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ARTICLE

The long shadow of woody encroachment: An integrated approach to modeling grassland songbird habitat

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Abstract

Animals must track resources over relatively fine spatial and temporal scales, particularly in disturbance-mediated systems like grasslands. Grassland birds respond to habitat heterogeneity by dispersing among sites within and between years, yet we know little about how they make post-dispersal settlement decisions. Many methods exist to quantify the resource selection of mobile taxa, but the habitat data used in these models are frequently not collected at the same location or time that individuals were present. This spatiotemporal misalignment may lead to incorrect interpretations and adverse conservation outcomes, particularly in dynamic systems. To investigate the extent to which spatially and temporally dynamic vegetation conditions and topography drive grassland bird settlement decisions, we integrated multiple data sources from our study site to predict slope, vegetation height, and multiple metrics of vegetation cover at any point in space and time within the temporal and spatial scope of our study. We paired these predictions with avian mark-resight data for 8 years at the Konza Prairie Biological Station in NE Kansas to evaluate territory selection for Grasshopper Sparrows (*Ammodramus savannarum*), Dickcissels (*Spiza americana*), and Eastern Meadowlarks (*Sturnella magna*). Each species selected different types and amounts of herbaceous vegetation cover, but all three species preferred relatively flat areas with less than 6% shrub cover and less than 1% tree cover. We evaluated several scenarios of woody vegetation removal and found that, with a targeted approach, the simulated removal of just one isolated tree in the uplands created up to 14 ha of grassland bird habitat. This study supports growing evidence that small amounts of woody encroachment can fragment landscapes, augmenting conservation threats to grassland systems. Conversely, these results demonstrate that drastic increases in bird habitat area could be achieved through relatively efficient management interventions. The results and approaches reported pave the way for more efficient conservation efforts in grasslands and other systems through spatiotemporal alignment of habitat with animal behaviors and simulated impacts of management interventions.

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KEYWORDS
conservation, grassland birds, Great Plains, tallgrass prairie, woody plants

INTRODUCTION

Relationships between species distributions and landscape attributes shed light on factors shaping current distributions, characterize use within those distributions, and better predict changes in future distributions (Matthiopoulos et al., 2020). Organisms in dynamic systems, such as many mid-continental grasslands, exhibit phenotypic plasticity in their phenology (Wagle et al., 2019), physiology (Bachle & Nippert, 2022), and behavior (McMillan et al., 2021; McNew et al., 2013) in response to environmental variability over space and time. Mobile species (e.g., grassland birds) may also alter their dispersal and settlement decisions, tracking conditions that presumably increase their survival and reproduction (Kentie et al., 2014).

Conditions that are “favorable” vary among species (Wiens, 1969), locations (Verheijen et al., 2021) and periods of the annual cycle (Gehrt et al., 2020). Many grassland bird species rely on multiple vegetation cover types for successful nesting and foraging, but the specific attributes of vegetation height and composition selected are species-specific (e.g., Chapman et al., 2004; Conover, 2009; Duchardt et al., 2020; Wiens, 1969). Interactions between fire, large grazers (e.g., cattle, bison), and weather can alter the availability of these habitat types. Frequent fires (e.g., 1–2 years) favor high grass cover, while infrequent fires generally increase species richness, forb cover, and woody plant cover (Collins & Calabrese, 2012). Grazing decreases the cover of dominant grasses, promoting plant species richness (Collins & Calabrese, 2012). However, grazers (i.e., cattle and bison) generally favor recently burned areas, creating interactive effects of fire and grazing (Fuhlendorf & Engle, 2004). These processes are further complicated because vegetation can be influenced by lagged or legacy effects of prior events (Broderick et al., 2022; Dudney et al., 2017; Sherry et al., 2008). Ultimately, the presence and proportion of vegetation cover types drive nest site and territory selection in many grassland bird species (e.g., Hansen et al., 2016; Rader et al., 2007; Ruth & Skagen, 2017).

While grassland birds exhibit species-specific responses to herbaceous vegetation, responses to woody vegetation tend to be negative across grassland bird communities (Bakker, 2003). Trees and shrubs are expanding in many grasslands, and woody plant encroachment has been implicated in the decline of grassland-dependent birds (Coppedge et al., 2001; Lautenbach et al., 2020). Woody vegetation in grasslands is associated with lower occurrence, abundance, nest densities, and nest survival (Bakker, 2003; Coppedge et al., 2001; Ellison et al., 2013; Graves et al., 2010; Lautenbach et al., 2020). Territory selection may also relate to topography, although few studies have analyzed this relationship (see Renfrew & Ribic, 2002). Grassland birds may choose flatter territories to avoid predators having better vantage points or optimize nest microclimate. Flatter areas may also have different vegetation structures than steep slopes because slope affects cattle and bison grazing behavior (Bruggeman et al., 2007; Koczura et al., 2019) and sloped areas retain less moisture (Condon & Maxwell, 2015), potentially leading to changes in perceived habitat quality.

Despite the ability of mobile grassland birds to cope with changing conditions via their high mobility (Herkert, 2007), almost 75% of North American grassland bird species have declined in abundance since 1970 (Rosenberg et al., 2019). Although these declines are often attributed to habitat loss, many grassland species are even disappearing in protected areas, suggesting an important role of local management (With et al., 2008) and regional connections between multiple sites. Habitat selection studies are essential to understanding which management actions result in the most positive population-level responses, but it is often challenging to collect auxiliary data, such as vegetation measurements, over space and time that are co-located with animal observations. This can lead to misalignment between animal observations and habitat covariates (i.e., spatiotemporal misalignment) because environmental data are seldom collected at the exact same time and place an animal is observed (Gotway & Young, 2002). Spatiotemporal misalignment can produce inaccurate inferences about species distributions and resource selection (Pacifici et al., 2019), which can lead to misguided conservation actions.

We aimed to determine the extent to which vegetation and topography drive grassland bird settlement decisions, characterize the attributes associated with territory occupancy, and simulate conservation scenarios to improve territory availability at the Konza Prairie Biological Station in Northeast Kansas between 2014 and 2021. We first combined multiple data sources including ground surveys, weather, and remotely sensed data to predict vegetation height, vegetation cover, and slope at any point in space and time within our study area and over the duration of our study. We then integrated these predictions with avian mark-resight data collected from

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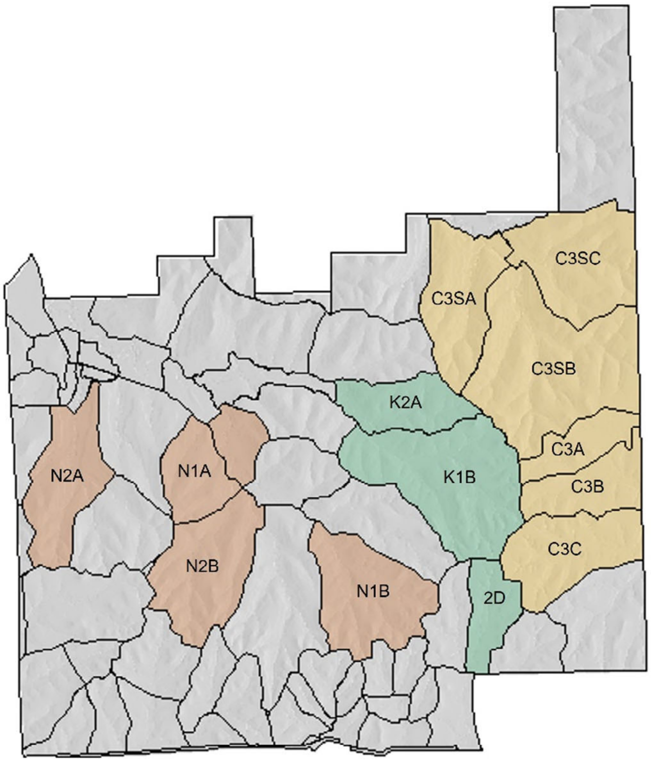
May to July in all years of the study for three of the most common grassland species in the Central Great Plains: Grasshopper Sparrows (*Ammodramus savannarum*), Dickcissels (*Spiza americana*), and Eastern Meadowlarks (*Sturnella magna*) to assess the attributes associated with territory occupancy. Based on prior studies, we expected each species to select for different territory attributes, but all would avoid sloped topography and woody vegetation. Finally, we used predictions from our Grasshopper Sparrow territory selection model to simulate the effect of shrub and tree removal on Grasshopper Sparrow territory availability across our study area. By quantifying habitat selection in multiple species, across multiple management regimes, and over a relatively long time period, we contribute to a more comprehensive understanding of grassland bird habitat use and shed light on how to slow and potentially reverse grassland bird declines.

METHODS

Study site

We conducted our study on the Konza Prairie Biological Station within the Flint Hills ecoregion near Manhattan, Kansas (39°05′ N, 96°33′ W). The Konza Prairie encompasses 3487 ha of native tallgrass prairie divided into 46 experimental study units; each unit is patch-burn grazed by cattle (i.e., one-third of the pasture is burned each year, leading to a 3-year fire return interval) or is either bison grazed or ungrazed with a fire return interval of 1, 2, 4, or 20 years. We collected vegetation and bird data on 13 of these study units, reflecting patch-burn grazed units and bison-grazed and ungrazed units burned every 1 or 2 years (Figure 1). Burns occurred in March and April before the nesting season began. Cattle grazed from April through September, and bison grazed year-round. Dominant grasses included big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), buffalo grass (*Bouteloua dactyloides*), blue grama (*B. gracilis*), hairy grama (*B. hirsuta*) and sideoats grama (*B. curtipendula*). Dominant forbs included goldenrod (*Solidago canandensis*, *S. missouriensis*), ironweed (*Vernonia baldwinii*), lead plant (*Amorpha canescens*), white heath aster (*Aster ericoides*), scurfpea (*Psoralidum tenuiflorum*), and ragweed (*Ambrosia psilotachya*). Shrub and tree cover have increased at the site over the last four decades (Ratajczak et al., 2014), particularly in less frequently burned units. Woody species that have increased include rough-leafed dogwood (*Cornus drummondii*),



Unit	Fire return interval	Grazing regime
2D	2 years	Ungrazed
C3A/C3B/C3C	3 years	Patch-burn grazed
C3SA/C3SB/C3SC	3 years	Patch-burn grazed
K1B	1 year	Ungrazed
K2A	2 years	Ungrazed
N1A	1 year	Bison-grazed
N1B	1 year	Bison-grazed
N2A	2 years	Bison-grazed
N2B	2 years	Bison-grazed

FIGURE 1 Experimental fire and grazing regimes in sampled units at the Konza Prairie Biological Station in NE Kansas. Vegetation and bird data were collected on units reflecting 1–3-year fire return intervals and ungrazed (green), bison grazed (brown), and cattle grazed (i.e., patch-burn grazed; gold) pastures. Units filled in gray were unsampled.

