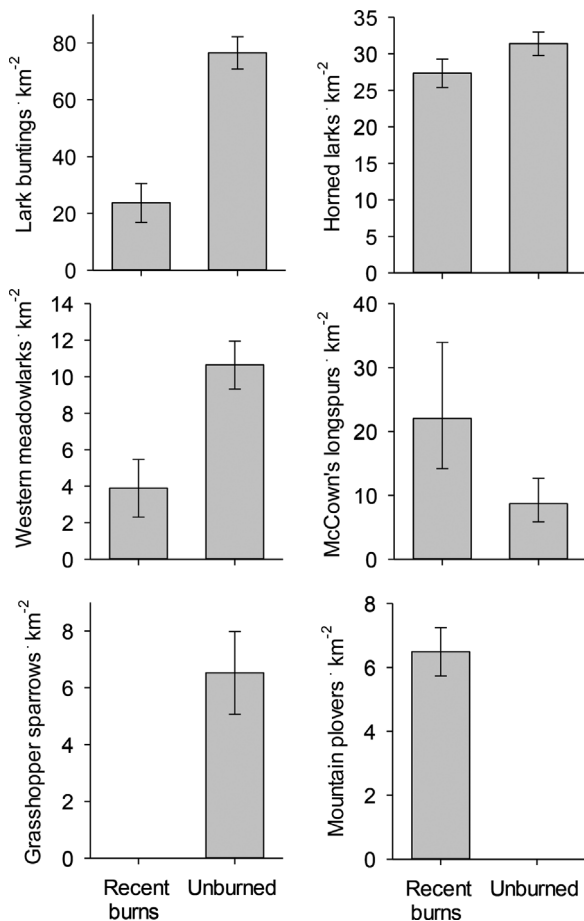


Figure 2. Comparison of breeding-season densities of 6 grassland bird species in recently burned patches versus unburned grassland, averaged over 4 years (2008–2011) in the shortgrass steppe of northeastern Colorado. Error bars show ± 1 standard error.

DISCUSSION

Patch-burn grazing management in shortgrass steppe generated short, sparse vegetation in recent burns, which was effective in creating breeding habitat for mountain plovers. However, despite the finding that cattle increased grazing time on burned patches compared to the remainder of the patch-burned pastures (Augustine and Derner 2014), vegetation structure did not increase outside of the burned patches. Because patch burning has a weaker effect on ungulate grazing patterns compared to mesic rangelands (Allred et al. 2011 vs. Augustine and Derner 2014), consequences for vegetation structure and heterogeneity differ. In mesic grasslands, the attraction of large herbivores to burned patches is so strong that adjacent unburned patches experience minimal grazing pressure, thereby allowing vegetation height and density in these unburned patches to increase significantly above levels found in treatments with more homogenous grazing distribution (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006). We documented that in the semi-arid shortgrass steppe, vegetation in patch-burned pastures encompassed a gradient from short to moderate height and density but did not include patches that increased in vegetation height and density above levels found in unburned pastures (Fig. 1). Patch burns also reduced prickly pear cactus abundance (Augustine and Derner 2015), which contributed to reduced vegetation structure on older burns compared to unburned pastures. Thus, relative to the traditional, prevailing management regime in this semi-arid grassland, patch-burn grazing management increased pasture-scale heterogeneity by creating short and sparse structure in recent burns but not by creating tall and dense structure in unburned patches.

Avian responses to patch-burn grazing were generally consistent with effects on vegetation structure. Mountain plovers were found exclusively on recent burns, consistent with previous findings based on a larger sample of prescribed burns and wildfires (Augustine and Derner 2012). Conversely, species that rely on tall and dense vegetation for nest concealment exhibited significant declines in abundance on recent and 2-year-old burns (Fig. 3). Lark buntings were the most abundant species in unburned pastures, and were most abundant in the wettest years (2009 and 2010), when vegetation cover and height was greatest. In years of peak

