RESEARCH ARTICLE

A multiscale assessment of tree avoidance by prairie birds

Sarah J. Thompson,[1]***, Todd W. Arnold,**[1] **and Courtney L. Amundson**[2]

[1] Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, Saint Paul, Minnesota, USA
[2] U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska, USA
* Corresponding author: thom1253@umn.edu

ABSTRACT

In North America, grassland bird abundances have declined, likely as a result of loss and degradation of prairie habitat. Given the expense and limited opportunity to procure new grasslands, managers are increasingly focusing on ways to improve existing habitat for grassland birds, using techniques such as tree removal. To examine the potential for tree removal to benefit grassland birds, we conducted 446 point counts on 35 grassland habitat patches in the highly fragmented landscape of west-central Minnesota during 2009–2011. We modeled density of four grassland bird species in relation to habitat composition at multiple scales, focusing on covariates that described grass, woody vegetation (trees and large shrubs), or combinations of grass and woody vegetation. The best-supported models for all four grassland bird species incorporated variables measured at multiple scales, including local features such as grass height, litter depth, and local tree abundance, as well as landscape-level measures of grass and tree cover. Savannah Sparrows (*Passerculus sandwichensis*), Sedge Wrens (*Cistothorus platensis*), and Bobolinks (*Dolichonyx oryzivorus*) responded consistently and negatively to woody vegetation, but response to litter depth, grass height, and grassland extent were mixed among species. Our results suggest that reducing shrub and tree cover is more likely to increase the density of grassland birds than are attempts to improve grass quality or quantity. In particular, tree removal is more likely to increase density of Savannah Sparrows and Sedge Wrens than any reasonable changes in grass quality or quantity. Yet tree removal may not result in increased abundance of grassland birds if habitat composition is not considered at multiple scales. Managers will need to either manage at large scales (80–300 ha) or focus their efforts on removing trees in landscapes that contain some grasslands but few nearby wooded areas.

Keywords: Bobolink, Clay-colored Sparrow, fragmentation, grassland birds, N-mixture model, Savannah Sparrow, Sedge Wren, woody vegetation

Evaluación a múltiples escalas de la elusión de árboles por parte de las aves de pastizal de América del Norte

RESUMEN

En América del Norte, las abundancias de las aves de pastizal han declinado, probablemente como resultado de la pérdida y degradación de los ambientes de pradera. Debido al costo y a las limitadas oportunidades de procurar nuevos pastizales, los gestores se enfocan cada vez más en modos de mejorar los ambientes existentes para las aves de pastizal usando técnicas como la remoción de árboles. Para examinar el potencial beneficio que tiene la remoción de árboles para las aves de pastizal, realizamos 446 puntos de conteo en 35 parches de ambiente de pastizal en el paisaje altamente fragmentado del centro oeste de Minnesota durante 2009–2011. Modelamos la densidad de cuatro especies de aves de pastizal en relación con la composición del hábitat a múltiples escalas, enfocándonos en covariables que describiesen el pastizal, la vegetación leñosa (árboles y arbustos grandes), o combinaciones de pastizal y vegetación leñosa. El modelo con mayor soporte para las cuatro especies de aves de pastizal incorporó variables medidas a múltiples escalas, incluyendo rasgos locales como altura del pasto, profundidad de la hojarasca y abundancia local de árboles, así como también medidas a escala de paisaje de cobertura de pastos y árboles. *Passerculus sandwichensis*, *Cistothorus platensis* y *Dolichonyx oryzivorus* respondieron consistente y negativamente a la vegetación leñosa, pero la respuesta a la profundidad de la hojarasca, la altura del pasto y la extensión del pastizal fue diferente entre las especies. Nuestros resultados sugieren que la reducción de la cobertura de arbustos y árboles tiene más probabilidades de aumentar la densidad de las aves de pastizal que los intentos de mejorar la calidad o cantidad del pasto. En particular, la remoción de árboles tiene más probabilidades de aumentar la densidad de *P. sandwichensis* y *C. platensis* que cualquier modificación razonable en la calidad o cantidad del pasto. A pesar de esto, la remoción de árboles puede no incrementar la abundancia de las aves de pastizal si no se considera la composición del hábitat a múltiples escalas. Los gestores necesitarán realizar manejo ya sea a grandes escalas (80–300 ha) o enfocar sus esfuerzos en la remoción de árboles en paisajes que contengan algo de pastizal, pero pocas áreas arboladas vecinas.

INTRODUCTION

Population declines of North American grassland birds are likely driven by extensive loss of grassland habitat (Igl and Johnson 1997, Sauer et al. 2011). Additionally, many remnant and restored prairies across North America are small and isolated, lack fire or grazing disturbances, and are under pressure from invasive species and encroaching woody vegetation (Samson and Knopf 1994). As rural landscapes come under increasing pressure to produce food and energy, grassland management and conservation will need to become more strategic (Fargione et al. 2009). Conservation efforts will need to focus on optimization of available habitat as opportunities to protect or restore additional lands become increasingly scarce (Secchi and Babcock 2007).

Trees have been widely planted in grasslands to reduce soil erosion in agricultural regions or to protect homes and communities from wind and weather (Tibke 1988). Additionally, humans have planted trees and shrubs on conservation lands to provide shelter for desired game species such as white-tailed deer (*Odocoileus virginianus*) and Ring-necked Pheasant (*Phasianus colchicus*; Martin 1980, Yahner 1983, Kelsey et al. 2006). The presence of woody vegetation on grasslands can reduce the diversity of native grassland plants, reduce forage quality, alter hydrologic processes, alter predator communities, and reduce grassland carbon sequestration capacity (Grover and Musick 1990, Archer et al. 2001, Jackson et al. 2002, Huxman et al. 2005, Renfrew and Ribic 2008, Ellison et al. 2013). Once trees and shrubs become established, treatments such as fire or grazing are unlikely to reverse the progression of woody vegetation. Therefore, maintaining treeless grasslands generally requires intentional, mechanical tree removal (Briggs et al. 2005). Mechanical removal of established tree groves is expensive and disruptive, often requiring many years and subsequent treatments to successfully eradicate the woody vegetation and regrowth (Quamen 2007, Ellison et al. 2013). Control and removal of lone trees and shrubs is less costly and disruptive but requires consistent vigilance and effort to prevent recolonization (S. Vacek, U.S. Fish and Wildlife Service, personal communication).

