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Research Article

Semi-Arid Grassland Bird Responses to Patch-Burn Grazing and Drought

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ABSTRACT As grassland birds of central North America experience steep population declines with changes in land use, management of remaining tracts becomes increasingly important for population viability. The integrated use of fire and grazing may enhance vegetation heterogeneity and diversity in breeding birds, but the subsequent effects on reproduction are unknown. We examined the influence of patch-burn grazing management in shortgrass steppe in eastern Colorado on habitat use and reproductive success of 3 grassland bird species, horned lark (*Eremophila alpestris*), lark bunting (*Calamospiza melanocorys*), and McCown's longspur (*Rhynchophanes mccownii*), at several spatial scales during 2011 and 2012. Although no simple direct relationship to patch-burn grazing treatment existed, habitat selection depended on precipitation- and management-induced vegetation conditions and spatial scale. All species selected taller-than-expected vegetation at the nest site, whereas at the territory scale, horned larks and McCown's longspurs selected areas with low vegetation height and sparse cover of tall plants (taller than the dominant shortgrasses). Buntings nested primarily in unburned grassland under average rainfall. Larks and longspurs shifted activity from patch burns during average precipitation (2011) to unburned pastures during drought (2012). Daily survival rate (DSR) of nests varied with time in season, species, weather, and vegetation structure. Daily survival rate of McCown's longspur nests did not vary with foliar cover of relatively tall vegetation at the nest under average precipitation but declined with increasing cover during drought. At the 200-m scale, increasing cover of shortgrasses, rather than taller plant species, improved DSR of larks and longspurs. These birds experience tradeoffs in the selection of habitat at different spatial scales: tall structure at nests may reduce visual detection by predators and provide protection from sun, wind, and rain, yet taller structure surrounding territories may host nest predators. Patch-burn grazing management in combination with other strategies that retain taller-structured vegetation may help sustain a diversity of breeding habitats for shortgrass birds under varying weather conditions. Published 2017. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS daily survival rate, drought, grazing, horned lark, McCown's longspur, nest-site selection, prescribed fire, rainfall, shortgrass steppe.

The conservation of biodiversity requires a variety of approaches, from maintaining species and populations to addressing the dynamic ecosystem processes underlying distribution patterns of organisms (Franklin 1993, Pimm et al. 1995, Poiani et al. 2000). The vegetative structure of interior grasslands of North America varies spatially and temporally in response to influences of climatic gradients, seasonal weather patterns, herbivory, and fire (Knopf and Samson 1997, Askins et al. 2007, Fuhlendorf et al. 2012). Avian species have responded to this ecological heterogeneity through partitioning of breeding habitats and microhabitats (Wiens 1973, 1974). Over recent decades, grassland birds have been one of the most rapidly declining guilds of North

American breeding birds (Brennan and Kuvleskey 2005, Askins et al. 2007). Although some populations have stabilized in recent years, other species, including horned lark (*Eremophila alpestris*), lark bunting (*Calamospiza melanocorys*), and McCown's longspur (*Rhynchophanes mccownii*), which breed in midcontinental grasslands, continue to decline (North American Bird Conservation Initiative 2014). Presently, avian conservation interests emphasize the need to minimize the conversion of grasslands to other land uses, to maintain grassland structural heterogeneity required by the diverse suite of grassland birds in the region (Knopf 1994, Fuhlendorf et al. 2006, Toombs et al. 2010), and to foster the necessary ecosystem processes and management actions to do so (Knopf 1996, Samson et al. 2004, Derner et al. 2009, Fuhlendorf et al. 2012).

Grassland management in the North American Great Plains prioritizes cattle production and ranch profitability on privately owned lands (Hart and Waggoner 1988, Hart and

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Ashby 1998). Traditional range management using optimal moderate stocking rates and continuous season-long grazing can lead to homogeneity in grassland structure (Holechek et al. 2004, Fuhlendorf and Engle 2012, Allred et al. 2014). Rangeland management approaches that integrate the use of grazing and fire, known as patch-burn grazing or pyric herbivory (Fuhlendorf et al. 2009), allow grazers to selectively forage on recently burned areas and can potentially generate a shifting pattern of disturbance across the landscape, thereby increasing heterogeneity in vegetation structure. This shifting mosaic can potentially create habitat for avian species that breed in sparse, short-statured vegetation and species that breed in taller, denser mixtures of shrubs, forbs, and midgrasses (Fuhlendorf et al. 2009, Augustine and Derner 2015). Increased species diversity under patch-burn grazing management and enhanced reproductive performance of grassland birds, such as dickcissel (*Spiza americana*) and grasshopper sparrow (*Ammodramus saviannarum*), support the biodiversity goals of this management approach in tallgrass prairie (Churchwell et al. 2008, Coppedge et al. 2008), but few studies have addressed the role of patch-burn grazing in semi-arid grasslands.

Augustine and Derner (2015) reported on vegetation responses and avian abundance patterns in a patch-burn grazing experiment in the shortgrass steppe. They found that heterogeneity increased at the short-sparse end of the vegetation structure continuum, but tall dense structure did not increase relative to grazed-only areas. Further, lark buntings were significantly less abundant in recently burned patches compared to unburned patches, whereas abundances of McCown's longspurs and horned larks were not significantly affected by time since burning. However, their analysis focused only on avian densities and did not examine nest-site habitat selection or reproductive performance. We expanded on the experimental study described in Augustine and Derner (2015) to examine the effects of patch-burn grazing management and rainfall on habitat use and aspects of reproductive success of avian species in the semi-arid shortgrass steppe of Colorado, USA. Because habitat selection behavior in birds can differ across spatial scales, between nest and territory scales and among microhabitat, macrohabitat, and landscape scales (Orians and Wittenberger 1991, Saab 1999, Ruth and Skagen 2017), we evaluated vegetation structure at several scales.

We examined the general hypothesis that patch-burn grazing management in a semi-arid grassland would favor the breeding performance of a suite of avian species that collectively requires heterogeneity in grassland structure. Specifically, we predicted that recently burned patches would attract McCown's longspurs and horned larks which use short sparse vegetation for breeding, and that taller denser vegetation would be available to lark buntings. We examined apparent nest density of avian species relative to patch-burn grazing management, and we examined nest-site and territory habitat selection patterns relative to habitat structure. Further, we posited that nest survival of longspurs and larks would be optimized in recently burned

patches and short-statured vegetation. Because weather variability strongly influences grassland structure, bird response, and nest predation (Skagen and Yackel Adams 2012, Conrey et al. 2016), we incorporated daily and seasonal weather information into analyses to account for yearly variation that was not associated with management activities.

