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Habitat Relations

Habitat and Landscape Effects on Abundance of Missouri's Grassland Birds

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ABSTRACT Of 6 million ha of prairie that once covered northern and western Missouri, <36,500 ha remain, with planted, managed, and restored grasslands comprising most contemporary grasslands. Most grasslands are used as pasture or hayfields. Native grasses largely have been replaced by fescue (*Festuca* spp.) on most private lands (almost 7 million ha). Previously cropped fields set aside under the Conservation Reserve Program (CRP) varied from a mix of cool-season grasses and forbs, or mix of native warm-season grasses and forbs, to simple tall-grass monocultures. We used generalized linear mixed models and distance sampling to assess abundance of 8 species of breeding grassland birds on 6 grassland types commonly associated with farm practices in Missouri and located in landscapes managed for grassland-bird conservation. We selected Bird Conservation Areas (BCAs) for their high percentage of grasslands and grassland-bird species, and for <5% forest cover. We used an information-theoretic approach to assess the relationship between bird abundance and 6 grassland types, 3 measures of vegetative structure, and 2 landscape variables (% grassland and edge density within a 1-km radius). We found support for all 3 levels of model parameters, although there was less support for landscape than vegetation structure effects likely because we studied high-percentage-grassland landscapes (BCAs). Henslow's sparrow (*Ammodramus henslowii*) counts increased with greater percentage of grassland, vegetation height-density, litter depth, and shrub cover and lower edge density. Henslow's sparrow counts were greatest in hayed native prairie. Dickcissel (*Spiza americana*) counts increased with greater vegetation height-density and were greatest in planted CRP grasslands. Grasshopper sparrow (*A. savannarum*) counts increased with lower vegetation height, litter depth, and shrub cover. Based on distance modeling, breeding densities of Henslow's sparrow, dickcissel, and grasshopper sparrow in the 6 grassland types ranged 0.9–2.6, 1.4–3.2, and 0.1–1.5 birds/ha, respectively. We suggest different grassland types and structures (vegetation height, litter depth, shrub cover) are needed to support priority grassland-bird species in Missouri.

KEY WORDS *Ammodramus henslowii*, *Ammodramus savannarum*, Bird Conservation Area, dickcissel, grasshopper sparrow, grassland birds, habitat, Henslow's sparrow, Missouri, *Spiza americana*.

The tallgrass prairie region of the United States has lost 98% of its native grassland (Samson and Knopf 2004). At the time of settlement by Europeans, over 6 million ha of tallgrass prairie were in Missouri (Missouri Department of Conservation 1999) but <36,500 ha remain, with <9,000 ha in public ownership (Missouri Department of Conservation 1999). Most contemporary grasslands have been planted and are managed as pasture or hayfields. Native grasses largely have been replaced by fescue (*Festuca arundinacea* and *F. pratensis*) on approximately 6.9 million ha of private land (Roberts 2000). Under the U.S. Department of Agriculture (USDA) Conservation Reserve Program (CRP), previously cropped fields have been restored using a mix of cool-season grasses and forbs, a mix of native warm-season grasses and forbs, or tall-grass monocultures.

Concomitant with the loss of prairie grasslands was the decline of prairie birds (Askins et al. 2007). Since the mid-1960s, grassland bird populations have declined more consistently and ubiquitously than any other suite of avian species associated with a specific habitat or landscape (Vickery et al. 2000). Recent analysis of the Breeding Bird

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Survey (BBS) reveals negative range-wide population trends for many grassland-bird species during 1966–2009 (Sauer et al. 2011). These included easily observed species such as northern bobwhite (*Colinus virginianus*), dickcissel (*Spiza americana*), bobolink (*Dolichonyx oryzivorus*), and eastern meadowlark (*Sturnella magna*), as well as more cryptic species such as grasshopper sparrow (*Ammodramus savannarum*) and Henslow's sparrow (*A. henslowii*). However, in Missouri from 1987 to 2007, Henslow's sparrow and bobolink increased 9.8% and 6.6% per year, respectively (Sauer et al. 2011). These increases were likely a response to increased grassland area resulting from CRP restorations (Herkert 2007).