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smooth sumac (*Rhus glabra*), Eastern red cedar (*Juniperus virginiana*), and a diverse set of deciduous trees. The terrain of the site is characteristic of the Flint Hills region; steeply rolling hills range in elevation from 320 to 444 m, punctuated by flat lowlands, mid-elevation benches, and uplands (Brunsell et al., 2008).

Study species

Grasshopper Sparrows (*A. savannarum*) are small (~17 g), ground-nesting grassland sparrows that breed in grasslands across North America and winter in the southern United States and in Mexico (Vickery, 2021). They exhibit high rates of inter- and intra-annual dispersal, apparently spurred by nest failures or changes in vegetation structure (Silber et al., 2023; Williams & Boyle, 2018). Sparrows construct domed nests on the ground using dry grasses from previous growing seasons. At our site, territories average 43 ± 2 m in diameter (Williams & Boyle, 2018). Across North America, Grasshopper Sparrow populations have declined by 72% in the last 50 years and continue to decline by 3.1% each year (Road to Recovery, 2022).

Eastern Meadowlarks (*S. magna*) are relatively large (~120 g), grassland-dependent songbirds of central and eastern North America. Eastern Meadowlarks are present at our study site year-round, although interannual site fidelity is low, and wintering individuals may differ from breeding individuals. They require dead grass grown in previous breeding seasons to construct domed nests on the ground and tall perches from which males can sing and defend territories. Territory size varies across the species' range from 1.2 to 4.8 ha (Francq, 1972; Wiens, 1969). Across North America, Eastern Meadowlark populations have declined by 76% in the last 50 years and continue to decline by 2.0% each year (Road to Recovery, 2022).

Dickcissels (*S. americana*) are ubiquitous, medium-sized (~32 g) grassland songbirds of the Great Plains prairies. They are long-distance migrants, wintering in Venezuela and breeding throughout most of the central United States (Fretwell, 1986). They build open cup nests in dense forbs or small shrubs, on or near the ground (Gross, 1968). Territory sizes range from 0.22 to ≥0.95 ha (Harmeson, 1974; Schartz & Zimmerman, 1971; Verheijen et al., 2022). Dickcissel populations declined by 12% in the last 50 years but have recently increased by 2.4% each year since 2009 (Road to Recovery, 2022).

Data collection

We studied Grasshopper Sparrows from 2014 to 2021, and Dickcissels and Eastern Meadowlarks from 2019 to 2021. Throughout each breeding season (late April to early August), we intensively captured and surveyed randomly located 10 ha plots within each study unit. We prioritized efforts on plots to ensure we thoroughly sampled a consistent area, but also sampled the entire unit several times per season.

To capture breeding males, we placed a 12 × 2.5 m mist net (Ecotone, Gdynia, Poland; 32 mm mesh size) adjacent to preferred perches of territorial males. At the base of each net, we placed a small audio player and speaker broadcasting conspecific songs to lure territorial males. We fit each bird with a uniquely numbered aluminum band from the United States Geological Survey and unique combinations of three plastic color bands (a total of two bands/leg). We determined sex by looking for brood patches (female) or cloacal protuberances (male). Before releasing, we collected morphometric measurements, feather samples, and blood samples for other projects.

We aimed to capture and mark all territorial male Grasshopper Sparrows within our 13 study units (Figure 1). Due to high abundances of Eastern Meadowlarks and Dickcissels, we focused sampling for those species within six units: one set of patch-burn grazed units (i.e., three units); one annually burned, ungrazed unit; one biennially burned, ungrazed unit; and one annually burned, bison-grazed unit. Due to high frequencies of within-season dispersal, we returned to each study unit multiple times throughout the season to capture, band, and resight adults. All aspects of this study were approved through the Kansas State University IACUC (protocols 3260, 3733, and 4250) and the North American Bird Banding Laboratory (permit 23836).

We surveyed all units to resight color-banded adults approximately every 10 days from late April to the beginning of August 2014–2021. Starting 30 min before sunrise, technicians chose a haphazard route throughout the study unit, walking within at least 300 m of every point, looking and listening for focal species. Observers used 8 × 42 binoculars and 10× spotting scopes to record the color band combination of each bird they detected and recorded GPS waypoints at all observed perches. If birds were unbanded, observers marked their location on a map and returned later to band the individual. Observers did not conduct surveys during precipitation or in wind exceeding 35 kph because the focal species are unlikely to sing in these conditions, reducing bird detection.

We conducted vegetation surveys within each unit once per month in May, June, and July. We repeatedly collected vegetation measurements at three (2014–2017) or 10 randomly located points (2018–2021). We measured visual obstruction by placing a Robel Pole at each point and measuring the vegetation height from all four cardinal directions from a distance of 4 m and a height of 1 m

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(Robel et al., 1970). We then placed the Robel Pole 5 m distant from the central point in each of the cardinal directions and measured visual obstruction at a further 4 m distance from the central point for a total of eight visual obstruction measurements per point. We placed a 20 × 50 cm quadrat (i.e., Daubenmire frame) at the center point to estimate percent cover to the nearest 5% of standing dead grass, live grass (green, not brown/dry), other dead veg (standing dead forbs and shrubs), forbs/flowering veg, bare ground (bare soil or rocks), litter (horizontal dead plant material), and shrubs/woody veg >0.5 m. We repeated this measurement at four additional locations, 5 m distant from the central point in each cardinal direction, collecting a total of five sets of cover measurements per point.

Territory selection analyses

We fit generalized additive models (GAMs) to predict vegetation height (dry matter) and percent cover for live grass, live forbs, bare ground, and dead grass/litter across our study units. We included the following as linear predictors for vegetation height and composition: precipitation, fire, grazing, month, elevation, and slope. We included three metrics of local precipitation as linear predictors for vegetation height and cover: spring (1 March–1 May) precipitation, breeding season (i.e., 1 May–15 August) precipitation lagged 1 year, and breeding season precipitation lagged 2 years. We included multiple metrics for precipitation because they each relate to different metrics of vegetation height and composition. Spring precipitation at the beginning of the growing season increases plant biomass (Darenova et al., 2017) and species richness (Ladwig et al., 2016), and precipitation can have legacy effects of at least 2 years on vegetation (Tenhumberg et al., 2018). Fire and grazing also affects plant composition and aboveground biomass, so we included a binary variable for whether or not the unit was burned that breeding season and a variable for the management regime. We included management regimes (e.g., bison grazed, annual burn) as a combined, factorial variable instead of separately including fire return interval and grazer identity because not all combinations of fire and grazing are reflected in our study units. We sampled two replicates per management regime (Figure 1) previously shown to provide suitable grassland bird habitat (Powell, 2008; Powell & Busby, 2013), except annually burned, ungrazed units, where we ceased sampling in all but one of these units by 2020 due to extremely low focal bird densities. We included month as a linear predictor because vegetation grows throughout the season, and the prevalence of vegetation cover types can change due to plant phenology. We included elevation and slope as linear predictors, as they are associated with soil types and grazer foraging choices. We included smooth terms for space (i.e., UTM easting and northing) and time, as we expected there to be some degree of spatial and temporal autocorrelation (Hefley et al., 2017; Wood, 2017). We also included observer as a random effect to account for differences among the 41 observers that contributed to vegetation data collection. We then fit a separate model for each vegetation response variable (i.e., vegetation height, percent live grass cover, percent live forb cover, percent dead grass and litter cover, and percent bare ground cover) to predict vegetation height and composition across our study area, at a daily, 4 m^2 resolution.

We evaluated the predictive accuracy of our vegetation model using a hold-out dataset of vegetation height and composition observations in 2022. We predicted the vegetation height and percent cover at 450 random points during the 2022 breeding season. We then calculated the mean absolute error (MAE) for vegetation height and each cover type between the observed values and our predictions $\left(\text{i.e., MAE} = \frac{\sum_{i=1}^{n}|y_i - x_i|}{n}\right)$, where n is the number of observations, y_i is the observed measurement, and x_i is the prediction. Pastures at our site exhibit small-scale patch structures, with high variability among soil types, resource availability (e.g., soil N), and management regimes (Collins & Calabrese, 2012; Koerner & Collins, 2013), challenging spatial predictive accuracy. However, grassland birds often exhibit site preferences for vegetation cover within ~15%–30% and vegetation height up to ~0.25–0.5 m (Dieni & Jones, 2017; Larned et al., 2020), necessitating some degree of predictive accuracy for correct interpretation of territory selection. Therefore, we considered our model to be a good predictor of vegetation height with an MAE ≤0.3 m, a satisfactory predictor with an MAE >0.3 and ≤0.8 m, and a poor predictor with an MAE >0.8 m. We considered our vegetation composition models to be a good predictor of a given cover type with an MAE ≤15%, a satisfactory predictor with an MAE >15% and ≤30%, a poor predictor with an MAE >30%.