STUDY AREA

We conducted our research at the Central Plains Experimental Range (CPER), which is a United States Department of Agriculture (USDA) Long-term Agroecosystem Research site located approximately 12 km northeast of Nunn, Colorado, USA (40°50'N, 104°43'W). The property encompasses ~6,300 ha of flat to gently rolling terrain at elevations of 1,500–1,700 m managed for beef cattle production. Soils in the study area consisted of deep, well-drained, fine sandy loams on convex alluvial flats and upland plains. The climate is characterized by a strong annual cycle (mean daily min. and max. temperatures of -12–4°C in Jan and 15–26°C in Jul), frequent and persisting dry weather, and occasional intense storms. Long-term (1939–2016) annual precipitation averaged 341 ± 96 mm (SD), and mean precipitation during the growing season (Apr–Aug) was 240 ± 83 mm; Fig. S1, available online in Supporting Information). During 2008–2012, annual precipitation was 330 mm, 436 mm, 360 mm, 356 mm, and 206 mm, respectively, and growing season precipitation was 240 mm, 352 mm, 285 mm, 245 mm, and 116 mm, respectively.

Vegetation in this grassland was characterized structurally as a matrix of short-statured grasses punctuated by individuals and patches of taller vegetation consisting of the mid-height grasses plus cactus, forbs, subshrubs, and shrubs. Two perennial C₄ shortgrasses (blue grama [*Bouteloua gracilis*] and buffalograss [*B. dactyloides*]) and a short-statured C₃ perennial sedge (needleleaf sedge [*Carex duriuscula*]) dominated the vegetation (>70% of annual net primary productivity; Lauenroth and Burke 2008). We refer to these 3 species, along with an annual plant, 6-weeks fescue (*Vulpia octoflora*), collectively as shortgrasses. Less abundant but widespread plant species provided taller vertical structure than the dominant shortgrasses. The midgrasses included C₃ perennial grasses (western wheatgrass [*Pascopyrum smithii*], needle and thread [*Hesperostipa comata*], and squirreltail [*Elymus elymoides*]) and C₄ bunchgrasses (purple threeawn [*Aristida purpurea*], sand dropseed [*Sporobolus cryptandrus*]). Other taller-structured plant species include plains prickly-pear cactus (*Opuntia polyacantha*), forbs (>20 species, the most abundant being scarlet globemallow [*Sphaeralcea coccinea*]), subshrubs (broom snakeweed [*Gutierrezia sarothrae*], buckwheat [*Eriogonum effusum*], and fringed sage [*Artemisia frigida*]), and shrubs (fourwing saltbush [*Atriplex canescens*] and rubber rabbitbrush [*Ericameria nauseosa*]; Lauenroth and Burke 2008). Dominant fauna at the site include cattle and pronghorn (*Antilocapra americana*). The most common avian predators include thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), swift foxes (*Vulpes*

velox), striped skunks (*Mephitis mephitis*), and bull snakes (*Pituophis melanoleucus*; With 1994).

METHODS

During 2007–2011, we implemented a patch-burn grazing management regime in each of 3 replicate 65-ha pastures. The patch-burn treatment consisted of prescribed burning of 25% of each pasture (16.25 ha, square shape) during the autumn (Oct or Nov) preceding the growing seasons of 2008, 2009, 2010, and 2011, such that the entire area of each pasture was burned once during the 4-year period. During the last year of the patch-burning regime (2011) and the first year after the patch-burning regime ended (2012), we studied grassland bird nest-site selection and nest survival rates in the 3 patch-burned pastures and 6 unburned pastures of the same area (65-ha). 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/ha, which results in approximately 40% forage utilization (Hart and Ashby 1998). Before the study, these pastures had been grazed at this moderate stocking rate for >10 years with no burns. No portion of control pastures were burned during the study. Augustine et al. (2014) provide details on fuel loads and burn characteristics, and Augustine and Derner (2014) provide details for responses of cattle in terms of grazing distribution and weight gains.

Vegetation Measurements

Each study pasture was divided into 4 16.25-ha quarters corresponding to the distribution of the burns in the patch-burned pastures. We measured vegetation structure and conducted searches for bird nests in each of the 4 quarters of the patch-burned pastures and within 1 randomly selected 16.25-ha quarter of each unburned 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. We permanently marked each location with a nail and a 3-cm diameter washer and determined its location with a global positioning system (GPS) recording device with sub-meter accuracy (Trimble GeoXT or GeoExplorer, Trimble Navigation, Sunnyvale, CA, USA). In June of each year, we visually estimated plant canopy cover by species in a 50 × 20-cm quadrat placed at each location. We also measured vegetation visual obstruction (VO), a measure of height and vertical density of standing vegetation, by placing a visual obstruction pole (Robel et al. 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.

In 2011, each of the 3 patch-burned pastures contained a recently burned patch (burned in November 2010) plus

2-year-old, 3-year-old, and 4-year-old burn patches. Thus, the study area consisted of 3 patches (16.25 ha each) of each of 4 time-since-burn treatments plus 6 patches (16.25 ha each) that had not been burned, which resulted in 293 ha with 648 vegetation sampling locations. In 2012, the 4 time-since-burn treatments were 2- to 5-year-old burn patches.

Grassland Bird Nests and Weather

From 17 May (2011) and 10 May (2012) through early July of each year, we searched for nests using a rope-dragging technique (Winter et al. 2003) in each of the pasture quarters where we also conducted the vegetation structure measurements. Nests of larks and longspurs generally are at ground level and relatively exposed with the tallest vegetation at the nest averaging 10–15 cm; lark bunting nests are at or above ground level under nest vegetation averaging >30 cm (S. K. Skagen, U.S. Geological Survey, unpublished data). We used the number of nests found per species within each pasture as the apparent nest density because nest search effort was similar across treatments (4–5 searches/pasture during a breeding season).

We determined incubation stage by floating 2 eggs from each nest using the technique described in Skagen and Yackel Adams (2012). We obtained scientific collecting permits from the United States Fish and Wildlife Service Region 6 and Colorado Parks and Wildlife, and all animal handling methods (floating eggs for aging clutches) and protocols were approved by the Institutional Animal Care and Use Committee of the United States Geological Survey Fort Collins Science Center. We monitored nests and counted eggs and chicks every 2–4 days until nests were empty. We recorded signs of success (parents feeding young or calling in vicinity, fecal droppings outside of nest) or failure (eggshell fragments, nest damage) and considered nests successful if ≥1 young fledged as determined by field cues. We assumed the number of fledglings to be the number alive at the last visit when the nest was active. Adult birds were unmarked. We mapped nest locations with a GPS recording device with sub-meter accuracy.