Grassland bird species have varying preferences or sensitivity to grass type or grassland extent, but avoidance of woody vegetation is relatively consistent for most species and landscapes (Bakker 2003). Thogmartin et al. (2006) found that forest cover was negatively associated with abundance of several grassland bird species at multiple scales from 800 to 80,000 ha, and in the case of the Grasshopper Sparrow (*Ammodramus savannarum*) measures of forest cover were more important predictors of abundance than measures of grass cover. For 9 of 10 species of grassland birds in North Dakota, Grant et al. (2004) found that percent woody cover within 500 m of a survey point was the strongest predictor of occurrence. Renfrew and Ribic (2008) noted that abundance of Savannah Sparrow and Bobolink was less sensitive to patch size when tree cover in the area (1,200-m buffer) was low, but as tree cover increased, both species sought larger core grassland areas. Conversely, different grassland bird species have different preferences for vegetation structure (e.g., grass height and litter depth) and, therefore, management directed at these elements is unlikely to be beneficial for overall grassland bird abundance or diversity (Sample and Mossman 1997). Thus, tree removal has become a preferred method to improve habitat quality for grassland birds on degraded grasslands (U.S. Fish and Wildlife Service 2003); however, few studies have examined the strength and scale of tree avoidance with the explicit goal of informing management decisions.

Our primary objective was to examine patterns of grassland bird density, with a focus on how density varies in response to woody vegetation. We also wanted to compare the relative strength of tree avoidance versus other habitat preferences, and to identify the scale(s) at which these relationships were strongest. Our ultimate goal was to provide information to managers interested in planning targeted tree removal that would be most likely to benefit grassland birds. For example, if grassland birds avoid trees at landscape scales, then tree removal in small grassland patches may not affect grassland birds' habitat use because woodlots or shelterbelts remain on nearby private lands. Conversely, if grassland birds preferentially select habitat primarily on the basis of local fine-scale habitat features (e.g., avoiding single trees, selecting for grass height or litter depth), then predictions about habitat preferences based on landscape-level data (e.g., National Land Cover Database, Fry et al. 2011) may be less valuable than on-site assessments of vegetation composition.

METHODS

Study Area

We conducted point counts on grasslands owned and managed by the U.S. Fish and Wildlife Service in west-central Minnesota, USA. The study area was located in an ecological transition zone between tallgrass prairie to the west and eastern deciduous forest to the east (Ricketts et al. 1999) and, thus, provided an excellent location for

studying gradients of woody vegetation. The landscape surrounding study sites was predominantly row-crop agriculture, including corn and soybeans (60%), spring wheat (5%), pasture and hay (4%), and other row crops (3%). The remainder of the landscape was composed of wetlands and restored grasslands (16%), woody vegetation (2%), and developed areas (10%) (Fry et al. 2011).

Exotic grass and forb species such as smooth brome (*Bromus inermis*), sweetclover (*Melilotus* spp.), and alfalfa (*Medicago sativa*) dominated some study sites, whereas others had been restored using native warm-season grasses such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and numerous native forbs. Common tree species in the region included native trees that are often considered invasive, such as eastern redcedar (*Juniperus virginiana*), boxelder (*Acer negundo*), and less invasive native species such as green ash (*Fraxinus pennsylvanica*) and eastern cottonwood (*Populus deltoides*). Common shrubs included native wild plum (*Prunus americana*) and sandbar willow (*Salix interior*), as well as invasive Russian olive (*Elaeagnus angustifolia*) and common buckthorn (*Rhamnus cathartica*). Land managers used a combination of prescribed fire, herbicide, and mechanical removal to control trees and shrubs (U.S. Fish and Wildlife Service 2003).

Site and Survey Point Selection

We selected study sites with >20 ha of grassland that maximized variation in woody vegetation in four counties in west-central Minnesota. To generate point-count locations, we used ArcMap version 9.0 (ESRI, Redlands, California, USA) to randomly place points within study sites such that they were ≥200 m apart and not located within a wetland or woodlot. Because woodlots and scattered trees made up a small percentage of the landscape (2%), we purposefully added additional point-count locations near trees when randomly placed points did not adequately sample these areas.

Point-Count Surveys

At each location, we conducted a 5-min point count, recording all birds detected by sight or sound within 100 m (Hutto et al. 1986). We conducted bird surveys from May 30 to June 30, 2009–2011, during morning hours (0459–1215 hours; only 5% of surveys took place after 1030 hours), on days with winds <40 km h^{-1} and without precipitation (Ralph et al. 1995). The survey crew consisted of four individuals: two in 2009, one in 2010, and one in 2011. Surveyors were instructed to avoid double counting a bird within a survey and to exclude birds that were only observed flying overhead (e.g., swallows). We divided surveys into two distance bins (0–50 m and 51–100 m) and assigned each bird to a distance bin based on initial detection location (Buckland et al. 2001). Before beginning

surveys, observers used laser rangefinders to determine distances to reference objects (e.g., shrubs, grass clumps, rocks) to assist in accurately determining distances to birds. When possible, rangefinders were also used to measure distances to birds during the survey.

Vegetation Surveys

Vegetation surveys were limited to habitat measurements consistently found to be important in previous studies of grassland-bird habitat selection (Fisher and Davis 2010). We assessed vegetation characteristics at the center of each point-count circle, 25 m north of center, and 25 m south of the center. We measured litter depth to the nearest 0.5 cm (Smith et al. 1995) and measured grass height and density (i.e. visual obstruction readings [VOR]) to the nearest 0.5 dm (Robel et al. 1970). We used the mean of the three litter and three VOR measurements to generate a single mean litter and VOR value for each point-count location. Observers also conducted a tree and shrub survey at each point-count location. We defined shrubs as perennial woody vegetation 1–4 m in height (generally extending above the mean height of grass) and trees as perennial woody vegetation >4 m in height (Thompson et al. 2012). Observers counted all shrubs within 50 m and all trees within 100 m of the point-count location. Because of their smaller size and tendency to be found in greater numbers, we truncated shrub counts at 50 m. When visual barriers (woody vegetation, topography) made counting difficult, the observer would walk through the survey area, counting woody vegetation and getting better height estimates as necessary.