The sentinel species depicting the decline in grassland birds is greater prairie-chicken (*Tympanuchus cupido*). This species was historically abundant but now persists only in small, isolated, and endangered populations in Illinois, Iowa, and Missouri (Vodehnal and Haufler 2007). Loss of adequate nesting and brood-rearing habitat was the most important factor that led to the species' decline (Wisdom and Mills 1997, Westemeier et al. 1998). To conserve and increase habitat for greater prairie-chickens, as well as other grassland species, conservation planners since the late 1990s have focused management within designated finite landscapes, each referred to as a Bird Conservation Area (BCA; Fitzgerald and Pashley 2000). Each landscape designated as a BCA had >800 ha of grassland.

We sought to determine the effects of grassland type, vegetative structure, and landscape context on abundance of grassland birds. We used an information-theoretic approach to examine how these factors affected relative abundance of grassland-bird species. We also estimated the density of commonly detected grassland-bird species within grassland types located within BCA landscapes in western and northern Missouri.

STUDY AREA

We conducted this study on private and state lands located within 4 focal areas (Western Cherokee Grasslands, Marmaton/Wah'Kon-Tah, Cole Camp/High Lonesome, and Grand River Grasslands) of the Missouri Grasslands Coalition (Johnson 2008). Focal areas (Fig. 1) ranged in area from 5,438 ha to 18,952 ha and were located within a mosaic of grassland, cropland, and forest. Focal areas were selected because of ancillary objectives to monitor each of these sites as a BCA (Fitzgerald and Pashley 2000); this selection technically limits statistical inference from this study to these focal areas. However, because focal areas were large and geographically dispersed, and patches of grassland types were randomly selected within them, we believe our results are relevant to grassland bird conservation in similar landscapes in Missouri. We divided each focal area into 4 quadrants and randomly selected 1 >16-ha patch of each grassland type for up to 6 types in each quadrant.

We classified grassland types based on species composition (native prairie vs. introduced cool-season grasslands), history of use during prior years (hayed vs. grazed), and identification of CRP (cool-season and warm-season) plantings. These categories captured major differences in composition, structure, and management that we hypothesized would affect bird abundance. Grassland types were: grazed native prairie (NPG), hayed native prairie (NPH), grazed cool-season grasses and forbs (CSG), hayed cool-season grasses and forbs (CSH), warm-season CRP fields (WSCRP), and cool-season CRP fields (CSCRP). Because not all 6 grassland types were present in each quadrant, we selected only 70 grassland patches for study. We obtained data on haying and grazing activities on each patch during the previous 3–5 yr from landowners.

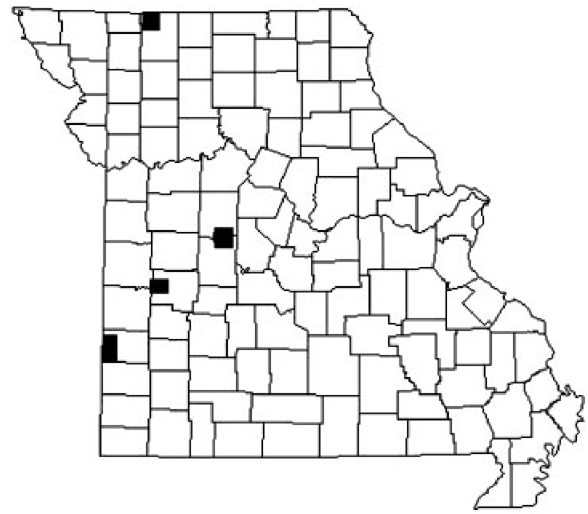

Figure 1. Location of 4 study sites in Missouri on which we surveyed grassland bird abundance to relate to grassland type, vegetation, and landscape structure in 2001–2003.

All native prairie patches were historically tallgrass prairie and had never been plowed. Because cutting native prairie for hay usually occurred in late summer, our study patches were not cut during the survey period we used. Cool-season patches were dominated by fescue or a combination of orchard grass (*Dactylis glomerata*), timothy (*Phleum pratense*), and fescue, and often with a mix of legumes such as alfalfa (*Medicago sativa*) and/or red clover (*Trifolium pratense*). During the 3 yr of the study, grazing occurred on the NPG and cool-season grazed CSG patches either before, during, or after the patch was surveyed, or a combination of all 3 grazing periods.