At each nest site, we measured vegetation composition and structure by centering a 50 × 20-cm quadrat over the nest and recording visual estimates of canopy and basal cover of each plant species, and placing a visual obstruction pole at the edge of the nest bowl in each of 4 cardinal directions and recording VO. We repeated these measurements 5 m away from the nest in 1 randomly selected cardinal direction. We completed all measurements within 7 days of nest failure or success. We also calculated the distance from the nest to each of the vegetation measurement locations distributed in the systematic grids to calculate compositional and structural attributes of the vegetation at varying distances from each nest site.

We obtained daily precipitation and temperature values from on-site weather stations administered by the Shortgrass Steppe Long Term Ecological Research project and the USDA Agricultural Research Service. We determined the distances of nests to the nearest weather station with ArcGIS (Environmental Systems Research Institute, Redlands, CA,

USA). We summed daily precipitation from 15 May to 15 July (encompassing >90% of the nesting season) to quantify rainfall during the breeding season. We assigned seasonal precipitation as the total amount of rainfall during the breeding season from each weather station weighted by the number of nests nearest the station. We assigned values for daily precipitation and temperatures to nests based on the nearest weather stations (\bar{x} distance = 2.0 km \pm 1.2, range = 0.4 to 5.5 km).

Data Analyses

We analyzed variation in vegetation structure (VO) across the time-since-burn gradient and among years with a 2-way, repeated-measures analysis of variance (ANOVA) that included patch type, year, and their interaction (both as nominal variables) as fixed effects, and we accounted for pasture as the subject on which repeated measures were performed. For this ANOVA, the response variable was mean VO within each replicate 16-ha patch in the experiment. We constructed histograms illustrating the range of small-scale (individual quadrat) variation pooled across all 3 replicates within each patch-burn treatment per year to illustrate the amount of variability within the different patch types. We conducted analyses in JMP[®] version 12.0.1 (SAS Institute, Cary, NC, USA).

We analyzed variation in the number of nests detected (apparent nest density) across the time-since-burn treatment for larks and longspurs in each year using a generalized linear mixed model that assumed a negative binomial distribution for nest density with a log link (Proc GLIMMIX, SAS v9.4, SAS Institute). We tested for effects of species, burn treatment (years since burn [YSB]), year, YSB \times year, and YSB \times species. We used $\alpha = 0.1$ as the threshold for evaluating potentially important interaction terms (Meredith and Stehman 1991), and evaluated main effects at $\alpha = 0.05$.

For horned larks, lark buntings, and McCown's longspurs, we calculated means and 95% confidence intervals for vegetation attributes measured at the nest microsites, within 50 m of nests, and within 100 m of nests. For each species, we then compared values to the 95% confidence interval for all plots within the study area that were >100 m distant from nests, to provide a *post hoc* evaluation of how nest microsites and the area surrounding the nest (an approximation of the territory) compared to one another and to the unused area. The 50-m and 100-m radius circles (\sim 0.8 ha and 3 ha) encompass the range of territory sizes of grassland and shrubsteppe birds in general (Wiens et al. 1985, Shane 2000, Jones 2011); thus, we refer to these scales when referencing the territory.

We analyzed vegetation structure in terms of VO. We measured vegetation composition in terms of canopy cover of the 6 plant functional groups consisting of shortgrasses, midgrasses, cactus, forbs, subshrubs, and shrubs. We determined differences in vegetation structure and percent foliar cover of tall-structure plant functional groups (the sum of cactus, midgrasses, subshrub, shrubs and forbs) across spatial scales for all 3 bird species in 2011 and for 2 bird species in 2012 (because of the lack of nesting lark buntings in the 2012 drought).

We estimated daily survival rates (DSR) of horned lark and McCown's longspur nests using the nest survival model in Program MARK version 6.2 (White and Burnham 1999). We were primarily interested in the influence of patch-burn grazing and vegetation structure on nest DSR. However, we recognized that several other factors influence DSR in grassland and shrubsteppe birds (Rotenberry and Wiens 1989, George et al. 1992, Dinsmore et al. 2002, Skagen and Yackel Adams 2012). The inclusion of additional intrinsic and extrinsic information could reduce error variance and improve our ability to detect a treatment effect. Therefore, before we evaluated potential vegetation effects, we incorporated 5 categories of initial variables, including age of the nest (linear and quadratic), time in season (day of yr; linear and quadratic), bird species, seasonal precipitation, and daily weather into our modeling process. We used a hierarchical model selection procedure using Akaike's Information Criterion for small sample sizes (AIC_c) to infer support for models (Burnham and Anderson 2002). Within each category of initial variables, we ran univariate models to determine the best expression (lowest AIC_c including the constant model) to carry forward to more inclusive models. We then chose the most parsimonious model representing initial variables as a base model. This hierarchical approach allowed us to reduce the overall number of models while identifying variables that best contributed to model fit. We did not combine highly correlated variables ($|r| > 0.7$) in the same model.

Using the base model, we evaluated the influence of habitat variables on DSR of nests at 4 spatial scales. We selected the largest scale, the pasture quarter (16.25 ha), because that was the scale at which treatments were applied; habitat variables included recent burn (a binary variable) and years since burn. We analyzed 3 finer spatial scales (nest site, within 50 m of the nest, and within 200 m of the nest) corresponding to the nest site, the center of the territory, and vegetation beyond the territory. For each nest site and the areas within 50 m and 200 m of the nest, we evaluated 4 vegetation structure variables: VO, cover of bare ground, foliar cover of relatively tall-structured vegetation (ln-transformed to improve linearity of the models), and cover of shortgrass. Tall-structured vegetation included midgrasses, cactus, forbs, subshrubs, and shrubs. Using the best models incorporating the vegetation metrics at each of the 3 spatial scales, we tested 2 interactions: (species \times seasonal precipitation) and (vegetation structure \times seasonal precipitation). We calculated nest success as DSR^{*x*}, where *x* was the total length of the incubation and nestling stages combined. We used the following numbers of days for incubation and nestling periods, respectively, based on Baich and Harrison (1997): horned lark (12, 10), lark bunting (12, 8), and McCown's longspur (12, 10). We considered findings statistically significant at $P < 0.05$ or when 95% confidence intervals were non-overlapping; marginally significant trends were denoted at $P < 0.1$.

RESULTS

The 2 years of study differed in growing season precipitation, with 2011 accruing a near average amount (245 mm), and

2012 falling far below average (116 mm; drought conditions). Only 4 years covered by long-term records (1939, 1954, 1960, and 1964) were drier during the growing season than 2012 (Fig. S1). Variation in mean vegetation VO among the patch-burn treatments did not vary by year (YSB \times yr: $F_{4, 26} = 0.75$, $P = 0.56$). Mean vegetation VO increased across the time-since-burn gradient in both years ($F_{4, 26} = 3.49$, $P = 0.021$) and declined in all treatments from 2011 to 2012 ($F_{1, 26} = 16.61$, $P < 0.001$). Although we detected clear and statistically significant patterns of variation in mean VO among the types of burn patches and between years, we still observed notable variability among these means at the scale of individual quadrats within each patch-burn treatment, with variability greater in 2011 than in 2012 (Fig. 1).