For woody vegetation, we used a classification map that combined high-resolution aerial data and machine learning to estimate land cover of the site at a 2 m^2 resolution, with land cover classes of grassland, shrub dominated, deciduous tree dominated, evergreen tree dominated, or other (mostly a mix of roads and open water; Noble, 2023). The user accuracy of this product is >95% based on a hold-out dataset of 90,113 samples (Noble, 2023). We used this classification map to calculate the proportion of shrub and tree cover in each territory and create two additional rasters: the distance of each 2 m^2 pixel to the closest shrub and the distance of

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each 2 m^2 pixel to the closest tree. We calculated the slope from a dataset of gridded elevation across the Konza Prairie (Blackmore, 2019). We obtained elevation from a 2 m^2 resolution digital elevation model, produced using a 2010 LiDAR digital elevation model collected according to United States Geological Survey protocols. We then calculated a matrix containing the derivative of elevation (i.e., slope) for each grid cell.

We characterized the territories of each territorial male using GPS waypoints collected during surveys and banding efforts. We first calculated the Euclidean distance between each GPS waypoint collected for a territorial male each year. If the Euclidean distance between waypoints was farther than the expected territory size (i.e., 40 m for Grasshopper Sparrows, 60 m for Dickcissels, and 100 m for Eastern Meadowlarks), we considered the points to be within different territories. For all waypoints with a Euclidean distance less than or equal to the average territory size, the territory location was calculated as the centroid between the points. We repeated this procedure with all points for an individual in a given year to establish unique territories. We did not calculate the centroid for all waypoints for an individual within an entire breeding season because ~52% of male Grasshopper Sparrows disperse each month (Williams & Boyle, 2018). We created a buffer (20 m for Grasshopper Sparrows, 30 m for Dickcissels, and 50 m for Eastern Meadowlarks) around the territory centroids, matching each species' average territory size. If an individual was observed in a territory on several days, we assigned the earliest date the individual was observed there to represent the date it was selected. These buffered areas (i.e., territories) were then considered the "use" locations for our resource selection analysis.

To create "available," or pseudo-absence, locations for our resource selection analyses, we randomly sampled coordinates throughout our study units (Pearce & Boyce, 2006) between May and July, 2014 and 2020. This period reflects the peak breeding season at our site throughout the extent of our study. For each "available" point, we created buffers (as with observed territories) to create the same number of "available" territories as "used" (i.e., observed) territories in the species dataset.

To integrate predictions from our habitat variables (i.e., vegetation height and composition, topography, and woody plant cover) into the resource selection model, we predicted vegetation height, percent live grass, percent live forbs, percent bare ground, percent dead grass and litter, slope, proportion of territory with shrub cover, proportion of territory with shrub cover, distance to the closest shrub, and distance to the closest tree for each territory (observed and pseudo-absence). We fit a GAM for each bird species to model our response variable (i.e., present or absent) with a Bernoulli distribution (Fithian & Hastie, 2013; Pearce & Boyce, 2006). We included a smoothed effect for UTM easting and nothing to account for spatial autocorrelation in territory locations (Winnicki et al., 2020) and a separable smoothed effect for time (i.e., numeric day since the onset of the project) to account for temporal autocorrelation (Hefley et al., 2017; Wood, 2017).

We evaluated the predictive accuracy of our territory selection model using a hold-out dataset of observed Grasshopper Sparrow territories in 2021. Grasshopper Sparrows had the largest sample size, collected over 8 years and across 13 study units (vs. 3 years of data across six study units for Dickcissels and Eastern Meadowlarks), allowing for a hold-out dataset while still having a large sample size for model fitting. We predicted our habitat variables (i.e., vegetation height and composition, topography, and woody plant cover) for every observed Grasshopper Sparrow territory (i.e., "use" territories) in 2021 and an equal number of randomly sampled (i.e., "available") territories. We used these predictions to estimate relative territory selection for every "use" and "available" territory in our study area. To quantify the concordance between the integrated resource selection model's predicted territory selection and the observed Grasshopper Sparrow territories, we calculated the Brier score, or the mean-squared difference between the predictions and observed outcomes (Brier, 1950; Harrell et al., 1996).

Simulated woody plant removal

We simulated several scenarios of shrub and tree removal to assess management strategies that may increase territory availability for Grasshopper Sparrows. Using our vegetation model, we predicted the relative probability of Grasshopper Sparrow territory selection for every 4 m^2 pixel in four study units (patch-burn grazed [C3A/C3B/C3C], annually burned and bison grazed [N1B], annually burned and ungrazed [K1B], and biennially burned and ungrazed [2D]) for the middle of the 2020 breeding season (June 15). These study units are geographically near each other (Figure 1) and represent two units with substantial (>10%) woody encroachment (C3A/C3B/C3C and N1B) and two units with minimal (≤6%) woody encroachment (K1B and 2D). We used these probabilities as baseline spatial predictions of where Grasshopper Sparrows were likely to select territories. We then simulated four scenarios of woody vegetation removal: (1) removal of one small, contiguous shrub patch, less than ~10 m diameter, isolated from another

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woody cover (i.e., shrub island); (2) removal of one tree, isolated from other woody cover; (3) removal of all shrubs in the upland portions of unit (areas with <10% slope and >400 m in elevation); and (4) removal of all trees in upland areas. We targeted upland prairies instead of riparian areas for our removal scenarios because we suspected uplands would be the preferred Grasshopper Sparrow habitat. We then calculated the area over which predicted territory selection increased (i.e., the area of improved habitat) from the baseline predicted territory selection (i.e., predicted territory selection prior to simulated woody plant removal).

RESULTS

We captured 1200 male Grasshopper Sparrows in our study units between 2014 and 2020, and 95 male Eastern Meadowlarks and 180 male Dickcissels between 2019 and 2021. We surveyed each study unit approximately once every 9.6 days (SD = 4.5) for an average of nine times (range: 8–10) per season. We observed each Grasshopper Sparrow at up to 57 locations (mean = 3.34, SD = 4.68) over 1–6 years. We observed Eastern Meadowlarks up to 16 times (mean = 2.29, SD = 2.35) and Dickcissels up to 21 times (mean = 2.58, SD = 2.81) over the course of the 3 years they were sampled. We documented 2057 Grasshopper Sparrow territories, 128 Eastern Meadowlark territories, and 239 Dickcissel territories. Within each month in which an individual was observed, we collected up to 26 waypoints for each Grasshopper Sparrow (mean = 2.6, SD = 2.8), up to five waypoints for each Eastern Meadowlark (mean = 1.4, SD = 1.0), and up to four waypoints for each Dickcissel (mean = 1.3, SD = 0.8).

Territory selection analyses

We measured vegetation height and composition at 1812 points between 2014 and 2021. Vegetation height ranged from 0 to 30 dm (mean = 3.15, SD = 2.70), live grass ranged from 0% to 100% cover (mean = 25%, SD = 18%), live forbs ranged from 0% to 100% cover (mean = 19%, SD = 17%), bare ground ranged from 0% to 99% cover (mean = 32%, SD = 28%), and dead grass/litter ranged from 0% to 96% cover (mean = 19%, SD = 21%). In burn years, vegetation was shorter and dominated by live grass, forbs, and bare ground. Live grass cover was greatest in ungrazed watersheds, while dead grass cover was greatest following years of more precipitation (i.e., precipitation lagged 1 and 2 years). Annually burned, bison-grazed watersheds had the shortest vegetation and greatest forb cover (Appendix S1: Table S1).

In 2020, approximately 76% of Konza consisted of grassland, followed by shrubs (~12%), trees (~10%), and roads, rivers, or buildings (<1%). Across the entire site, the average distance to shrubs was 18 m (SD = 20, range = 0–191 m), and the average distance to trees was 45 m (SD = 44, range = 0–320). Slope ranged from 0 to 2.5 m rise per meter run (mean = 0.15, SD = 0.11).

The predictive accuracy of our vegetation height and composition models varied by management type, with the highest accuracy in bison-grazed units with a 2-year fire return interval and the lowest accuracy in the patch-burn grazed units (Appendix S1: Table S2). Our models were a good predictor of bare ground cover (MAE = 7%) and dead grass/litter cover (MAE = 14%), a satisfactory predictor of live grass cover (MAE = 26%) and vegetation height (MAE = 0.38 m), and a poor predictor of live forb cover (MAE = 45%).

The mean vegetation conditions and slopes within each bird species' selected territories differed from the means within "available" (i.e., pseudo-absence) territories (Table 1). However, Grasshopper Sparrows, Eastern Meadowlarks, and Dickcissels all selected territories with different vegetation characteristics from each other (Figures 2 and 3; Appendix S1: Table S3). Grasshopper Sparrows selected territories in areas with higher forb and dead grass cover than live grass and bare ground, while Dickcissels were more generalist, exhibiting positive relationships with live grass, live forbs, and dead grass (Figures 2 and 3; Appendix S1: Table S3). Eastern Meadowlarks did not exhibit a statistically significant relationship with any herbaceous cover type (Figures 2 and 3; Appendix S1: Table S3). In some ways, the three species' territory selection was alike; they all primarily occupied flatter areas with less than 6% shrub cover and less than 1% tree cover, while the average shrub cover in the "available" territories was 10% and the average tree cover was 9% (Table 1). There was also more bare ground in the "available" territories (mean = 34%) than in each of the species' territories (Grasshopper Sparrows: 16%; Eastern Meadowlarks: 12%; Dickcissels: 21%; Table 1). Some vegetation cover types produced very large beta coefficient and uncertainty estimates for Dickcissels and Eastern Meadowlarks (Figures 2 and 4). This is likely a product of "complete separation," in which a variable has minimal variation in its response, leading to perfect prediction. Complete separation frequently results from small sample sizes (Albert & Anderson, 1984).

In 2021, we observed 192 Grasshopper Sparrows which occupied 284 territories over the season. The integrated resource selection model performed well in terms of predicting where Grasshopper Sparrows would select territories; the average relative probability of a sparrow selecting territory calculated over all pixels in the study area in 2021 was 35% (SE = 30%). By contrast, the mean

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TABLE 1 Model-predicted averages for habitat variables in Grasshopper Sparrow territories ($n = 2057$; 2014–2020), Eastern Meadowlark territories ($n = 128$; 2019–2021), and Dickcissel territories ($n = 239$; 2019–2021) at the Konza Prairie Biological Station.