Landscape Analysis

We digitized study sites and surrounding regions manually with ArcMap using aerial imagery from the first year that a site was surveyed. For sites that we surveyed in >1 yr, we examined aerial images annually, but we found little change in land cover type and therefore utilized a single digitized layer for all years. We categorized land cover as perennial grass (i.e. grassland, pasture, hay fields, and ditches), wetland (vegetated wetland and open water), woody vegetation (woodlots, shelterbelts, and large individual trees), crop, or other (farms, roads, and gravel pits). We used this data layer to generate percent cover statistics for the 100-m-radius count circle and areas within 500 m and 1000 m of the count center (i.e. 3.14, 78.5, and 314 ha, respectively). Most grassland bird studies have utilized similar radii or areas; the smallest areas generally describe vegetation within the point-count circle, and larger areas span from radii of 500 m (Grant et al. 2004), 1,000 m (Fletcher and Koford 2002), 1,200 m (Renfrew and Ribic 2008), to as large as 1,600 m (Bakker et al. 2002, Cunningham and Johnson 2006). To reduce issues of multicollinearity, we only considered proportion grass and

tree and did not include crop, wetland, or other features in any models, and we did not combine the 500-m and 1,000-m scales in any single model (reviewed in Graham 2003).

Statistical Analysis

We employed the hierarchical multinomial-Poisson and multinomial-negative binomial mixture models of Royle (2004) and Chandler et al. (2011) as implemented in program R (R Foundation for Statistical Computing, Vienna, Austria) with package Unmarked (i.e. modules distsamp and gdistsamp; Fiske and Chandler 2011). This model framework allowed us to account for variables that affected detection rates and concurrently consider covariates that influenced abundance or density (Royle et al. 2004). We used the closed-population formulation of both models, which assumed that birds did not move into or out of the survey area during the 5-min interval (Buckland et al. 2001).

Spatial autocorrelation was an issue with our study design and is a common issue in point-count studies (Thogmartin et al. 2004; see review by Dormann et al. 2007). Spatial clustering of survey points and repeated visits can lead to lack of independence of counts within sites. The Unmarked package does not accommodate random effects; however, independence of surveys is assumed to be achieved if the same birds are not counted from multiple survey points. Moreover, nonindependence should be revealed by lack-of-fit, and so standard methods for evaluating fit (e.g., parametric bootstrapping) should be useful for assessment of the independence assumption (Royle et al. 2004; J. A. Royle, U.S. Geological Survey, personal communication). Additionally, the negative binomial distribution accounts for some forms of spatial autocorrelation by including an overdispersion term (White and Bennetts 1996).

We truncated outliers and standardized all continuous covariates prior to analysis to facilitate model convergence and reduce bias in parameter estimates (Zuur et al. 2010, Chandler 2014). To identify outliers, we examined histograms of predictor variables; we truncated litter depth at 15 cm (3 measurements), tree and shrub counts at 45 (10 measurements each), and VOR at 8 dm (1 measurement). We imputed missing data for litter depth ($n = 3$) and VOR ($n = 4$) using standardized mean covariate values of zero. Proportion grassland within 500 m was strongly correlated with proportion grassland at 1,000 m ($R^2 = 0.77$), as were proportions of trees at 500 and 1,000 m ($R^2 = 0.68$); thus, we did not combine these two spatial scales (500 and 1,000 m) in any single model. We noted moderate correlations between variables at 100 and 500 m ($R^2 = 0.45$ for grass and $R^2 = 0.33$ for tree), but did not restrict these variables from co-occurring in models. Because primary observers ($n = 4$) differed among years, year and observer

effects were confounded and included together in what we hereafter refer to as "year effects."

Model Selection

We began by examining detection functions for each species. We used the half-normal detection function for all species because preliminary assessments showed that it provided the best fit of all available options in Unmarked (i.e. half-normal, hazard-rate, uniform, or exponential). We then selected detection covariates for each species. We hypothesized that wind (WIND; Beaufort class 1–7), year (YEAR; $n = 3$), Julian date (DATE; May 28 = 1), cloud cover (SKY; percent of sky that was cloudy), and time of day (TIME; 0500–1230 hours) had the greatest potential to influence detection of birds (Table 1). We were concerned that detection rate could be negatively affected by the presence of woody vegetation because woodlots and trees contain a novel community of birds that may distract observers or block visual detections. Thus, we included the proportion of trees within 100 m (PTREE100) as a potential detection covariate. To avoid spurious conclusions about factors influencing detection probability, we used a moderately parameterized density model while we assessed support for detection covariates (Survey + Landscape; Barker et al. 2005; Table 2). We considered a set of models that included every potential one- or two-covariate combination of detection covariates. We then selected the detection model resulting in the lowest AIC value for each species as the basis for comparing a priori habitat models (Burnham and Anderson 2002). With only two distance bins in our dataset, we believed that one- or two-covariate detection models adequately accounted for variation in detection without overfitting models (Giudice et al. 2012).

After assessing detection covariates, we examined whether the Poisson or negative binomial distribution provided a better model fit for density as determined by lowest AIC value (Royle et al. 2004, Chandler et al. 2011). Also, before proceeding to selection of a priori density models, we examined overall model fit for each species using a parametric bootstrap technique (White et al. 2001). We simulated data (200 iterations) using a highly parameterized density model (Full; Table 2) and then refit the model to the simulated data. This generated a sampling distribution of chi-square statistics that could be compared to the chi-square value from the original model (Fiske and Chandler 2011). We assumed adequate model fit when tests comparing these statistics resulted in a P value >0.05.

We considered seven a priori models to describe potential preference for grass and/or avoidance of woody vegetation (Burnham and Anderson 2002; Table 2). We limited our model set to these seven models (1) to avoid redundant models resulting from collinearity, (2) to create a straightforward message for managers by avoiding

TABLE 1. Variables used to model detection and density for four species of grassland songbirds. We conducted point-count surveys ($n = 446$) from 2009–2011 in west-central Minnesota. Variables VOR through PTREE1000 affected habitat selection and therefore influenced bird density, and variables DATE through TIME potentially influenced detection rates of birds. Columns labeled 10th, 50th, and 90th represent percentiles.