Nest-Site Selection

We measured vegetation attributes for 69 McCown's longspur, 26 horned lark, and 20 lark bunting nests in 2011 (average precipitation), and for 66 McCown's longspur and 28 horned lark nests in 2012 (drought). Lark buntings

were extremely rare during the drought in 2012 ($n = 2$ nests) and were not included in the 2012 analyses.

For larks and longspurs, a generalized linear mixed model of apparent nest density did not support species \times year or species \times YSB treatment interactions ($P > 0.70$). Nest density was lower for larks (0.37 nests/16 ha) compared to longspurs (1.26 nests/16 ha; $F_{1, 61} = 14.18$, $P < 0.001$), but the lack of a species \times treatment interaction indicated that both species responded to patch-burn treatments in a similar manner. We identified a potentially important interaction between year and burn treatment ($F_{4, 61} = 2.01$, $P = 0.10$). Apparent nest density was >5 times greater in unburned patches in the drought (2012) versus the average (2011) year ($F_{1, 61} = 4.11$, $P = 0.047$), declined by a marginally significant amount ($F_{1, 61} = 3.34$, $P = 0.073$) from 2011 to 2012 in the most recently burned patches, and did not vary between years in the remaining patch types (Fig. 2). In other words, during a year of normal precipitation, the greatest nest density occurred in the most recently burned patches and generally declined across the time-since-burn gradient, whereas during the drought, nest density was lowest in

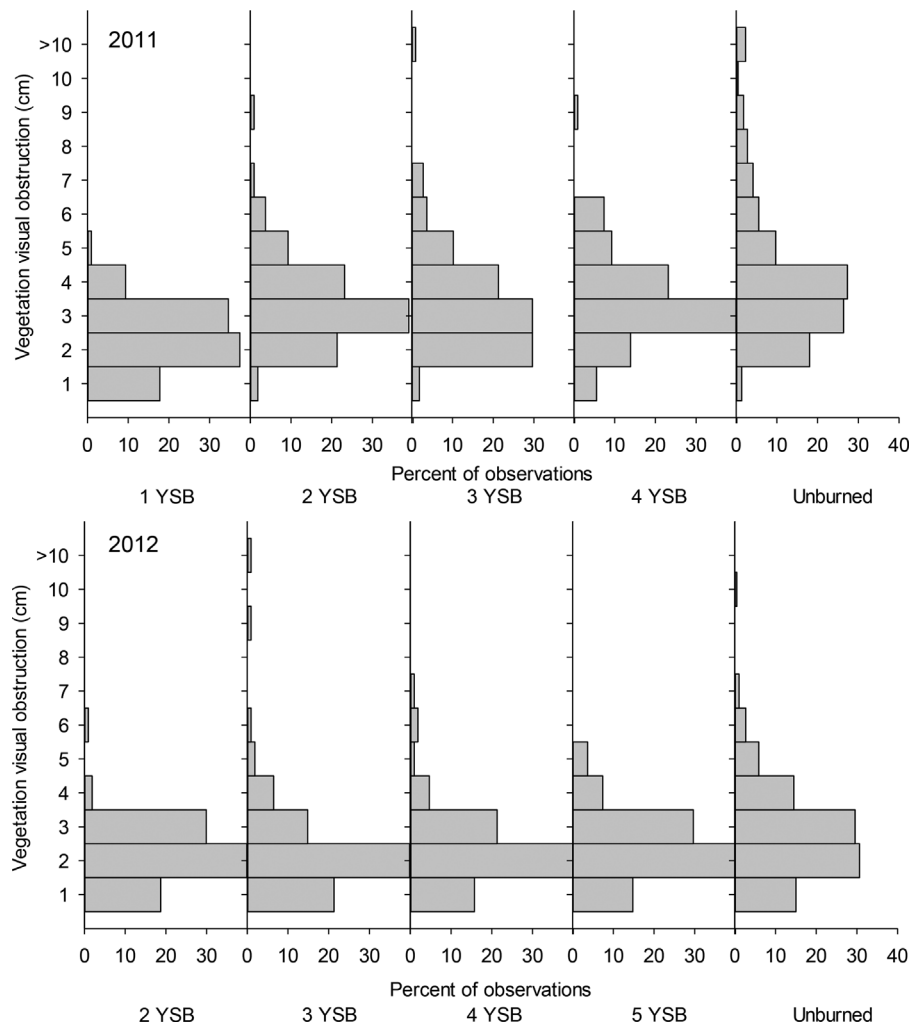


Figure 1. The frequency distribution of visual obstruction readings measured in each patch-burn grazing treatment in 2011 (average precipitation) and 2012 (drought) in the shortgrass steppe of northeastern Colorado, USA. YSB = years since burning.

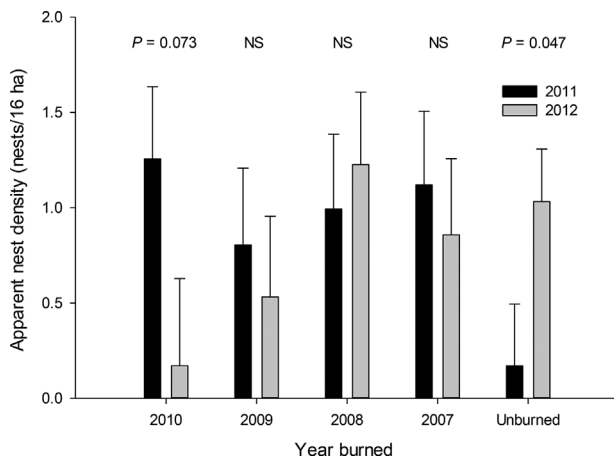


Figure 2. Variation in apparent density of McCown's longspur and horned lark nests across a time-since-burn gradient in shortgrass steppe of northeastern Colorado, USA, during an average precipitation year (2011) and a severe drought (2012). Bars show least square means \pm 1 standard error. NS indicates comparisons with $P > 0.10$. Note that burns were conducted in the autumn of the year listed on the x -axis, such that patches burned in 2010 first initiated regrowth in the spring of 2011.

recently burned patches and generally increased across the time-since-burn gradient (Fig. 2). We did not analyze apparent nest density of buntings statistically because of low sample size, but we note that 12 of the 20 (60%) bunting nests in 2011 occurred in unburned grassland sites that comprised only 33% of the total area searched.