	Random territories		Grasshopper sparrows		Eastern meadowlarks		Dickcissels	
Covariate	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Slope (%)	16	8	9	6	8	5	10	6
Vegetation height (dm)	2.80	1.10	2.71	0.85	2.68	0.86	2.78	0.97
Live grass (%)	24%	11%	22%	9%	36%	10%	36%	10%
Live forbs (%)	16%	5%	16%	5%	22%	4%	23%	5%
Bare ground (%)	34%	15%	25%	12%	20%	9%	21%	10%
Dead grass and litter (%)	24%	17%	33%	18%	11%	5%	10%	4%
Proportion of shrubs (%)	10%	14%	3%	7%	3%	6%	6%	9%
Proportion of trees (%)	9%	23%	<1%	4%	<1%	<1%	<1%	<1%
Distance to shrubs (m)	16.98	16.60	27.24	17.29	32.59	18.99	23.37	19.13
Distance to trees (m)	47.98	41.31	75.52	43.78	92.21	48.12	76.92	48.12

estimated relative probability of territory selection at locations where we observed territories in 2021 was 93% (SE = 8%). The model exhibited high concordance (i.e., predictive accuracy) with observed territories (Brier score = 0.11), where a score of 0 indicates perfect accuracy and a score of 1 indicates perfect inaccuracy (Brier, 1950; Harrell et al., 1996).

Simulated woody plant removal

The amount of grassland bird habitat increased under each of the four woody vegetation removal scenarios we tested (Figure 5; Appendix S1: Table S4, Figures S2–S5). Simulated removal of an isolated shrub island increased the likelihood of Grasshopper Sparrow territory selection from 0.20 ha in the annually burned, ungrazed unit (K1B) to 0.76 ha in the patch-burn grazed unit (C3A/C3B/C3C). Simulated removal of one isolated tree increased the probability of territory selection from 2.12 ha in the patch-burn grazed unit (C3A/C3B/C3C) to up to 14.64 ha in the annually burned, ungrazed unit (K1B). Simulated removal of all shrubs in flat, high-elevation areas increased the probability of territory selection by 11.49 ha in the biennially burned, ungrazed unit (2D) to 97.76 ha in the patch-burn grazed unit (C3A/C3B/C3C). Simulated removal all trees in the flat, high elevation areas resulted in a 22.41 ha increase in the biennially burned, ungrazed unit (2D), where only about 0.02 upland hectares were encroached. In the patch-burn grazed unit (C3A/C3B/C3C), where approximately 1.01 ha of the uplands were encroached by trees, removing all trees in the flat, high-elevation areas resulted in improved habitat across 103.19 ha.

DISCUSSION

Grasshopper Sparrows, Eastern Meadowlarks, and Dickcissels made settlement decisions based on topography and vegetation structure, particularly woody plant cover. All three species primarily selected territories with less than 6% shrub cover and less than 1% tree cover, highlighting an immediate need to limit woody encroachment in the Central Great Plains. While all three species avoided woody vegetation, they each selected different herbaceous vegetation cover types. Therefore, mosaics of fire and grazing regimes that support heterogeneous vegetation and suppress woody encroachment will more likely support diverse communities of grassland birds. Furthermore, our integrated resource selection model combined multiple environmental datasets to predict grassland bird territory selection with remarkably high accuracy. Models such as the one presented in this study are powerful tools to leverage multiple datasets, assess species–habitat relationships, and simulate the potential impact of conservation initiatives for declining taxa (Linden et al., 2018; Royle et al., 2013).

Grasshopper Sparrows, Eastern Meadowlarks, and Dickcissels all tended to select territories in relatively flat areas. These findings contradict previous reports that Eastern Meadowlarks prefer slopes as opposed to tops of hills or flat valleys (Roseberry & Klimstra, 1970). Selection may vary geographically based on grazing intensity, as many flat areas can be intensively grazed leaving slopes with more preferable vegetation cover. Although our study investigated territory selection and not nest site selection, territory selection constrains nest selection, therefore territory characteristics correlate with nest site characteristics (e.g., Jones & Robertson, 2001;

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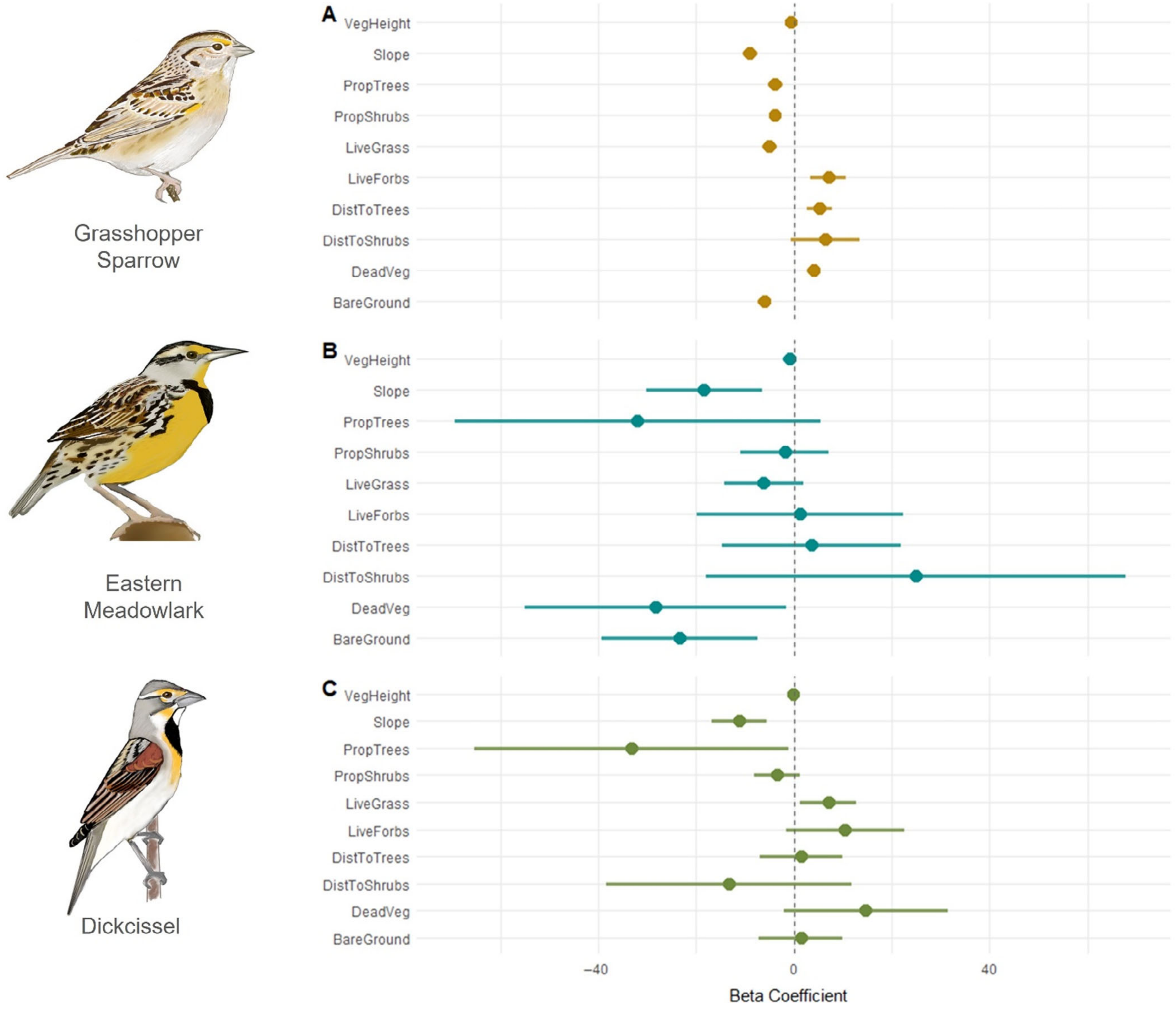

FIGURE 2 Resource selection coefficients for Grasshopper Sparrows (A; yellow; $n = 2057$; 2014–2020), Eastern Meadowlarks (B; blue; $n = 128$; 2019–2021), and Dickcissels (C; green; $n = 239$; 2019–2021) at the Konza Prairie Biological Station. Lines represent 95% confidence intervals around the resource selection coefficients. Species illustrations by Katy M. Silber.

Ruth & Skagen, 2017). Slopes may affect nest success through nest microclimate (Rauter et al., 2002) or risk of predation by providing more sunning spots for reptiles or crevices for mammal burrows. Grassland birds may also avoid steep areas for the same reason they avoid tall structures and trees; high perches may increase the risk of predation (Pitman et al., 2006). Finally, slope may indirectly impact territory selection via vegetation structure, as sloped and flat areas may have different plant biomass and community composition (Collins & Calabrese, 2012; Liu et al., 2019), including woody vegetation (Jones et al., 2023). Many shrub and tree patches in the Great Plains are more likely to occur on moderate or steep slopes (e.g., Kaskie et al., 2022). Because all three bird species avoided shrubs and trees, woody vegetation may underlie grassland birds' aversion to slopes.

Although Grasshopper Sparrows, Eastern Meadowlarks, and Dickcissels all breed in grasslands, they have different preferences for vegetation cover within their breeding territories. Grasshopper Sparrows selected territories composed primarily of dead grass and forbs, supporting previous studies noting higher abundance in grazed pastures with a 2–3 year fire return interval, but not during the year that pastures burn (Augustine & Derner, 2015; Powell, 2008). Nevertheless, relationships between territory selection and forb cover should be interpreted with caution because of the high degree of uncertainty in the underlying vegetation predictions.