Covariate	Description	Min.	10th	50th	Mean	90th	Max.
VOR	Visual obstruction reading (dm)	0	1.2	2.4	2.5	3.8	15.7
LITTER	Litter depth (cm)	0	1.9	5.2	5.4	9	36.3
SUMSHRUB	Count of shrubs within 50 m	0	0	0	4.3	15	104
SUMTREE	Count of trees within 100 m	0	0	0	4.7	13	70
PGRASS100	Proportion grass within 100 m	0.32	0.51	0.83	0.79	0.98	1.00
PGRASS500	Proportion grass within 500 m	0.16	0.25	0.44	0.45	0.65	0.93
PGRASS1000	Proportion grass within 1,000 m	0.08	0.16	0.27	0.30	0.48	0.67
PTREE100	Proportion tree cover within 100 m	0.00	0.00	0.00	0.02	0.07	0.39
PTREE500	Proportion tree cover within 500 m	0.00	0.00	0.02	0.03	0.07	0.12
PTREE1000	Proportion tree cover within 1,000 m	0.00	0.00	0.03	0.029	0.06	0.14
DATE [a]	Date (1 = May 29)	May 29	June 3	June 12	June 13	June 23	June 30
WIND	Beaufort wind speed	0	0	2		3	6
YEAR [a]	Year	$n = 3$	–	–	–	–	–
SKY	Percent cloud cover	0	0	50	50.8	100	100
TIME	Initiation time of survey	0459	0631	0757	0836	1013	1215

[a] In the case of Sedge Wrens, DATE and YEAR were also considered in models of density because of late arrival at breeding sites in 2011.

interactions and complex combinations of scales, and (3) because our model set allowed for nested comparisons (e.g., between scales, between tree- or grass-related covariates, or between single- and multiple-scale models). We focused on percent grass cover within concentric circles to avoid the issue of patch delineation. We hypothesized that suitable habitat (grass) and hostile habitat (trees) were the most important drivers of habitat use and focused on modeling these features exclusively. Preliminary examination of scatterplots and loess curves did not reveal any compelling evidence for nonlinear patterns (Zuur et al. 2010); thus, we did not consider quadratic or cubic terms.

We included the proportion of the point-count area (100-m radius) composed of grass (PGRASS100) in every model to account for survey areas that were not entirely composed of suitable habitat for grassland birds (e.g., open water or crop fields). We considered three models that examined support for three separate scales of habitat measurement that included grass and woody vegetation descriptors: Survey-point (100 m), Patch (500 m), and Landscape (1,000 m). Two additional models contained variables combining both grass and woody vegetation descriptors from more than one scale; Survey + Patch and Survey + Landscape (we omitted Patch + Landscape because of previously described collinearity between variables measured at these two scales). Finally, the last two models contained only grass or only tree-related variables (Grass only, Tree only) from two scales (Survey-point and Landscape). We ranked models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002).

TABLE 2. A priori model structures for comparing grassland songbird density in relation to habitat characteristics. We included percent grass at the 100-m scale as an offset in all models to account for point-count areas that were not entirely composed of grass. We used the full model to assess overall model fit, but this model was not considered in model selection procedures. See Table 1 for a description of covariates.

Model name	Covariate structure
Survey-point	VOR + LITTER + SUMSHRUB + SUMTREE + PTREE100
Patch	PGRASS500 + PTREE500
Landscape	PTREE1K + PGRASS1K
Survey + Patch	VOR + LITTER + SUMSHRUB + SUMTREE + PTREE100 + PGRASS500 + PTREE500
Survey + Landscape	VOR + LITTER + SUMSHRUB + SUMTREE + PTREE100 + PGRASS1K + PTREE1K
Grass only	VOR + LITTER + PGRASS1K
Tree only	SUMSHRUB + SUMTREE + PTREE100 + PTREE1K
Full	$PGRASS100 + PGRASS100^2 + LITTER + VOR + SUMSHRUB + SUMTREE + SUMTREE^2 + PTREE100 + PTREE100^2 + PTREE500 + PTREE1K + PGRASS500 + PGRASS1K + PGRASS1K \times SUMTREE + PGRASS1K \times PTREE1K$

TABLE 3. Information from preliminary-stage models examining factors affecting detection probability and abundance of four grassland bird species in western Minnesota. In stage 1, we individually assessed each detection covariate and retained those that improved model fit over a null detection model (based on AIC). In stage 2, all stage 1 covariates were compared in all possible combinations with the best-supported detection model retained (based on AIC). The third step was to select the better-fitting error distribution for density: negative binomial (NB) or Poisson. Finally, we used the best detection model from stage 2, the better-fitting distribution from stage 3, and a full model (see Table 2) to test goodness-of-fit (GOF). The final rows show apparent values of birds ha^{-1} and then estimates based on the best-supported model at mean covariate values.

Species	Bobolink	Clay-colored Sparrow	Savannah Sparrow	Sedge Wren
Stage 1 (detection)	DATE (−)	DATE (+)	YEAR	WIND
	Sky (−)	WIND (−)	PTREE100 (−)	
	TIME (+)	YEAR		
	YEAR			
Stage 2 (detection)	DATE	YEAR + DATE	YEAR	WIND
Stage 3 (distribution)	NB (AIC Δ8.49)	Poisson (2. 00)	NB (24.45)	NB (4.16)
GOF test result	p = 0.13	p = 0.36	p = 0.21	p = 0.21
Apparent density	0.34 (SD = 0.45)	0.41 (SD = 0.40)	0.18 (SD = 0.31)	0.32 (SD = 0.49)
Estimated density (95% CI)	0.54 (0.44–0.66)	0.56 (0.46–0.67)	0.38 (0.29–0.50)	2009: 0.49 (0.37–0.65)
				2010: 0.72 (0.57–0.92)
				2011: 0.16 (0.10–0.26)

We generated model-based predictions of abundance for each species with the best-supported model. When comparing the impact of grass-related versus woody-vegetation-related covariates, we varied all covariates in one group (e.g., grass-related) from the 10th to 90th percentile while holding the covariates in the other group (e.g., tree-related) at mean values. For example, if the best-supported model was Survey + Patch, predictions examining the impact of grass-related descriptors would increase VOR, LITTER, and PGRASS500 from the 10th to the 90th percentile while SUMSHRUB, SUMTREE, PTREE100, and PTREE500 would be held constant at mean values. In all predictions, we held PGRASS100 and any detection covariates constant at mean values. When YEAR affected detection probabilities, we selected the year with the median detection value. Numbers in parentheses are 95% confidence intervals unless otherwise noted.