Patterns of nest-site selection were apparent for vegetation attributes that reflect spatial variation in plant height and density (Figs. 3 and 4). Distinctive overall patterns were apparent for foliar cover of all tall-structured plant functional groups combined (i.e., the sum of cactus, midgrass, forb, subshrub, and shrub cover; Figs. 3 and 4). This metric, foliar cover of the tall-structured plant functional group, provides a measure of the abundance of plants that create vertical and horizontal cover extending above the shortgrass layer. During the year with average precipitation (2011), lark buntings selected nest sites and territories (50-m and 100-m radius) with distinctly different vegetation structural attributes than McCown's longspurs and horned larks. Cover of tall-structured functional groups and VO were greater at lark bunting nest sites and territories than for the other 2 species (Fig. 3, Table S1, available online in Supporting Information). Lark bunting territories were associated with greater cover of midgrasses and cactus than unused areas; nest sites had greater cover of midgrasses and shrubs than territories, and greater cover of subshrubs and less shortgrass than unused areas (Table S1). In 2012, there was little habitat available within the range of VO used by lark buntings the prior year (Figs. 1 and 3; Table S2, available online in Supporting Information).

Scale-related differences were evident in the nesting habitat selection patterns of all 3 species and differed with average precipitation versus drought. Under average precipitation in 2011, both VO and foliar cover of tall-structured plants at lark bunting nest sites and the area within a 50-m radius of

nests were greater than in areas >100 m from bunting nests (Fig. 3). In the same year (2011), nest microsites of horned larks and McCown's longspurs were similar in structure (VO) to areas >100 m from nests, yet both species placed their nests where surrounding vegetation out to a 100-m radius was shorter and contained less cover of tall-structured plant species than areas >100 m from nests (Fig. 3). During the 2012 drought when vegetation VO declined across all burn treatments (Fig. 1), longspurs and larks placed their territories in areas with similar VO but lower tall-plant cover as areas distant from nests, and selected nest microsites with taller vegetation than the areas surrounding nests and beyond (Fig. 4).

In 2011, territories of McCown's longspurs contained low cover of midgrasses and greater cover of shortgrass than areas outside territories, whereas nest sites had greater cover of midgrasses and cactus than territories and non-use areas (Table S1). In 2012, both species selected nest sites with more midgrasses, but territories contained less midgrass cover than non-use areas (Table S2). McCown's longspur territories contained less midgrass and more shortgrass than non-use areas (Table S2).

Daily Survival Rate and Overall Nest Success

The base model for evaluating daily survival rates of nests included age of the nest (quadratic), time in season (quadratic), species, seasonal precipitation, and daily precipitation (Tables 1 and S3). Nest age and time-in-season quadratic effects were represented by equations describing curves that were concave upward (indicated by positive coefficients of the squared terms; Table 2). Daily survival rates declined throughout incubation and increased as the nestling period progressed. In general, horned larks had greater DSRs than McCown's longspurs, DSR was greater in the year of average rainfall rather than the drought year, and high daily precipitation depressed nest survival (Tables 2 and 3). Although the preliminary model including daily maximum temperature was nearly as well supported as the model containing daily precipitation (Table S3), we did not include both factors in the base model because rainy days were generally cooler than dry days. A *post hoc* substitution of daily temperature for daily precipitation in the final top model yielded a negative relationship ($\beta = -0.053 \pm 0.033$ SE) with 95% confidence intervals that were asymmetrically distributed around zero ($-0.117, 0.011$).

Neither of the variables that quantified treatment at the pasture scale, recent burn (binary) or years-since-burn, nor at the territory scale (50 m) improved upon the base model (Table S3). The most parsimonious models ($w_i > 0.05$) for DSR included habitat structure variables at 2 spatial scales, foliar cover of tall-structured vegetation at the nest and cover of shortgrass within 200 m of the nest (Table 1). The species \times precipitation interaction appeared in the best performing models at both spatial scales with McCown's longspur exhibiting the lowest DSR during the dry year (Tables 1 and 3). At the nest site scale, the vegetation \times precipitation interaction was also supported (Table 2). The DSR of horned lark nests did not vary with cover of tall

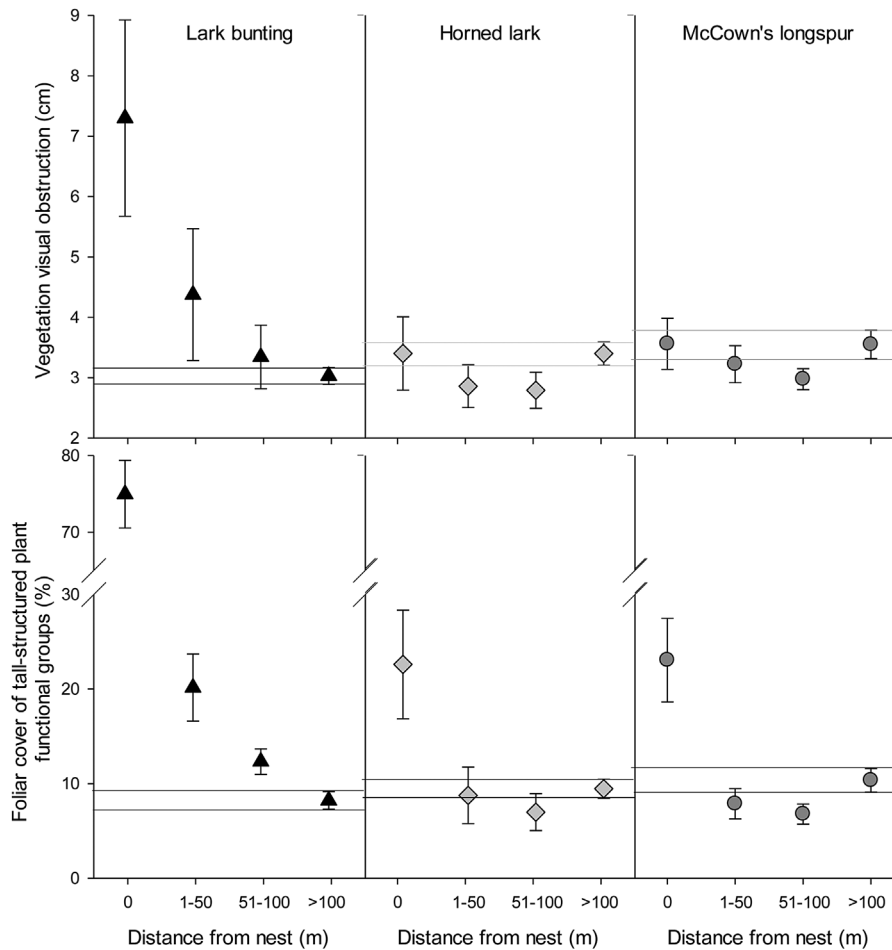


Figure 3. Scale-dependent nesting habitat selection by 3 passerines in the shortgrass steppe of northeastern Colorado, USA, under average precipitation conditions in 2011. The symbols show means (and 95% CI) for nest sites (0 m), territories (1–50-m, 51–100-m radii), and unused areas (>100 m from nests). For ease of comparison, the double lines extend the 95% confidence intervals around the mean value for unused areas.