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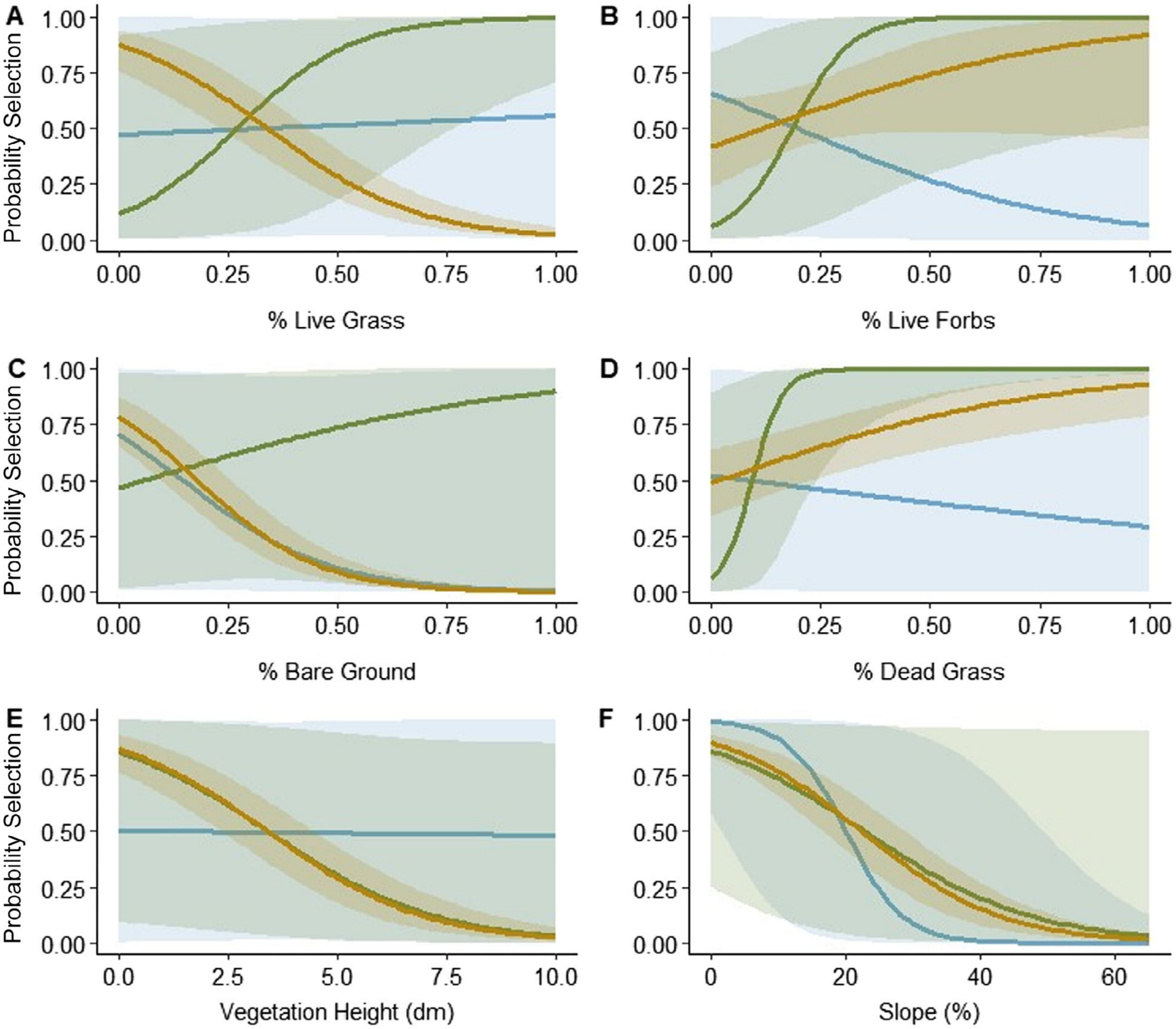

FIGURE 3 Relative probability of territory selection as a function of vegetation cover (A–D), vegetation height (E), and slope (F) for Grasshopper Sparrows (yellow; $n = 2057$; 2014–2020), Eastern Meadowlarks (blue; $n = 128$; 2019–2021) and Dickcissels (green; $n = 239$; 2019–2021) at the Konza Prairie Biological Station. Solid lines are model-predicted responses and shading indicates 95% confidence intervals.

Eastern Meadowlarks did not exhibit strong preferences for any one cover type except an aversion to areas with predominantly dead grass cover, supporting previous findings that they occupy both burned and unburned pastures (Powell, 2008). Dickcissels are considered grassland-facultative (Gross, 1968), and our findings support the conclusion that they are generalists when it comes to vegetation selection and preferred management (Powell, 2008; Verheijen et al., 2019). Although Dickcissels preferred areas with ample grass cover, they had no other strong associations with herbaceous vegetation cover. Unlike the sparrows and meadowlarks, they did not avoid territories near shrubs. The lack of strong preferences in herbaceous plant cover in Eastern Meadowlarks and Dickcissels may be a product of small sample sizes within statistical analyses (e.g., complete or quasicomplete separation; Albert & Anderson, 1984), uncertainty surrounding vegetation predictions, or these species' relatively large territories that may encompass a range of cover types. Further analyses of use within territories may yield stronger preferences. Alternatively, these results may indicate these species select territories based on landscape features other than herbaceous plant cover. Differences in territory selection among species likely reflect differences in life histories and nesting strategies, as Grasshopper Sparrows and Eastern Meadowlarks are ground-nesting birds that primarily construct nests from grasses (Roseberry & Klimstra, 1970; Wiens, 1969), whereas Dickcissels use a variety of nest construction materials, and sometimes place nests up to 126 cm above the ground in shrubs or small trees (Gross, 1968; Overmire, 1962). While each species had different

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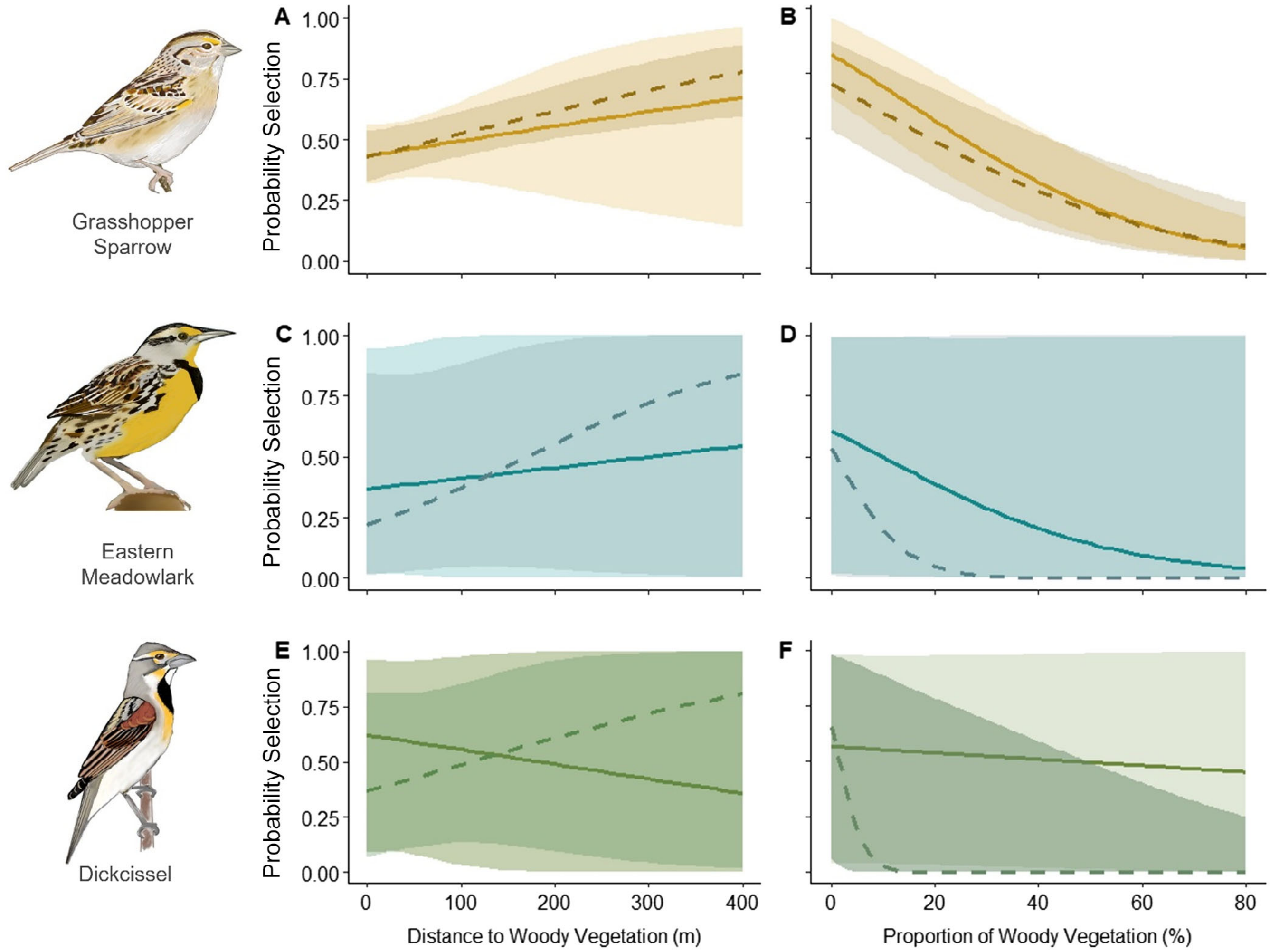

FIGURE 4 Relative probability of territory selection as a function of distance to shrubs (solid line) and trees (dashed line) for Grasshopper Sparrows (A) and proportion of shrubs (solid line) and trees (dashed line) for Grasshopper Sparrows (B) at the Konza Prairie Biological Station, 2014–2020. Relative probability of territory selection as a function of distance to shrubs (solid line) and trees (dashed line) for Eastern Meadowlarks (C) and proportion of shrubs (solid line) and trees (dashed line) for Eastern Meadowlarks (D), 2019–2021. Relative probability of territory selection as a function of distance to shrubs (solid line) and trees (dashed line) for Dickcissels (E) and proportion of shrubs (solid line) and trees (dashed line) for Dickcissels (F), 2019–2021. Species illustrations by Katy M. Silber.

preferences for cover types, the average vegetation height for all three species was ~25 cm, which was congruent with the average vegetation height within our study units. Given that some common grass species in tallgrass prairies can reach over 75 cm by July (Nippert et al., 2011), grazing is essential to keep vegetation at heights that are preferable for grassland birds throughout the breeding season.