RESULTS

During 2009–2011, we conducted 446 point counts on 35 grassland sites (50 site–year combinations) with an average of 8.9 point counts site^{-1} year^{-1} (range: 2–20). We visited 24 sites in 1 yr, 7 in 2 yr, and 4 in all 3 yr of the study. The most frequently observed grassland birds were Clay-colored Sparrow (*Spizella pallida*; n = 570), Bobolink (n = 478), Sedge Wren (n = 443), and Savannah Sparrow (n = 255). Other grassland birds were observed rarely (n ≤ 40), and therefore only these four species were included in our analyses. Other frequently observed species included Red-winged Blackbird (*Agelaius phoeniceus*; n = 1,008), Common Yellowthroat (*Geothlypis trichas*; n = 533), and Common Grackle (*Quiscalus quiscula*; n = 363).

Bobolink

The best-supported model for Bobolinks was Survey + Patch (preliminary model fitting: Table 3; a priori model selection results: Table 4). Bobolink detection probabilities ranged from 0.68 (0.55–0.78) for early surveys (June 2, 10th percentile) to 0.34 (0.28–0.42) for later-season surveys (June 22, 90th percentile). Bobolink density was negatively associated with all woody vegetation covariates included in the best-supported model (Figure 1 and Table 5). Density was predicted to decrease from 0.86 (0.69–1.07) to 0.21 (0.15–0.32) birds ha^{-1} when woody vegetation covariates increased from the 10th to the 90th percentile (Figure 2). Bobolink density was positively associated with all grass-related covariates and was predicted to increase with increasing grass extent, litter depth, and grass height. Density increased from 0.30 (0.22–0.42) to 0.98 (0.73–1.31) birds ha^{-1} as grass-related covariates increased from the 10th to the 90th percentile (Figure 2).

Clay-Colored Sparrow

The best-supported Clay-colored Sparrow density model was Survey + Landscape (Tables 3 and 4). Detection rates varied by year and increased with Julian date (β = 0.15; SE = 0.07); detection rates increased throughout the season from 0.70 (0.49–0.84; June 2) to 0.85 (0.64–0.94; June 22) during the year with the greatest detection probability (2010). In 2011, the year with the lowest estimated detection probability, detection increased from 0.50 (0.34–0.65) to 0.71 (0.53–0.83) during the same period.

Clay-colored Sparrow density was positively associated with most habitat variables in the best-supported model, including both grass- and tree-related covariates (Table 5 and Figure 1). The best-supported model predicted that Clay-colored Sparrow density would increase from 0.52 (0.42–0.63) to 0.65 (0.52–0.82) birds ha^{-1} as all woody

TABLE 4. Model results, including ΔAIC, number of parameters (k), and model weight (w_i) from models of abundance for four species of grassland birds surveyed during 446 point counts in western Minnesota, 2009–2011. Models included variables from three scales: Survey (100-m radius), Patch (500-m radius), and Landscape (1,000-m radius). At each scale, variables described characteristics of woody vegetation or grass quantity or quality. Bold indicates model set changing to new species and best-supported model for that species.

Species	Model	k	ΔAIC [a]	w_i
Bobolink	**Survey + Patch**	**12**	**0.00**	**0.800**
Negative binomial	Survey + Landscape	12	2.78	0.200
Detection model: DATE	Survey-point	10	19.15	0.000
	Tree only	9	27.43	0.000
	Patch	7	31.05	0.000
	Landscape	7	38.80	0.000
	Grass only	8	45.59	0.000
	Detection	4	96.17	0.000
	Null	3	114.82	0.000
Clay-colored Sparrow	**Survey + Landscape**	**13**	**0.00**	**0.473**
Poisson	Survey + Patch	13	2.01	0.173
Detection model:	Grass only	9	2.58	0.130
DATE + YEAR	Survey-point	11	2.95	0.108
	Tree only	10	3.77	0.072
	Landscape	8	5.34	0.033
	Patch	8	7.44	0.012
	Detection	5	59.91	0.000
	Null	2	76.92	0.000
Savannah Sparrow	**Survey + Patch**	**13**	**0.00**	**0.724**
Negative Binomial	Survey + Landscape	13	2.49	0.208
Detection model: YEAR	Tree only	10	5.13	0.056
	Survey-point	11	8.32	0.011
	Patch	8	12.87	0.001
	Landscape	8	17.75	0.000
	Grass only	9	27.46	0.000
	Detection	5	37.53	0.000
	Null	3	38.98	0.000
Sedge Wren	**Survey + Landscape** [b]	**17**	**0.00**	**0.990**
Negative Binomial	Tree only [b]	14	8.87	0.012
Detection model: WIND	Landscape [b]	12	13.61	0.001
	Survey-point [b]	15	22.18	0.000
	Survey + Patch [b]	17	25.44	0.000
	Grass only [b]	13	31.44	0.000
	Patch [b]	12	86.77	0.000
	Null	3	114.27	0.000
	Detection [b]	4	115.72	0.000

[a] AIC score for the best-supported models: Bobolink = 1,337.24, Clay-colored Sparrow = 1,781.54, Savannah Sparrow = 1,047.1, and Sedge Wren = 1,323.04.
[b] Sedge Wren a priori model set included an interaction of DATE × YEAR in the abundance model to account for late arrival of the species on the breeding grounds in 2011.

vegetation covariates increased, and that density would also increase from 0.44 (0.34–0.58) to 0.73 (0.56–0.94) birds ha^{-1} as grass-related covariates increased (Figure 2).

Savannah Sparrow

For Savannah Sparrows, the best-supported density model was Survey + Patch (Tables 3 and 4). Detection probability varied annually, ranging from a high of 0.52 (0.37–0.66) in 2011 to a low of 0.33 (0.25–0.42) in 2010. Savannah Sparrow density was negatively associated with all woody vegetation covariates and had mixed associations with grass covariates (Table 5 and Figure 1). Density decreased

from 0.70 (0.52–0.93) to 0.12 (0.07–0.21) birds ha^{-1} as woody vegetation covariates increased but was also predicted to decrease from 0.52 (0.33–0.81) to 0.47 (0.30–0.73) birds ha^{-1} as grass-related covariates increased (Figure 2).