Most CRP patches were approximately 3- to 5-yr-old plantings. These patches frequently included tall, weedy annual plants or standing dead vegetation. Some CRP patches were cut in past summers to encourage growth of planted perennial species. The seed mixtures (5–30 species) used to plant WSCRP patches were considerably less diverse than native prairies. The CSCRP seed mixtures included cool-season grasses and legumes, although some also had robust annual plants or standing dead vegetation mixed in with the perennial planting.

METHODS

Bird Surveys

We surveyed bird abundance at 4 points in each of the grassland patches 2 times per breeding season during 19

May–29 June 2001, 21 May–24 June 2002, and 19 May–25 June 2003. We counted all adult male and female birds detected within 100 m during a 5-min survey. Observers received several days of training in bird identification and distance estimation prior to conducting surveys. In 2001, we recorded detections at 0–50 m and 51–100 m from the point whereas in 2002–2003, we recorded detections at 0–25 m, 26–50 m, 51–75 m, and 76–100 m from the point. Surveys started in the southernmost sites and proceeded to the north (375 km), the second visit repeating this same order. We surveyed hayed grassland types early to reduce the probability of haying before our visits.

Vegetation and Landscape Measurements

We measured vegetation structure at 4 randomly selected distances (between 5 m and 95 m) from each bird-survey point during each visit and calculated the mean of these for each point visit. Litter depth was the height of dead vegetation measured to the nearest cm. We took 4 measurements of vegetation height-density (nearest dm) in cardinal directions from each of the points with a Robel pole (Robel et al. 1970). We estimated the area of shrub cover that exceeded 2 m in height within the 100-m radius point count areas by visually estimating the length and width (nearest m) of patches of woody vegetation. We rationalized this technique was more accurate than estimating percent cover and, because shrub cover was limited and in discrete patches, line-transect approaches would have frequently missed these patches.

We developed landcover maps from USDA Farm Service Agency Common Land Unit data (USDA Farm Service Agency 2010) that identified grassland, cropland, forest, water, and developed landcover. Common Land Unit data consisted of digitized farm tract and field boundaries with associated attributes in a Geographic Information System. We verified and edited field boundaries and landcover types during field visits. We estimated the percent of grassland and edge density (m/ha) within 1 km of each bird survey point. We defined edge as the boundary between grassland landcover and any other landcover type.

Regression Models

We selected 7 bird species identified as species of concern within the Dissected Till Plains and Osage Plains physiographic areas (Partners in Flight 2010) for which we had sufficient data for analysis: northern bobwhite, field sparrow (*Spizella pusilla*), grasshopper sparrow, Henslow's sparrow, dickcissel, eastern meadowlark, and bobolink. We also included brown-headed cowbird (*Molothrus ater*) in our analyses because it is a brood parasite that could affect populations of these host species.

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate hypotheses concerning factors affecting bird abundance. We evaluated models that assessed the hypotheses that 1) bird abundance varied among grassland types, 2) species responded to vegetation structure as defined by our measurements of vegetation height, litter depth, and shrub cover, and 3) grassland birds have greater abundance in landscapes with more grassland and less grassland edge. In addition, we evaluated models that combined grassland type, structure, and landscape context as well as a null model with only an intercept (Table 1). Before fitting models, we examined tolerance values for each continuous

Table 1. A priori candidate models of effects on counts of breeding birds in grassland habitats in Missouri, 2001–2003. Models are generalized linear mixed models with a Poisson distribution and random-intercept terms for points within sites, points within a patch and site, and visits to points within a patch and site. Models with a lower ΔAIC_c (change in Akaike's Information Criteria adjusted for small sample size) and a greater Akaike weight (w_i) have more substantial support. All models are based on $N = 1,612$ and k = number of estimated parameters. Models with $\Delta AIC_c \leq 4$ considered as a 95% confidence set for each species are indicated by *.