Vegetation structure at our site, like grasslands elsewhere, is mediated not only by fire and grazing, but also via interactions with weather (Collins & Calabrese, 2012). In particular, grasslands are responsive to concurrent and lagged precipitation (Blair et al., 2014; Dudney et al., 2017). Interannual variation in grassland bird densities and site fidelity can largely be attributed to weather variability; for example, indirect relationships between precipitation, vegetation, and grassland birds manifest as variation in grassland bird survival and emigration due to the lagged effects of precipitation on dead grass and other aspects of vegetation structure (Silber et al., 2023). Thus, management in combination with delayed consequences of precipitation acting via vegetation structure ultimately regulates local abundances.

While agriculture and human development are the commonly cited drivers of grassland bird declines (Samson & Knopf, 1994; With et al., 2008), our results reinforce the importance of controlling woody encroachment to conserve grassland bird habitat. Woody vegetation is increasing across the Great Plains and in grasslands around the world (Archer, 1995; Briggs et al.,

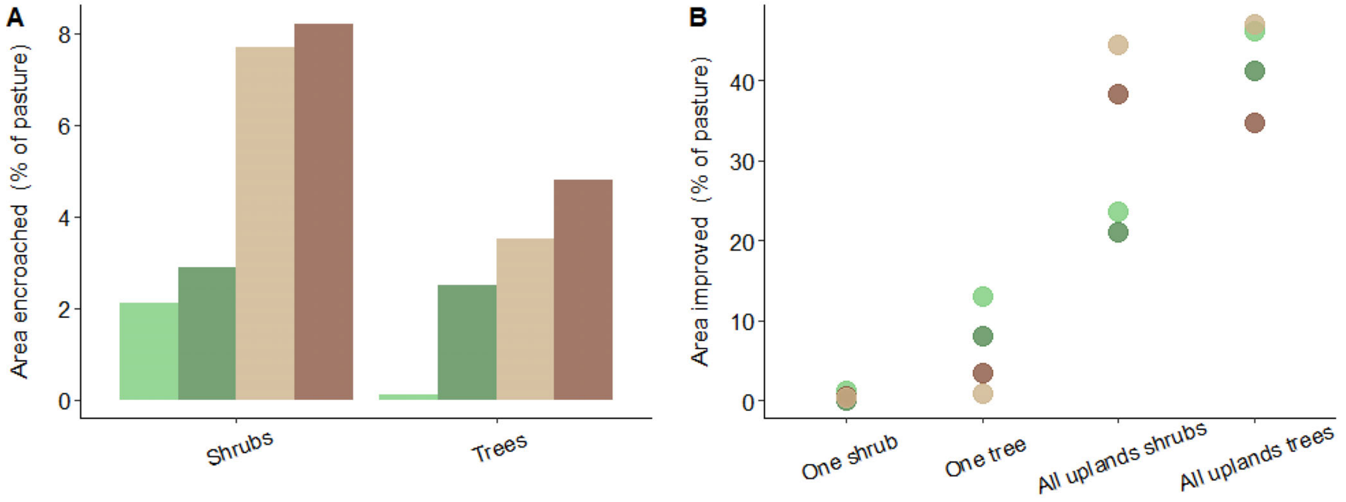

FIGURE 5 Shrub and tree encroachment (A) in a bison-grazed, 1-year fire return unit (N1B; 121 ha; brown bars), patch-burn grazed unit (C3A/C3B/C3C; 219 ha; tan bars), ungrazed, 1-year fire return unit (K1B; 180 ha; light green bars), and ungrazed, 2-year fire return unit (2D; 49 ha; dark green bars) at the Konza Prairie Biological Station in 2020. Grasshopper Sparrow habitat improvement under four simulated woody plant removal scenarios (B): removal of one shrub island, removal of one tree, removal of all shrubs in the uplands (areas with <10% slope and >400 m in elevation) and removal of all trees in upland areas. Dots indicate area within each unit that improved divided by the total unit area in a bison-grazed, 1-year fire return unit (N1B; brown dots), patch-burn grazed unit (C3A/C3B/C3C; tan dots), ungrazed, 1-year fire return unit (K1B; light green dots), and ungrazed, 2-year fire return unit (2D; dark green dots).

2005; Roques et al., 2001) with dire consequences for grassland-obligate birds (Coppedge et al., 2001). Variation in aversion to woody vegetation likely depends on species-specific behavior and natural history. In this work, the grassland-obligate species (Grasshopper Sparrows and Eastern Meadowlarks) nest on the ground and need herbaceous vegetation to form nest structures (Wiens, 1969), whereas Dickcissels build nests in vegetation above the ground and are more tolerant of shrubs, implicating nesting behavior in these differences. Regardless of nesting behavior, all three species declined as the proportion of trees and shrubs increased. This likely accounts for some of the staggering declines in grassland-obligate and grassland-facultative species. At our site, grass decreased by an astounding 29% between 2000 and 2013, primarily due to an increase in woody vegetation (Ratajczak et al., 2014). The mechanisms linking woody encroachment to grassland bird declines likely involve an increased risk of nest predation (Ellison et al., 2013; With, 1994) with concurrent lower nest survival (Graves et al., 2010), which explains avoidance behavior and lower fitness.

Fortunately, targeted removal of woody vegetation, especially in upland areas with isolated tree cover, has the potential for substantial and economically efficient conservation gains. As this study shows, multiple scenarios of woody vegetation removal increased grassland bird habitat. This supports the idea that effective grassland bird conservation defends "core" grassland areas by prioritizing removing isolated woody plants (Roberts et al., 2022). As grassland-to-tree edge densities increase, grassland bird abundances increase (e.g., Herse et al., 2018). However, in areas with severe woody encroachment, removing several woody plants was necessary to improve grassland bird habitat. These results suggest that conservation priorities for these bird species are (1) suppressing woody vegetation, (2) early detection of encroachment when shrubs and trees are more vulnerable to management interventions, and (3) when the first two strategies fail, targeted removal of shrubs and trees.

Frequent fires may limit the expansion of woody vegetation (Briggs et al., 2005) but are less successful in removing woody vegetation once it has become established (Collins et al., 2021). Extreme fire can sometimes reverse woody encroachment (Bielski et al., 2021; Twidwell et al., 2016) but may reduce grass abundance for years (Ratajczak et al., 2019). If woody encroachment is severe, a combination of fire, mechanical removal, and chemical removal will likely be necessary to suppress woody vegetation (Briggs et al., 2005). Fortunately, management that leads to suppression and removal of woody vegetation is a common interest for many stakeholders, given woody plants pose a threat to both conservation and ranching (Morford et al., 2022), paving the way for meaningful partnerships between ranchers and researchers.

While many North American birds have experienced steep declines since 1970, grassland birds are the most

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imperiled (Rosenberg et al., 2019). They inhabit largely human-dominated systems, privately owned land, and areas of intensive agriculture (Ahlering et al., 2019; White et al., 2000), and exhibit sharp declines in response to habitat loss, habitat degradation, and habitat fragmentation (Herkert, 1998; Stanton et al., 2018). Compared with most other remaining grassland taxa, such as insects and small mammals, grassland birds often require much larger areas. Furthermore, the losses are likely to continue given the common public perception of grasslands as "empty" and therefore available for exploitation. Understanding grassland bird habitat requirements will help us prioritize conservation initiatives, such as woody plant removal, to slow or reverse grassland bird declines. Restoration projects that prioritize grassland bird populations may ultimately benefit grassland organisms across multiple levels of ecological organization and the humans that depend on grassland landscapes.

AUTHOR CONTRIBUTIONS

KMS and WAB conceived the research question and hypotheses. WAB, TJH, and ZRR provided resources and funding. KMS, HNCM, and WAB contributed to data collection. KMS and TJH conceived the analyses. KMS and HNCM wrote the first draft of the manuscript. Species illustrations by KMS. All authors contributed to draft edits and approved the final version for submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (kmmsilber, 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.10426227.

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REFERENCES

Ahlering, M. A., D. H. Johnson, and L. H. Elliott. 2019. "Land Ownership and Use Influence Grassland Bird Abundance." *Journal of Wildlife Management* 83: 343–355.

Albert, A., and J. Anderson. 1984. "On the Existence of Maximum Likelihood Estimates in Logistic Regression Models." *Biometrika* 71: 1–10.

Archer, S. 1995. "Tree-Grass Dynamics in a Prosopis-Thornscrub Savanna Parkland: Reconstructing the Past and Predicting the Future." *Ecoscience* 2: 83–89.

Augustine, D. J., and J. D. Derner. 2015. "Patch-Burn Grazing Management, Vegetation Heterogeneity, and Avian Responses in a Semi-Arid Grassland." *Journal of Wildlife Management* 79: 927–936.

Bachle, S., and J. B. Nippert. 2022. "Climate Variability Supersedes Grazing to Determine the Anatomy and Physiology of a Dominant Grassland Species." *Oecologia* 198: 345–355.

Bakker, K. K. 2003. "The Effect of Woody Vegetation on Grassland Nesting Birds: An Annotated Bibliography." *Proceedings of the South Dakota Academy of Science* 82: 119–141.

Bielski, C., R. Scholtz, V. Donovan, C. Allen, and D. Twidwell. 2021. "Overcoming an 'Irreversible' Threshold: A 15-Year Fire Experiment." *Journal of Environmental Management* 291: 112550.

Blackmore, P. 2019. "GIS20 GIS Coverages Defining Konza Elevations. Environmental Data Initiative." *Environmental Data Initiative.* https://doi.org/10.6073/pasta/f11596621709ba6e4ac48e9f2e898a7a.

Blair, J., J. Nippert, and J. Briggs. 2014. "Grassland Ecology." In *Ecology and the Environment, The Plant Sciences*, Vol. 8, edited by R. Monson, 389–423. New York: Springer.

Brier, G. 1950. "Verification of Forecasts Expressed in Terms of Probability." *Monthly Weather Review* 75: 1–3.

Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. "An Ecosystem in Transition: Causes and Consequences of the Conversion of Mesic Grassland to Shrubland." *Bioscience* 55: 243–254.

Broderick, C. M., K. Wilkins, M. D. Smith, and J. M. Blair. 2022. "Climate Legacies Determine Grassland Responses to Future Rainfall Regimes." *Global Change Biology* 28: 2639–56.

Bruggeman, J. E., R. A. Garrott, P. J. White, F. G. R. Watson, and R. Wallen. 2007. "Covariates Affecting Spatial Variability in Bison Travel Behavior in Yellowstone National Park." *Ecological Applications* 17: 1411–23.

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Brunsell, N. A., J. M. Ham, and C. E. Owensby. 2008. "Assessing the Multi-Resolution Information Content of Remotely Sensed Variables and Elevation for Evapotranspiration in a Tall-Grass Prairie Environment." *Remote Sensing of Environment* 112: 2977–87.

Chapman, R. N., D. M. Engle, R. E. Masters, and D. M. Leslie. 2004. "Grassland Vegetation and Bird Communities in the Southern Great Plains of North America." *Agriculture, Ecosystems and Environment* 104: 577–585.

Collins, S. L., and L. B. Calabrese. 2012. "Effects of Fire, Grazing and Topographic Variation on Vegetation Structure in Tallgrass Prairie." *Journal of Vegetation Science* 23: 563–575.

Collins, S. L., J. B. Nippert, J. M. Blair, and J. M. Briggs. 2021. "Fire Frequency, State Change and Hysteresis in Tallgrass Prairie." *Ecology Letters* 24: 636–647. https://doi.org/10.1111/ele.13676.

Condon, L., and R. Maxwell. 2015. "Evaluating the Relationship between Topography and Groundwater Using Outputs from a Continental-Scale Integrated Hydrology Model." *Water Resources Research* 51: 6602–21.

Conover, R. R. 2009. "Grassland Bird Associations in a Managed Agricultural Matrix." PhD Dissertation, Iowa State University.

Coppedge, B. R., D. M. Engle, R. E. Masters, and M. S. Gregory. 2001. "Avian Response to Landscape Change in Fragmented Southern Great Plains Grasslands." *Ecological Applications* 11: 47–59.

Darenova, E., P. Holub, L. Krupkova, and M. Pavelka. 2017. "Effect of Repeated Spring Drought and Summer Heavy Rain on Managed Grassland Biomass Production and CO_2 Efflux." *Journal of Plant Ecology* 10: 476–485.

Dieni, J. S., and S. L. Jones. 2017. "Grassland Songbird Nest Site Selection Patterns in Northcentral Montana." *The Wilson Bulletin* 115: 388–396.

Duchardt, C. J., J. L. Beck, and D. J. Augustine. 2020. "Mountain Plover Habitat Selection and Nest Survival in Relation to Weather Variability and Spatial Attributes of Black-Tailed Prairie Dog Disturbance." *Condor* 122(1): 15.

Dudney, J., L. M. Hallett, L. Larios, E. C. Farrer, E. N. Spotswood, C. Stein, and K. N. Suding. 2017. "Lagging behind: Have we Overlooked Previous-Year Rainfall Effects in Annual Grasslands?" *Journal of Ecology* 105: 484–495.

Ellison, K. S., C. A. Ribic, D. W. Sample, M. J. Fawcett, and J. D. Dadisman. 2013. "Impacts of Tree Rows on Grassland Birds and Potential Nest Predators: A Removal Experiment." *PLoS One* 8: e59151.

Fithian, W., and T. Hastie. 2013. "Finite-Sample Equivalence in Statistical Models for Presence-Only Data." *The Annals of Applied Statistics* 7: 1917–39.

Francq, G. E. 1972. "Parental Care of the Eastern Meadowlark (*Sturnella magna*)." MSc Thesis, Kansas State Teachers College.

Fretwell, S. 1986. "Distribution and Abundance of the Dickcissel." *Current Ornithology* 4: 211–242.

Fuhlendorf, S. D., and D. M. Engle. 2004. "Application of the Fire-Grazing Interaction to Restore a Shifting Mosaic on Tallgrass Prairie." *Journal of Applied Ecology* 41: 604–614.

Gehrt, J. M., D. S. Sullins, and D. A. Haukos. 2020. "Looking at the Bigger Picture: How Abundance of Nesting and Brooding Habitat Influences Lek-Site Selection by Lesser Prairie-Chickens." *American Midland Naturalist* 183: 52–77.

Gotway, C. A., and L. J. Young. 2002. "Combining Incompatible Spatial Data." *Journal of the American Statistical Association* 97: 632–648.

Graves, B. M., A. D. Rodewald, and S. D. Hull. 2010. "Influence of Woody Vegetation on Grassland Birds within Reclaimed Surface Mines." *Wilson Journal Of Ornithology* 122: 646–654.

Gross, A. 1968. "Dickcissel." In *Life Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows and their Allies*, edited by O. L. Austin. Washington, D.C.: Smithsonian Institution Press.

Hansen, C. P., L. A. Schreiber, M. A. Rumble, J. L. Millspaugh, R. C. Gamo, J. W. Kehmeier, and N. Wojcik. 2016. "Microsite Selection and Survival of Greater Sage-Grouse Nests in South-Central Wyoming." *Journal of Wildlife Management* 80: 862–876.

Harmeson, J. P. 1974. "Breeding Ecology of the Dickcissel." *Auk* 91: 348–359.

Harrell, F., K. L. Lee, and D. B. Mark. 1996. "Multivariable Prognostic Models: Issues in Developing Models, Evaluating Assumptions and Adequacy, and Measuring and Reducing Errors." *Statistics in Medicine* 15: 361–387.

Hefley, T. J., K. M. Broms, B. M. Brost, F. E. Buderman, S. L. Kay, H. R. Scharf, J. R. Tipton, P. J. Williams, and M. B. Hooten. 2017. "The Basis Function Approach for Modeling Autocorrelation in Ecological Data." *Ecology* 98: 632–646.

Herkert, J. R. 1998. "The Influence of the CRP on Grasshopper Sparrow Population Trends in the Mid-Continental United States." *Wildlife Society Bulletin* 26: 227–231.

Herkert, J. R. 2007. "Evidence for a Recent Henslow's Sparrow Population Increase in Illinois." *Journal of Wildlife Management* 71: 1229–33.

Herse, M. R., K. A. With, and W. A. Boyle. 2018. "The Importance of Core Habitat for a Threatened Species in Changing Landscapes." *Journal of Applied Ecology* 55: 2241–52.

Jones, J., and R. J. Robertson. 2001. "Territory and Nest-Site Selection of Cerulean Warblers in Eastern Ontario." *The Auk* 118: 727–735.

Jones, S. A., S. R. Archer, K. A. Hartfield, and S. E. Marsh. 2023. "Topoedaphic Constraints on Woody Plant Cover in a Semi-Arid Grassland." *Ecological Indicators* 151: 110226.

Kaskie, K. D., M. C. Wimberly, and P. J. Bauman. 2022. "Predictive Mapping of Low-Density Juniper Stands in Prairie Landscapes of the Northern Great Plains." *Rangeland Ecology and Management* 83: 81–90.

Kentie, R., C. Both, J. C. E. W. Hooijmeijer, and T. Piersma. 2014. "Age-Dependent Dispersal and Habitat Choice in Black-Tailed Godwits *Limosa limosa limosa* across a Mosaic of Traditional and Modern Grassland Habitats." *Journal of Avian Biology* 45: 396–405.

Kmmsilber. 2023. "Kmmsilber/IntegratedResourceSelection: The Long Shadow of Woody Encroachment: An Integrated Approach to Modeling Grassland Songbird Habitat (IntegratedResourceSelection)." Zenodo. https://doi.org/10.5281/zenodo.10426227.

Koczura, M., B. Martin, M. Bouchon, G. Turille, J. Berard, A. Farruggia, M. Kreuzer, and M. Coppa. 2019. "Grazing Behaviour of Dairy Cows on Biodiverse Mountain Pastures Is more Influenced by Slope than Cow Breed." *Animal* 13: 2594–2602.

19395582, 2024, 3, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2954 by Kansas State University, Wiley Online Library on [08/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Koerner, S. E., and S. L. Collins. 2013. “Small-Scale Patch Structure in North American and South African Grasslands Responds Differently to Fire and Grazing.” *Landscape Ecology* 28: 1293–1306.

Ladwig, L. M., Z. R. Ratajczak, T. W. Ocheltree, K. A. Hafich, A. C. Churchill, S. J. K. Frey, C. B. Fuss, et al. 2016. “Beyond Arctic and Alpine: The Influence of Winter Climate on Temperate Ecosystems.” *Ecology* 97: 372–382.

Larned, A. F., E. L. Hewett Ragheb, K. E. Miller, and B. Lohr. 2020. “Nest Microhabitat Influences Nest-Site Selection in Dry Prairie but Not in Pasture Habitat for the Endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*).” *Avian Conservation and Ecology* 15: 20.

Lautenbach, J. M., N. Stricker, M. Ervin, A. Hershner, R. Harris, and C. Smith. 2020. “Woody Vegetation Removal Benefits Grassland Birds on Reclaimed Surface Mines.” *Journal of Fish and Wildlife Management* 11: 89–98.

Linden, D., A. Siren, and P. Pekins. 2018. “Integrating Telemetry Data into Spatial Capture Recapture Modifies Inferences on Multi-Scale Resource Selection.” *Ecosphere* 9: e02203.

Liu, J., L. Qiu, J. Chen, B. Zheng, X. Wei, H. Gao, Y. Zhang, and J. Cheng. 2019. “Responses of Plant Biomass and Nutrients to Fire Vary with Functional Group and Slope Aspect in a Semi-arid Restored Grassland on the Loess Plateau.” *Journal of Arid Environments* 171: 104008.

Matthiopoulos, J., J. Fieberg, and A. Geert. 2020. “Species-Habitat Associations: Spatial Data, Predictive Models, and Ecological Insights.” https://bookdown.org/jfieberg/SHABook/chapter1.html.