vegetation in either year (Fig. 5A,B). In contrast, although DSR of McCown's longspur nests did not vary with foliar cover of tall vegetation at the nest in the average precipitation year, it declined >0.10 as cover of tall vegetation at the nest increased during drought (Fig. 5C, D). During the drought, the average DSR of McCown's longspur nests was 0.920 (incubation) and 0.907 (nestling period) in low vegetation and dropped to 0.800 (incubation) and 0.760 (nestling period) in taller cover (50% cover of tall vegetation; Fig. 5C, D). The DSR of both species increased with increasing cover of shortgrass, rather than tall vegetation, at the 200-m scale (Table 2). Relationships of nest survival relative to vegetation structure did not vary between horned larks and McCown's longspurs; species \times vegetation interactions did not improve the most parsimonious models for either tall vegetation at the nest nor shortgrass at 200 m ($\Delta\text{AIC}_c > 1.0$; Table S3).

The inclusion of additional intrinsic and extrinsic factors improved our ability to detect vegetation effect. Without the additional non-vegetation factors we considered (nest age, time in season, species, weather), a nest-scale model containing the habitat covariate alone (cover of tall vegetation) had substantially worse fit than the more inclusive model ($\Delta\text{AIC}_c = 23.70$) and showed no trend

($\beta = -0.001 \pm 0.081$ SE). At the 200-m scale, although a model with the habitat variable alone (cover of shortgrass within 200 m) had considerably worse fit than the top more inclusive model ($\Delta\text{AIC}_c = 20.69$), a positive trend with DSR was apparent ($\beta = 0.035 \pm 0.012$).

Overall nest success was greatest for horned larks in the normal rainfall year and lowest for McCown's longspur in the drought. The number of fledglings per successful nest did not differ between species or years (Table 3).

DISCUSSION

In mesic grasslands of the North American Great Plains, managing vegetation for spatiotemporal heterogeneity in height and composition is important for sustaining habitat for a diverse suite of grassland birds (Davis 2005, Fuhlendorf et al. 2012, Lusk and Koper 2013). Few studies have examined this issue in more arid portions of the Great Plains where vegetation is considerably shorter and less productive, and hence the absolute magnitude of potential variation in vegetation structure is more limited. We previously showed that patch-burn grazing management in the semi-arid shortgrass steppe creates breeding habitat for the mountain plover (*Charadrius montanus*), a species of

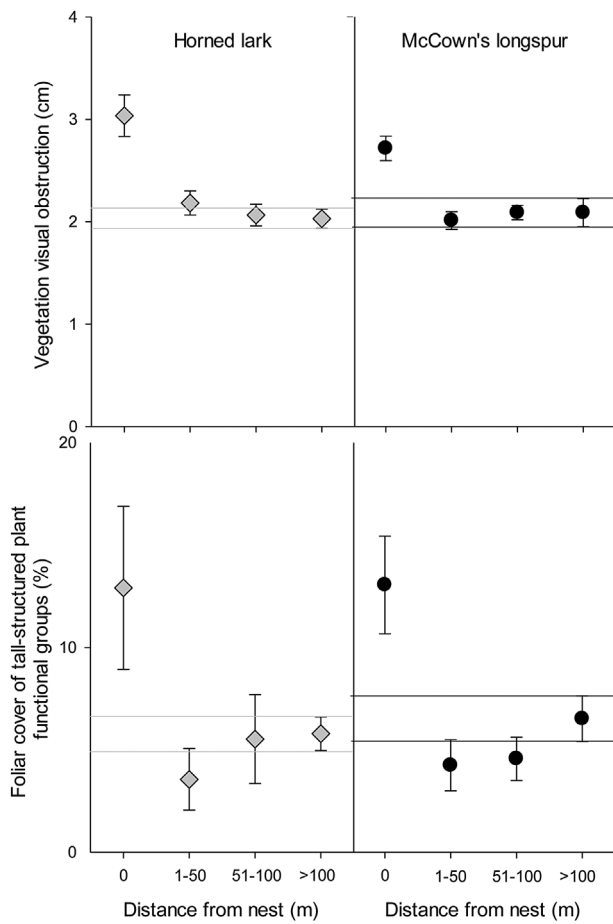


Figure 4. Scale-dependent nesting habitat selection by 2 passerines in the shortgrass steppe of northeastern Colorado, USA, in drought conditions in 2012. The symbols show means (and 95% CI) for nest sites (0 m), territories (1–50-m, 51–100-m radii), and unused areas (>100 m from nests). For ease of comparison, the double lines extend the 95% confidence intervals around the mean value for unused areas.

conservation concern in the region (Augustine and Derner 2012, Augustine and Skagen 2014). However, patch-burn grazing management can negatively affect local abundance of other bird species such as lark buntings and grasshopper

sparrows (Augustine and Derner 2015). We showed that patch-burn grazing management influenced the distribution of nesting effort by horned larks, lark buntings, and McCown's longspurs, but that the direction of such effects were contingent on weather patterns. Furthermore, we detected several scale-dependent influences of vegetation conditions on nest survival rates, which must be interpreted within the context of the influence of daily and seasonal weather effects.

Lark Buntings

As expected based on generalized habitat relationships of grassland birds (Knopf 1996), lark buntings selected substantially taller vegetation at the nest site and breeding territory compared to horned larks and McCown's longspurs. Lark buntings nested more frequently than expected in unburned grassland, selected nests sites with vegetation more than twice as tall as unused areas (primarily in association with midgrasses, cactus, subshrubs, or shrubs), and nested in territories with vegetation approximately 30% taller than unused areas.