Sedge Wren

We noted that most Sedge Wrens arrived late during the 2011 breeding season; to account for this, we tested an interaction of DATE and YEAR in the density model. The interaction was highly supported (ΔAIC of second-ranked model = 64.56), and we therefore included it in all
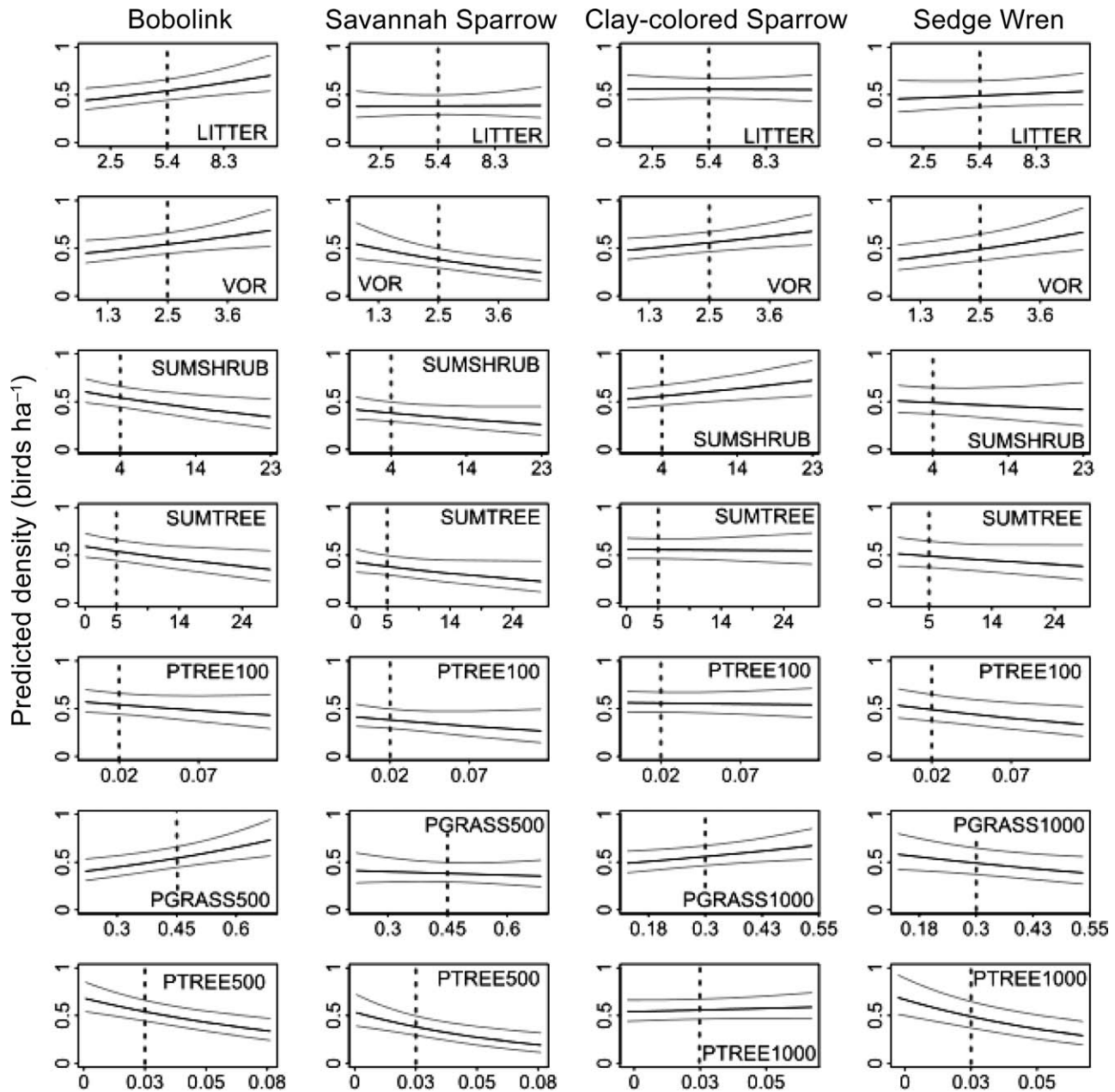
FIGURE 1. Expected density (birds ha^{-1}) and 95% confidence interval for four species of grassland songbirds when varying single covariates from the best-supported model (all other values held at mean). We varied the covariate of interest from its 10th to its 90th percentile. The vertical dotted line represents the mean value for the variable. The units of measure for covariates (x-axes) are detailed in Table 1.

subsequent models. The best-supported model was Survey + Landscape (Tables 3 and 4), and the best detection model included only WIND. Detection probability decreased from 0.57 (0.46–0.67) at low wind speeds (Beaufort scale 0) to 0.45 (0.37–0.53) at higher wind speeds (Beaufort scale 3).

Sedge Wren density was negatively associated with all woody vegetation covariates in the best-supported model and had mixed associations with covariates describing grass (Table 5 and Figure 1). Density was predicted to

decrease from 0.79 (0.60–1.04) to 0.23 (0.15–0.37) birds ha^{-1} as woody vegetation covariates increased and to increase from 0.44 (0.30–0.65) to 0.53 (0.38–0.75) birds ha^{-1} as grass-related covariates increased (Figure 2).

DISCUSSION

Our results demonstrate that grassland bird abundance was more strongly affected by negative effects of woody

TABLE 5. Covariate coefficient estimates (β) and standard errors (SE) for variables affecting detection rates (p) and density (λ) of four grassland bird species in Minnesota, 2009–2011. Estimates are based on the best-supported model for each species.