abundance, lark buntings were 2–3 times less abundant in 1–3-year-old burns compared to unburned pastures. Western meadowlarks were most abundant in 2011, when they exhibited nearly identical responses to patch-burn grazing management as lark buntings (Fig. 3). Peak grasshopper sparrow densities in 2010 were associated with taller and more homogeneous grassland swards resulting from the accumulation of residual standing dead vegetation (from the wet year in 2009) in unburned pastures. Thus, annual fluctuations in precipitation had varying effects on the abundance of each species (i.e., peak densities of lark buntings, grasshopper sparrow, and western meadowlarks in 2009, 2010, and 2011, respectively), but all 3 species consistently showed strong selection for unburned grassland in the years when they were most abundant. Consistent with our findings based on analyses at the patch scale, all 3 species exhibited reduced abundance in patch-burned pastures compared to unburned pastures. Based on these findings, we suggest that in years when lark buntings and grasshopper sparrows were less abundant within our study area, across the

broader landscape they may have been seeking even taller vegetation structure than that provided by the moderately grazed, unburned treatment. Furthermore, consistent with our findings, grasshopper sparrows have been shown to decline with increased grazing intensity in the northwestern Great Plains (Henderson and Davis 2014) and with patch-burn grazing in the southwestern Great Plains (Holcomb et al. 2014) suggesting across the broad geographic region of the semi-arid, western Great Plains, this species could benefit from practices that increase vegetation height and density. We also emphasize that our findings are from an ecosystem with a long evolutionary history of large herbivore grazing (Milchunas et al. 1988) and fire (Guyette et al 2012), and hence should not be extrapolated to other regions, such as the intermountain and southwestern United States, with different historical roles of grazing and fire.

McCown's longspurs and horned larks are typically associated with short, sparse grasslands during the breeding season (Knopf 1996), suggesting they could benefit from patch-burn grazing management. However, even though