Lark buntings exhibit low philopatry (Shane 2000). During the drought, they largely abandoned our study area, although small numbers still attempted to breed in those limited portions of our study area that retained tall, dense vegetation (this species returned to breed in the study area in 2013 and 2014, years with near-normal precipitation; D. J. Augustine, Agricultural Research Service, personal observation). Thus, our findings suggest that both patch-burn grazing management and drought have significant negative effects on lark bunting reproductive output within a given locale, and that management strategies to retain taller vegetation structure than occurs under patch-burn grazing management are needed to sustain habitat for this species. The value of retaining tall-structured vegetation during droughts to provide lark bunting breeding habitat remains unclear, however, as large-scale shifts in breeding distribution in such years may negate the value of unburned and lightly or ungrazed areas in drought-affected areas. Further research is needed to understand the influences of lark bunting nesting habitat selection at scales larger than our study area, and to

Table 1. Nest survival models for horned larks and McCown's longspurs in eastern Colorado, USA, 2011–2012, difference in corrected Akaike's Information Criterion (ΔAIC_c), AIC_c model weights (w_i), number of parameters (K), and model deviance. Models that improved upon the base model are presented. Quadratic terms were accompanied by lower order terms. All models included an intercept. AIC_c of top model = 576.491. See Table S3 for full model set.

Model ^a	ΔAIC_c	w_i	K	Deviance
Age ² Time ² Species Prec DaPrec Shtgr200 (Species × Prec)	0.000	0.139	10	556.339
Age ² Time ² Species Prec DaPrec NTallVeg (Species × Prec) (NTallVeg × Prec)	1.038	0.083	11	555.347
Age ² Time ² Species Prec DaPrec Shtgr200	1.215	0.076	9	559.582
Age ² Time ² Species Prec DaPrec Shtgr200 (Species × Prec) (Shtgr200 × Prec)	1.243	0.074	11	555.552
Age ² Time ² Species Prec DaPrec NTallVeg (NTallVeg × Prec)	1.724	0.059	10	558.063
Age ² Time ² Species Prec DaPrec Shtgr200 (Species × Shtgr200)	1.829	0.056	10	558.168
Age ² Time ² Species Prec DaPrec Shtgr200 (Shtgr200 × Prec)	2.435	0.041	10	558.774
Age ² Time ² Species Prec DaPrec (Base model)	2.833	0.034	8	563.225

^a Age² = quadratic of nest age, Time² = quadratic of time in season where day 1 = 10 May, Species is binary with horned lark = 1, Prec = seasonal precipitation, the sum of daily values for 15 May–15 July of each year, DaPrec = daily precipitation, Shtgr200 = cover of shortgrass within 200 m of nest. Models testing quadratic terms also include linear terms. NTallVeg = ln(cover of tall-structured plants) within nest plot.

Table 2. Coefficients (β estimates \pm SE, 95% CI) of variables included in top-ranked models (Akaike weight [w_i] > 0.05) of daily survival rate (DSR) of horned lark and McCown's longspur nests in eastern Colorado, USA, 2011–2012. Values are from the best model in which the variable occurred.

Variables: nest survival models ($n = 186$ nests)	$\beta \pm SE$	95% CI
Intercept	1.755 \pm 0.795	
Age	-0.216 \pm 0.075	-0.371, -0.077
Age ²	0.008 \pm 0.004	0.002, 0.015
Time in season	-0.041 \pm 0.032	-0.101, 0.024
Time in season ²	0.001 \pm 0.0005	0.000, 0.002
Species (horned lark = 1)	2.048 \pm 0.0869	0.345, 3.751
Seasonal precipitation (Prec)	0.006 \pm 0.005	-0.003, 0.015
Daily precipitation (DaPrec, mm)	-0.041 \pm 0.020	-0.080, 0.001
Cover of tall-structured vegetation in nest plot (ln-transformed; NTallVeg)	-0.776 \pm 0.353	-1.468, -0.084

determine where key breeding sites occur at the range-wide scale during droughts.

Horned Larks and McCown's Longspurs

Nesting habitat selection by horned larks and McCown's longspurs depended on precipitation- and management-induced vegetation conditions and the spatial scale considered. At the nest site, both species selected greater cover of tall herbaceous vegetation. Under average rainfall conditions (2011) and drought (2012), territories were placed in areas with overall shorter vegetation structure than what is found in unused areas, although in the drought year this trend was exhibited more strongly by foliar cover of tall plants than by VO. Consistent with these patterns for vegetation structure, both species exhibited greater nesting effort in patch-burned pastures and lower nesting effort in unburned grassland in the year of average precipitation, whereas the opposite was true during the drought.

Our results also provide insights into the tradeoffs that horned larks and McCown's longspurs face when breeding in such short-statured grasslands. Predation is a primary cause of nest failure in ground-nesting birds. Variation in arthropod abundance can also influence breeding birds, but we note that arthropod abundance varies only minimally across a broad gradient in grazing intensity and vegetation structure in the grasslands we studied (Newbold et al. 2014). Hence, we suggest that predator avoidance is likely a key influence on nest-site selection in ground-nesting passerines that breed in areas with sparse coverage of tall vegetation. Within and adjacent to a breeding territory, taller, more dense vegetation can host larger predator communities, and small patches of taller-structured vegetation within a mosaic of shortgrass can attract predators like ground squirrels and

snakes that are avoiding their own predators (Grant et al. 1982, With 1994, Dion et al. 2000, Klug et al. 2010, Lyons et al. 2015).

A tradeoff, however, also occurs in the selection of nest sites in that some structure immediately adjacent to the nest is necessary for protection from wind, rain, and solar radiation. Shortgrasses cannot provide this protection, and McCown's longspur and horned lark nest sites are typically associated with cactus or midgrasses that shade the nest during the hottest part of the day (With and Webb 1993). Our study site is located at the southern edge of the McCown longspur's range where effects of overheating on nest-tending birds may be particularly important (With and Webb 1993). Taller vegetation may also serve to hide nests from predators using visual cues and disrupt predator search activities. Thus, birds must balance selection of some cover at the nest site with selection of sparse cover within the surrounding area. During the drought year, taller vegetation structure at the nest site was associated with reduced probability of survival of McCown's longspur nests. Selection of excessively tall structure at nest sites in otherwise short-statured vegetation could potentially provide a cue to predators such as swift foxes that may search the area non-randomly by seeking out taller-than-average plants or patches.

McCown's longspur populations have been declining for the past 4 decades (Sauer et al. 2017), with this species on the State of the Birds 2014 Watch List (<http://www.stateofthebirds.org/2014/watch-list>) and identified as a species of conservation concern by state wildlife management agencies throughout its range in the United States, by multiple federal land management agencies (U.S. Forest Service, Bureau of Land Management, U.S. Fish and Wildlife Service), and by the Canadian government. As a result, there is considerable

Table 3. Daily survival rates (DSR), overall nest success, and productivity (fledglings per successful nest) of 218 grassland bird nests in eastern Colorado, USA, during a year of normal rainfall (2011) and a drought year (2012).