Covariate	Bobolink β	SE	Clay-colored Sparrow β	SE	Savannah Sparrow β	SE	Sedge Wren β	SE
Intercept (p)	4.06	0.08	4.26	0.13	3.76	0.08	4.02	0.07
DATE (p)	−0.23	0.05	0.15	0.07	–	–	–	–
YEAR2010 (p)	–	–	0.34	0.17	−0.03	0.09	–	–
YEAR2011 (p)	–	–	−0.04	0.14	0.30	0.13	–	–
WIND (p)	–	–	–	–	–	–	−0.08	0.04
Intercept (λ)	−0.61	0.10	−0.58	0.10	−0.96	0.13	−0.71	0.14
DATE (λ)	–	–	–	–	–	–	−0.37	0.09
YEAR2010 (λ)	–	–	–	–	–	–	0.39	0.14
YEAR2011 (λ)	–	–	–	–	–	–	−1.09	0.25
PGRASS100 (λ)	0.32	0.07	0.32	0.05	0.21	0.10	0.32	0.06
VOR (λ)	0.14	0.06	0.11	0.05	−0.26	0.09	0.18	0.06
LITTER (λ)	0.14	0.05	−0.01	0.05	0.01	0.09	0.05	0.06
PGRASS500 (λ)	0.19	0.06	–	–	−0.05	0.09	–	–
PGRASS1000 (λ)	–	–	0.10	0.05	–	–	−0.12	0.06
SUMSHRUB (λ)	−0.23	0.09	0.13	0.05	−0.26	0.09	−0.08	0.10
SUMTREE (λ)	−0.18	0.08	−0.01	0.05	−0.22	0.12	−0.10	0.08
PTREE100 (λ)	−0.12	0.09	0.02	0.06	−0.20	0.14	−0.20	0.09
PTREE500 (λ)	−0.23	0.06	–	–	−0.34	0.10	–	–
PTREE1000 (λ)	–	–	0.03	0.04	–	–	−0.31	0.08
YEAR2010 × DATE (λ)	–	–	–	–	–	–	0.32	0.12
YEAR2011 × DATE (λ)	–	–	–	–	–	–	1.05	0.20

vegetation than by positive effects of grass quality or quantity. Predicted densities of Bobolinks, Sedge Wrens, and Savannah Sparrows would increase twofold to fourfold if tree-related covariates were reduced from the 90th to the 10th percentile (Figure 2). Alternatively, attempts to improve grass quality by increasing litter depth, grass height, and grass extent would lead to increases in Bobolink density, marginal increases in Sedge Wren and Clay-colored Sparrow density, and reductions in density of Savannah Sparrow (Figure 2). Our results largely concur with findings from studies of experimental tree removal. Quamen (2007) found that grassland birds avoided wooded edges and redistributed themselves evenly in the study area after trees were removed. Ellison et al. (2013) found that grassland bird densities increased after removal of linear tree rows separating adjacent pastures. In the same landscape, Thompson (2013) found that grassland bird density decreased in the years immediately following experimental tree removal, likely in response to disturbance related to extensive tree removal, but eventually abundance increased on treated sites.

There are numerous underlying mechanisms that may cause grassland birds to avoid woody vegetation. A commonly hypothesized mechanism is that woody vegetation causes changes in predator communities by attracting more woodland-associated predators (e.g., raccoons [*Procyon lotor*], corvids, or raptors) or by altering the behavior of existing grassland predators (e.g., by providing perches for raptors or sheltered travel routes for mammalian predators). Bird density could be affected if arriving birds assess higher risk of mortality or reproductive failure near trees and then avoid settling there, or if birds that have experienced nest failure seek renesting sites farther from wooded edges (Bollinger and Gavin 2004). It is difficult to determine whether reduced density is the result of movements within a season, learning that has carried over between seasons, or innate habitat preferences. Furthermore, woody vegetation was not widespread in historical landscapes, and risks associated with nesting near wooded edges may have been much different in those landscapes. Avoidance of woody vegetation may no longer be an effective strategy, particularly considering the large distances that many predators are willing to travel and the highly fragmented state of modern grasslands (Renfrew et al. 2005). Most studies consistently find evidence that grassland bird density is reduced near wooded edges (Bakker 2003), but studies of nest survival are more variable. Some studies have documented increased risk of nest failure for grassland birds nesting near woody vegetation (Bollinger and Gavin 2004, Graves et al. 2010), but studies have also found no clear relationship (Renfrew et al. 2005, Winter et al. 2005) or a positive relationship between woody vegetation and nest survival (Grant et al. 2006, Thompson et al. 2012). Given these contrasting patterns, we believe that if risk of predation is a key driver of tree avoidance, it is likely an artifact of selection that occurred in historical landscapes (Renfrew et al. 2005). Other mechanisms for avoidance include
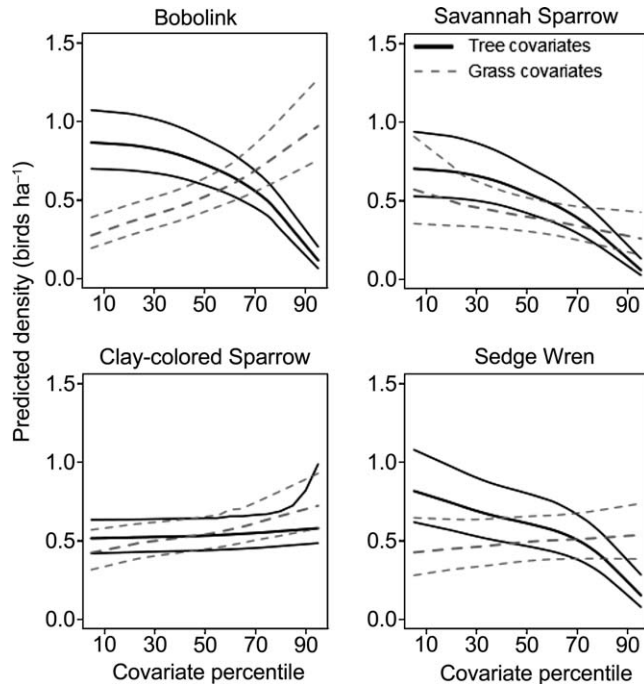
FIGURE 2. Plots comparing the effect of increasing grass variables (dashed gray lines; VOR, LITTER, and GRASS500 or GRASS1000) versus increasing woody vegetation variables (solid black lines; SUMSHRUB, SUMTREE, PTREE100, and PTREE500 or PTREE1000). Results are based on best-supported models for four grassland bird species from 446 point-count surveys conducted on 35 sites in western Minnesota, 2009–2011. Note that changing from the 10th to the 50th percentile involved little change in tree and shrub abundances, but large changes in grass quality and quantity (Table 1).

increased potential for brood parasitism near high perches, increased competition from generalist bird species, or altered habitat quality near wooded edges (Johnson and Temple 1990, Ribic et al. 2009).