McMillan, N. A., S. D. Fuhlendorf, B. Luttbeg, L. E. Goodman, C. A. Davis, B. W. Allred, and R. G. Hamilton. 2021. “Are Bison Movements Dependent on Season and Time of Day? Investigating Movement across Two Complex Grasslands.” *Ecosphere* 12: e03317.

McNew, L. B., A. J. Gregory, and B. K. Sandercock. 2013. “Spatial Heterogeneity in Habitat Selection: Nest Site Selection by Greater Prairie-Chickens.” *Journal of Wildlife Management* 77: 791–801.

Morford, S. L., B. W. Allred, D. Twidwell, M. O. Jones, J. D. Maestas, C. P. Roberts, and D. E. Naugle. 2022. “Herbaceous Production Lost to Tree Encroachment in United States Rangelands.” *Journal of Applied Ecology* 59: 2971–82.

Nippert, J. B., T. W. Ocheltree, A. M. Skibbe, L. C. Kangas, J. M. Ham, K. B. S. Arnold, and N. A. Brunsell. 2011. “Linking Plant Growth Responses across Topographic Gradients in Tallgrass Prairie.” *Oecologia* 166: 1131–42.

Noble, B. 2023. “Early Detection of Wildfire Risk in the Great Plains: Merging Machine Learning, Landscape Metrics, and Rich Data Sources.” MSc Thesis, Kansas State University.

Overmire, T. 1962. “Nesting of the Dickcissel in Oklahoma.” *Auk* 79: 115–16.

Pacifici, K., B. J. Reich, D. A. W. Miller, and B. S. Pease. 2019. “Resolving Misaligned Spatial Data with Integrated Species Distribution Models.” *Ecology* 10: 1–15.

Pearce, J., and M. Boyce. 2006. “Modelling Distribution and Abundance with Presence-Only Data.” *Journal of Applied Ecology* 43: 405–412.

Pitman, J. C., C. A. Hagen, B. E. Jamison, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2006. “Survival of Juvenile Lesser Prairie-Chickens in Kansas.” *Wildlife Society Bulletin (1973-2006)* 34(3): 675–681. http://www.jstor.org/stable/3784695.

Powell, A. 2008. “Responses of Breeding Birds in Tallgrass Prairie to Fire and Cattle Grazing.” *Journal of Field Ornithology* 79: 41–52.

Powell, A., and W. Busby. 2013. “Effects of Grassland Management on Breeding Birds at the Western Edge of the Tallgrass Prairie Ecosystem in Kansas Effects of Grassland Management on Breeding Birds at the Western Edge of the Tallgrass Prairie Ecosystem in Kansas.” *Natural Areas Journal* 33: 130–38.

Rader, M. J., L. A. Brennan, F. Hernandez, N. J. Silvy, and B. Wu. 2007. “Nest-Site Selection and Nest Survival of Northern Bobwhite in Southern Texas.” *Wilson Journal Of Ornithology* 119: 392–99.

Ratajczak, Z., A. C. Churchill, L. M. Ladwig, J. H. Taylor, and S. L. Collins. 2019. “The Combined Effects of an Extreme Heatwave and Wildfire on Tallgrass Prairie Vegetation.” *Journal of Vegetation Science* 30: 687–697.

Ratajczak, Z., J. B. Nippert, and T. W. Ocheltree. 2014. “Abrupt Transition of Mesic Grassland to Shrubland: Evidence for Thresholds, Alternative Attractors, and Regime Shifts.” *Ecology* 95: 2633–45.

Rauter, C. M., H. U. Reyer, and K. Bollmann. 2002. “Selection through Predation, Snowfall and Microclimate on Nest-Site Preferences in the Water Pipit *Anthus spinoletta*.” *Ibis* 144: 433–444.

Renfrew, R. B., and C. A. Ribic. 2002. “Influence of Topography on Density of Grassland Passerines in Pastures.” *American Midland Naturalist* 147: 315–325.

Road to Recovery. 2022. “The Road to Recovery Species Urgency List.” https://r2rbirds.org/resources/.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. “Relationships between Visual Obstruction Measurements and Weight of Grassland Vegetation.” *Journal of Range Management* 23: 295–97.

Roberts, C. P., D. R. Uden, S. M. Cady, B. Allred, S. Fuhlendorf, M. O. Jones, J. D. Maestas, et al. 2022. “Tracking Spatial Regimes as an Early Warning for a Species of Conservation Concern.” *Ecological Applications* 32: 1–10.

Roques, K. G., T. G. O’Connor, and A. R. Watkinson. 2001. “Dynamics of Shrub Encroachment in an African Savanna: Relative Influences of Fire, Herbivory, Rainfall and Density Dependence.” *Journal of Applied Ecology* 38: 268–280.

Roseberry, J., and W. Klimstra. 1970. “The Nesting Ecology and Reproductive Performance of the Eastern Meadowlark.” *The Wilson Bulletin* 82: 243–267.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, et al. 2019. “Decline of the North American Avifauna.” *Science* 366: 120–24.

Royle, J. A., R. B. Chandler, C. C. Sun, and A. K. Fuller. 2013. “Integrating Resource Selection Information with Spatial Capture–Recapture.” *Methods in Ecology and Evolution* 4: 520–530.

Ruth, J. M., and S. K. Skagen. 2017. “Territory and Nest Site Selection Patterns by Grasshopper Sparrows in Southeastern Arizona.” *Condor* 119: 469–483.

Samson, F., and F. Knopf. 1994. “Prairie Conservation in North America.” *Bioscience* 44: 418–421.

Schartz, R. L., and J. L. Zimmerman. 1971. “The Time and Energy Budget of the Male Dickcissel (*Spiza americana*).” *The Condor* 73: 65–76.

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Sherry, R. A., E. Weng, J. A. Arnone, D. W. Johnson, D. S. Schimel, P. S. Verburg, L. L. Wallace, and Y. Luo. 2008. “Lagged Effects of Experimental Warming and Doubled Precipitation on Annual and Seasonal Aboveground Biomass Production in a Tallgrass Prairie.” *Global Change Biology* 14: 2923–36.

Silber, K. M., N. M. Mohankumar, T. J. Hefley, and W. A. Boyle. 2023. “Emigration and Survival Correlate with Different Precipitation Metrics throughout a Grassland songbird’s Annual Cycle.” *Journal of Wildlife Management* 87: 1–17.

Stanton, R. L., C. A. Morrissey, and R. G. Clark. 2018. “Analysis of Trends and Agricultural Drivers of Farmland Bird Declines in North America: A Review.” *Agriculture, Ecosystems and Environment* 254: 244–254.

Tenhumberg, B., E. E. Crone, S. Ramula, and A. J. Tyre. 2018. “Time-Lagged Effects of Weather on Plant Demography: Drought and *Astragalus scaphoides*.” *Ecology* 99: 915–925.

Twidwell, D., W. E. Rogers, C. L. Wonkka, C. A. Taylor, Jr., and U. P. Kreuter. 2016. “Extreme Prescribed Fire during Drought Reduces Survival and Density of Woody Resprouters.” *Journal of Applied Ecology* 53: 1585–96.

Verheijen, B. H. F., H. L. Clipp, A. J. Bartolo, W. E. Jensen, and B. K. Sandercock. 2019. “Effects of Patch-Burn Grazing on Breeding Density and Territory Size of Dickcissels.” *Avian Conservation and Ecology* 14(1). https://doi.org/10.5751/ACE-01343-140107.

Verheijen, B. H. F., A. N. Erickson, W. A. Boyle, K. S. Leveritte, J. L. Sojka, L. A. Spahr, E. J. Williams, S. K. Winnicki, and B. K. Sandercock. 2022. “Predation, Parasitism, and Drought Counteract the Benefits of Patch-Burn Grazing for the Reproductive Success of Grassland Songbirds.” *Ornithological Applications* 124: 1–22.

Verheijen, B. H. F., R. T. Plumb, C. K. J. Gulick, C. A. Hagen, S. G. Robinson, D. S. Sullins, and D. A. Haukos. 2021. “Breeding Season Space Use by Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) Varies among Ecoregions and Breeding Stages.” *American Midland Naturalist* 185: 149–174.

Vickery, P. D. 2021. “Grasshopper Sparrow (*Ammodramus savannarum*), Version 1.0.” In Birds of the World. https://birdsoftheworld.org/bow/species/graspa/cur/introduction.

Wagle, P., P. H. Gowda, B. K. Northup, P. J. Starks, and J. P. S. Neel. 2019. “Response of Tallgrass Prairie to Management in the U.S. Southern Great Plains: Site Descriptions, Management Practices, and Eddy Covariance Instrumentation for a Long-Term Experiment.” *Remote Sensing* 11: 1–18.

White, R. P., S. Murray, and M. Rohweder. 2000. *Pilot Analysis of Global Ecosystems: Grassland Ecosystems*. Washington: World Resources Institute.

Wiens, J. A. 1969. “An Approach to the Study of Ecological Relationships among Grassland Birds.” *Ornithological Monographs* 8: 1–93.

Williams, E. J., and W. A. Boyle. 2018. “Patterns and Correlates of within-Season Breeding Dispersal: A Common Strategy in a Declining Grassland Songbird.” *Auk* 135: 1–14.

Winnicki, S. K., S. M. Munguía, E. J. Williams, and W. A. Boyle. 2020. “Social Interactions Do Not Drive Territory Aggregation in a Grassland Songbird.” *Ecology* 101: e02927.

With, K. A. 1994. “The Hazards of Nesting near Shrubs for a Grassland Bird, the McCown’s Longspur.” *Condor* 96: 1009–19.

With, K. A., A. W. King, and W. E. Jensen. 2008. “Remaining Large Grasslands May Not be Sufficient to Prevent Grassland Bird Declines.” *Biological Conservation* 141: 3152–67.

Wood, S. 2017. *Generalized Additive Models: An Introduction with R, Second Edition*. Boca Raton: Chapman and Hall/CRC Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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