	Lark bunting	Horned lark		McCown's longspur	
	2011 (normal rainfall)	2011 (normal)	2012 (drought)	2011 (normal)	2012 (drought)
DSR \pm SE (95% CI)	0.956 \pm 0.011 (0.934, 0.967)	0.954 \pm 0.010 (0.930, 0.970)	0.933 \pm 0.013 (0.902, 0.954)	0.923 \pm 0.010 (0.902, 0.941)	0.889 \pm 0.014 (0.858, 0.914)
Nest success (n) ^a	0.407 (32)	0.357 (25)	0.216 (28)	0.173 (69)	0.075 (64)
Fledglings/successful nest \pm SD (n)	3.4 \pm 1.06 (17)	2.4 \pm 0.63 (14)	2.1 \pm 0.64 (13)	2.2 \pm 0.88 (26)	2.2 \pm 0.44 (13)

^a Nest success is calculated as DSR^α , where $\alpha = 20$ for lark buntings and $\alpha = 22$ for horned larks and McCown's longspurs.

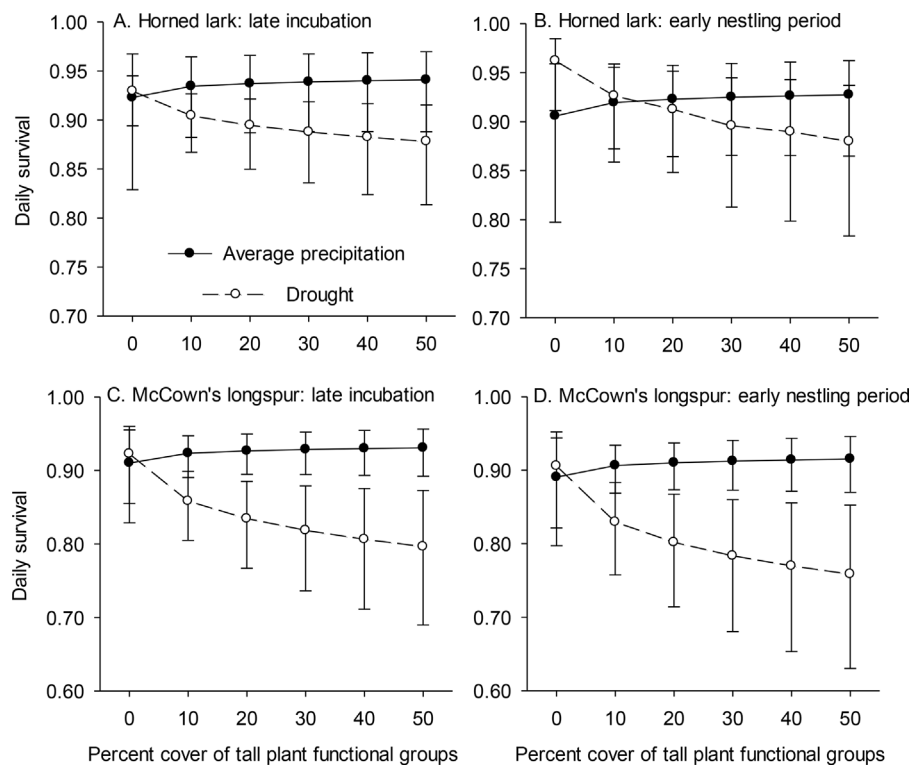


Figure 5. Modeled daily survival rates (DSR) of horned lark (A, B) and McCown's longspur (C, D) nests during a year of normal precipitation (2011) and drought year (2012) relative to coverage of tall vegetation structure (% cover of midgrasses, cacti, forbs, subshrubs, and shrubs) at nest sites. Values represent average DSR ($\pm 95\%$ CI) during late incubation (A, C; day 8 of incubation) and early nestling period (B, D; day 4 of nestling period) during mid-season.

interest in identifying habitat conditions that could maintain or enhance reproductive performance of this species. We showed that with average precipitation, McCown's longspurs established nesting territories in areas with mean vegetation VO less than 3 cm and where foliar cover of tall-structured plants was $< 9\%$.

During drought, when vegetation was more uniform and short, McCown's longspur established territories with mean vegetation VO of 2 cm and foliar cover of tall-structured plants of 4–6%, but nest survival rates declined substantially relative to the average-precipitation year (Table 3). Thus, we suggest that in the shortgrass steppe, McCown's longspur nesting habitat consists of shortgrass-dominated vegetation with mean VO of 2.5–3 cm, where shrubs are absent but shortgrasses are punctuated by small patches of taller-structured vegetation (cactus, midgrasses, or subshrubs) that comprise 4–9% foliar cover; these latter plant functional groups are important in providing nest sites. In general, these conditions are sustained in shortgrass steppe under average precipitation, particularly on loamy to clay soils where rangeland management strategies such as patch-burn grazing management prevent accumulation of excessive tall-structured vegetation. We predict that increased vegetation structure in years of above-average precipitation could reduce McCown's longspur habitat quality and nest survival rates, given the avoidance of taller-than-average vegetation structure in the average precipitation year, but additional studies are needed to address this.

Relationships between nest survival and vegetation structure are highly variable among grassland bird studies with no clear generalizations emerging. Such relationships are likely contingent upon context, not only the structure of local vegetation, but also weather, predator communities, bird densities, landscape structure, anthropogenic disturbance, and scale of measurement. For example, associations of vegetation structure and nest survival of horned larks were reported as neutral in Oregon and Colorado (Johnson et al. 2012, Conrey et al. 2016) and positive in Wyoming (Mahoney and Chalfoun 2016). For McCown's longspur, both neutral and negative relationships have been reported (Conrey et al. 2016, Mahoney and Chalfoun 2016). Evaluations of the influence of habitat structure on nest survival gain precision when additional intrinsic and extrinsic factors, such as nest age and prevailing weather, are considered. In this study, only after accounting for the variation in daily survival due to the additional factors did the importance of vegetation structure at the nest site emerge.

MANAGEMENT IMPLICATIONS

Conditions during the growing (and nesting) season are difficult to predict in the shortgrass steppe because most precipitation occurs as convective thunderstorms during May–August, and minimal precipitation is received during the winter and early spring preceding the growing and nesting season (Pielke and Doesken 2008). Land managers must therefore often make management decisions concerning stocking rates and prescribed burning treatments without

knowledge of impending growing season conditions. As a result, we suggest that at the scale of a large ranch or multiple adjacent ranches, employing a diversity of management strategies that includes patch-burn grazing management (applied to only a portion of the landscape) and other strategies that retain taller-structured vegetation on the landscape may be important to sustain breeding habitat for shortgrass birds under temporally varying weather conditions. By including areas of recently burned and unburned shortgrass steppe within the landscape each year, managers can increase the probability that vegetation conditions associated with enhanced McCown's longspur's reproductive success are present regardless of the weather conditions that occur during the ensuing growing season.

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