Although multiple scales are important, our results suggest that fine-scale habitat features are of primary importance as birds settle on territories. Best-supported models for each of the four species included grass and woody vegetation variables at multiple scales (Survey + Patch and Survey + Landscape). For Savannah Sparrow, Bobolink, and Clay-colored Sparrow, the finest-scale model was given the most support of models that incorporated a single scale (i.e. Survey-point, Patch, or Landscape; Table 3), indicating that for three of four species, the local habitat variables may be most important in determining settling patterns. Conversely, Sedge Wrens selected habitat at larger scales, and best-supported single-scale and overall models included landscape-level covariates. Bakker et al. (2002; South Dakota), Fletcher and Koford (2002; Iowa), and Cunningham and Johnson (2006; North Dakota) also noted that Sedge Wrens tended to select habitat at broader, landscape scales.

Although we expected all four species to show some variation in response to physical qualities of grass, we were surprised to also find a mixed response to measures of grass extent. Density of all species was strongly and positively associated with grass extent at 100 m, a proxy for the amount of habitat available in the count area. However, two species were negatively associated with grass extent in the surrounding area, Savannah Sparrow at the 500-m scale and Sedge Wren at the 1,000-m scale. Given the tendency of grassland songbirds to exhibit area sensitivity, it is counterintuitive that a location with more surrounding grassland would be associated with lower densities of some grassland bird species (Johnson and Igl 2001, Ribic et al. 2009). In the case of Sedge Wrens, one explanation is that more extensive grass cover may have been associated with fewer wetland edges, which is a preferred habitat for this species (Dechant et al. 2003). We conducted a post hoc analysis, examining a variety of model structures that included percent wetland at multiple scales and, contrary to expectations, found no support that wetland habitat was related to Sedge Wren density. However, our hand-digitized landscape layer combined open water with all other types of wetlands and, thus, was not optimal for this purpose. Another explanation is that grassland area at large spatial scales was positively correlated with woody vegetation and that tree avoidance is a potentially more important driver of habitat selection than grassland extent for some species. Proportion of grass at 500-m and 1,000-m scales was positively, albeit weakly, correlated with woody vegetation covariates for 7 of 10 combinations (r_{max} = 0.33). If tree avoidance is a strong driver of habitat selection, grassland birds may thus pass over larger grassland patches when they contain trees or are in proximity to wooded areas. Additionally, grassland birds may first settle into agricultural landscapes that represent the most open habitat, but then gravitate toward nearby isolated patches of grassland when they find bare dirt unsuitable. This could explain why small grasslands in open, agricultural landscapes may sometimes support higher-than-expected densities of grassland birds (e.g., Clower 2011, Dunlap 2014).

The remaining grassland patches in western Minnesota are, for the most part, publicly owned. These grasslands exist within a mosaic of private land that complicates endeavors to manage for grassland bird populations. Additionally, habitat manipulation is expensive, and budgets may limit the scale of management possible on public lands (S. Vacek, personal communication). Grassland management thus tends to occur primarily at the local or patch scale, and the greater landscape is largely excluded from management actions such as tree removal. Nevertheless, local management can be effective. For example, reducing only local woody vegetation from average to minimum values within a 3.14-ha area

(equivalent to the area of a point count) would require removing 4.3 shrubs, 4.7 trees, and 0.06 ha of woodlot. This local-scale reduction in woody vegetation would result in 28%, 32%, and 16% increases in predicted density of Bobolinks, Savannah Sparrows, and Sedge Wrens, respectively, and a 5% decrease in Clay-colored Sparrow density. Conversely, increasing grass extent within 500 m by 11.6 ha (1 SD above mean) or 23.4 ha (2 SD above mean) would lead to a 22% or 46% increase in Bobolink density and a 10% or 20% increase in Clay-colored Sparrow density. Conversely, these increases in grass extent would lead to predicted declines in Savannah Sparrow (6% or 8%) and Sedge Wren (13% or 23%) density in the 3.14-ha core area. Thus, managers can expect that removing shrubs, scattered trees, or woodlots at local scales and/or broader scales should lead to increased density for most grassland bird species (Figure 2). Conversely, any management action aimed at altering the physical qualities of grass would have a mixed response, and even attempts to increase grass extent at broad scales may not lead to expected benefits.

Because all best-supported models also incorporated broader-scale metrics, we can expect that the habitat configuration of surrounding landscapes will influence the efficacy of any local-scale management. In this region, landscapes with the fewest trees were usually dominated by agriculture and often contained little grassland. Landscapes with more extensive grasslands were often in areas that were less suitable for agriculture (e.g., steep slopes, poor soils, near riparian areas). For a variety of reasons, these largely unmanaged grasslands often contained more woody vegetation (e.g., due to intentional planting, encroachment, or proximity to wooded riparian zones). Our study suggests that, in some landscapes, grassland birds may not perceive large grassland patches as the best habitat, but that they may prefer more open landscapes even if grasslands are small and surrounded by agricultural fields. We recommend focusing tree removal on linear tree features because they affect a disproportionately large area in comparison to their size (i.e. they create more edge than a woodlot of equivalent size). We also recommend targeting woody features that are isolated from other wooded habitats (i.e. ≥500 m from other off-site woody vegetation), thereby maximizing percent reduction in woodland for that patch. Additionally, studies more commonly assess correlational evidence of habitat selection, as did our study, but experimental evidence is necessary to truly establish causation. Trees may be associated with other forms of degradation (e.g., infrequent fire), and removal may be only the first step toward restoring grassland quality. Finally, our results suggest that even in relatively open habitats, probability of detecting birds can vary both spatially (e.g., if observers are not randomly assigned to survey points) and temporally (e.g.,

year–observer and date effects), and confounding factors such as these should be examined when possible. In our study, not accounting for imperfect detection would have underestimated abundance by 15–69%, which is consistent with other studies that used distance methods to estimate detection probability during grassland bird surveys (Diefenbach et al. 2003, Lueders et al. 2006, Jacobs et al. 2012).

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