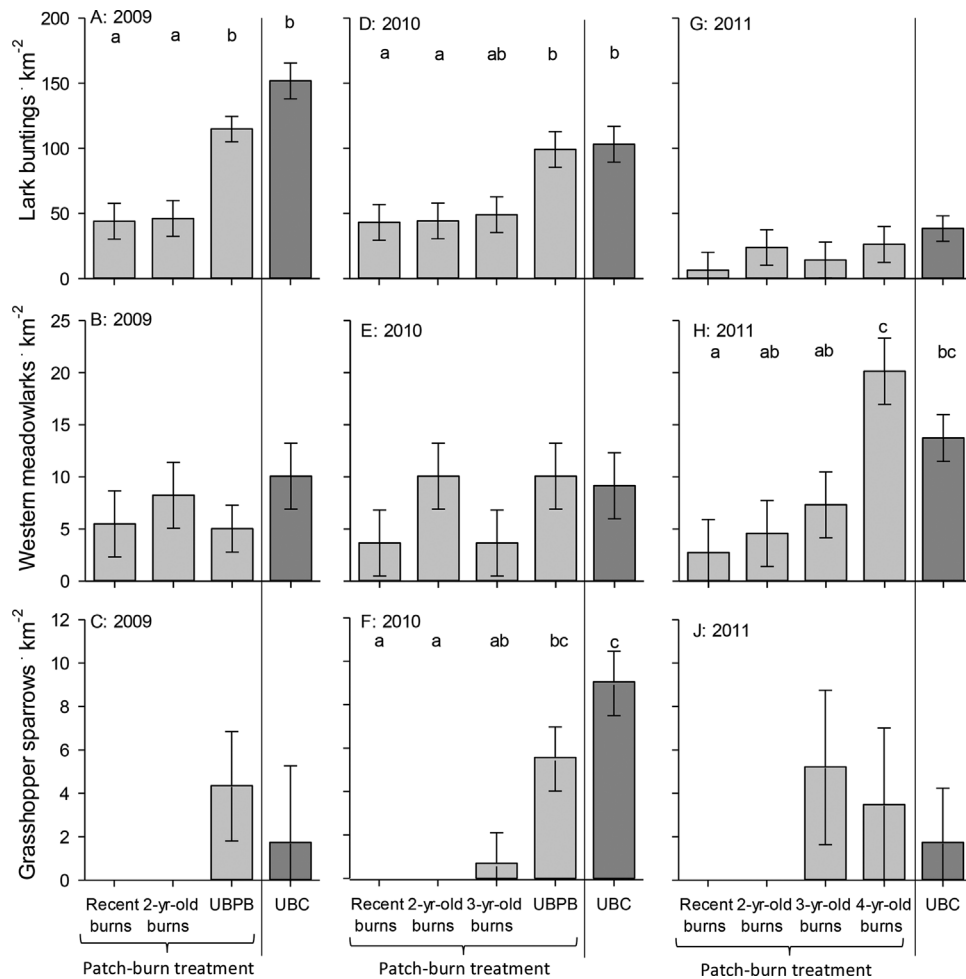


Figure 3. Variation in the breeding-season density of 3 grassland bird species in response to patch-burn grazing management during 2009–2011 in northeastern Colorado. Light gray bars show values for different types of patches within the patch-burned pastures; dark gray bars show values for unburned control pastures. UBPB = unburned patches in patch-burned pastures; UBC = unburned control pastures. Both the patch burned and unburned pastures received the same moderate cattle-stocking rate each year. Bars with different letters above them indicate significant differences ($P \leq 0.05$) based on Tukey's studentized range test; error bars show ± 1 standard error.

both species were consistently abundant in all 4 years of our study, we found no evidence that either species increased in response to patch-burn grazing. Wiens (1973) suggested that horned larks benefit from moderate levels of vegetation heterogeneity within their territories, such that the combination of reduced mean height and reduced variability in vegetation height within burned patches may be 1 reason horned larks did not increase in burns. For McCown's longspurs, nest survival has been shown to increase with reduced abundance of vegetation that provides cover for nest predators in the vicinity of nest sites (With 1994), so the lack of response to burned patches is surprising. We note that McCown's longspurs were patchily distributed across the study area, reflected in large standard errors for mean abundance (Fig. 2). This distribution was consistent across years in spite of the shifting location of patch burns, suggesting that philopatry, social interactions, or habitat features not influenced by burning may influence the species' local distribution and warrant further study. Another possibility both for McCown's longspur and horned larks is that patch-burn grazing management influenced nest survival rather than abundance, and more detailed studies examining measures of fecundity in response to management are needed (e.g., Hovick et al. 2012).

Recent studies in a range of grassland ecosystems provide quantitative support for the idea that increasing variability in vegetation structural characteristics (height and density), through grazing and fire disturbance that varies from recent and intense to lacking for ≥ 1 year, is important for sustaining the full suite of native grassland bird species. Examples include work in North American mixed-grass prairie (Lusk and Koper 2013, Holcomb et al. 2014, Henderson and Davis 2014), palouse prairie (Johnson et al. 2011, 2102), and tallgrass prairie (Fuhlendorf et al. 2006), as well as East African savannas (Gregory et al. 2010). Our work in the shortgrass steppe shows that patch-burn grazing management is an important strategy to create breeding habitat for disturbance-dependent species such as the mountain plover. However, patch-burn grazing did not enhance habitat for species associated with taller-structure habitats, such as lark buntings and grasshopper sparrows. As a result, we suggest that additional strategies, such as periodic rest from livestock grazing in areas not burned for > 3 years, be considered in combination with patch burn grazing to enhance habitat for the full grassland bird community. This is also supported by work in southern mixed-grass prairie, where patch-burn grazing enhanced lark sparrow (*Chondestes grammacus*) but reduced grasshopper sparrow abundance (Holcomb et al. 2014), and in northern mixed prairie where light stocking rates or multi-year rest from livestock grazing (in the absence of fire) enhanced habitat for 3 disturbance-sensitive grassland bird species (Lusk and Koper 2013, Henderson and Davis 2014). These findings emphasize the need for 1) studies that quantify tradeoffs between livestock production losses associated with reduced stocking or rested pastures and benefits to grassland birds, and 2) increased attention to mixed management strategies that generate a broader range of vegetation structural characteristics at the landscape scale.

MANAGEMENT IMPLICATIONS

Our findings indicate that in semi-arid grasslands of the North American Great Plains, patch-burn grazing management is an effective strategy to reduce vegetation structure and create breeding habitat for the mountain plover. However, under moderate cattle stocking rates, patch-burn grazing management did not result in areas with taller, more dense vegetation than occurs without patch burning. Shorter vegetation structure in areas burned in the past 1–3 years was associated with significant reductions in abundance of multiple grassland bird species (lark bunting, grasshopper sparrow, western meadowlark). These findings suggest that additional management strategies that generate taller, more dense vegetation structure than occurs under moderate cattle grazing may need to be considered in combination with patch-burn grazing management to generate landscape-scale vegetation heterogeneity that enhances breeding habitats for the full suite of native grassland bird species.

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