		Northern bobwhite		Field sparrow		Grasshopper sparrow		Henslow's sparrow	
Model[a]	k	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
Null	4	0.96	0.121*	38.42	0.000	149.08	0.000	45.01	0.000
Grassland type	9	0.05	0.191*	40.53	0.000	135.55	0.000	36.89	0.000
Landscape	6	1.11	0.113*	42.06	0.000	147.96	0.000	44.35	0.000
Structure	7	2.35	0.061*	0.00	0.653*	8.93	0.008	14.45	0.001
Grassland type + Landscape	11	0.63	0.143*	44.72	0.000	136.16	0.000	35.51	0.000
Grassland type + Structure	12	0.00	0.196*	2.26	0.210*	0.00	0.656*	6.03	0.046
Landscape + Structure	9	2.43	0.058*	3.42	0.118*	4.70	0.062	9.50	0.008
Grassland type + Landscape + Structure	14	1.05	0.116*	7.08	0.019	1.74	0.274*	0.00	0.945*

		Dickcissel		Bobolink		Eastern meadowlark		Brown-headed cowbird	
Model[a]	k	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
Null	4	33.66	0.000	1.92	0.113*	38.13	0.000	28.44	0.000
Grassland type	9	33.84	0.000	0.28	0.255*	17.61	0.000	37.81	0.000
Landscape	6	32.36	0.000	5.75	0.017	37.23	0.000	28.68	0.000
Structure	7	5.10	0.048	1.21	0.160*	27.04	0.000	0.00	0.521*
Grassland type + Landscape	11	32.20	0.000	4.35	0.033	18.73	0.000	38.22	0.000
Grassland type + Structure	12	2.62	0.166*	0.00	0.294*	0.00	0.656*	9.32	0.005
Landscape + Structure	9	2.56	0.171*	4.54	0.030	26.57	0.000	0.21	0.470*
Grassland type + Landscape + Structure	14	0.00	0.615*	2.21	0.097*	1.30	0.343*	9.46	0.005

[a] Fixed effects in each model were Null: intercept only; Structure: vegetation height-density, litter depth, shrub cover; Grassland type: 6 grassland type categories; Landscape: percent grassland, edge density; and 2- and 3-way combinations of Structure, Grassland type, and Landscape models.

variable to diagnose multicollinearity, wherein low tolerance values (<0.40) indicated a variable was highly linearly related to the remaining variables (Allison 1991).

We fit generalized linear mixed models with a Poisson distribution for the response variable for each species (GLIMMIX procedure, SAS 9.2, SAS Institute, Inc., Cary, NC). Each visit to a point was an observation in the analysis; however, we included 3 nested random-intercept effects so the model appropriately addressed correlation among repeated measures of points within sites, points within a patch and site, and visits to points within a patch and site. Preliminary analyses based on comparisons of Akaike's Information Criterion (AIC) and $\hat{c}$ (Pearson chi-square/Df) indicated this correlation structure was supported more than any reduced combination of random effects and a Poisson distribution was supported more than a negative binomial or normal distribution.

We compared support for the models by ranking models using AIC for small sample sizes (AIC_c; Burnham and Anderson 2002). We evaluated the goodness-of-fit of the global model by examining $\hat{c}$ to determine if it was close to 1 (Burnham and Anderson 2002) and by calculating correlations between predicted and observed values. Because model selection uncertainty was present, we averaged model-parameter estimates and model predictions. Several approaches exist to identify a confidence set of models for model averaging (Burnham and Anderson 2002). We included models with $\Delta AIC_c \leq 4$, which represented confidence sets with cumulative AIC_c weights of 0.92–1.00. We included zeros for parameters that did not appear in a model in the confidence set when model averaging (Burnham and Anderson 2002). We interpreted effects of variables that appeared in the confidence set and had model-averaged coefficients with 95% confidence intervals that did not overlap 0. In limited cases, we interpreted effects even if the confidence interval overlapped 0 if the magnitude of the effect was large enough to be biologically meaningful and it was in the confidence set of models; however, we clearly identified these cases. Arnold (2010) cautioned that in information-theoretic approaches, a parameter supported by the model-selection process should not necessarily be dismissed because its 95% confidence interval includes zero. To interpret effects, we plotted predicted counts and report percent change in counts over the observed range of a variable.

Distance-Based Analysis of Densities

We used program DISTANCE (Distance 5.0, Research Unit for Wildlife Population Assessment, University of St. Andrews, United Kingdom) to estimate detection probabilities and densities of focal species (Buckland et al. 2001, Thomas et al. 2005). We used only data from 2002 to 2003 because these data were recorded in 4 distance intervals. We fit 5 models for each species: 1) a uniform detection function, 2) a half-normal detection function with a cosine series expansion, and included 3) year, 4) grassland type, and 5) both year and grassland type as covariates in conjunction with the half-normal detection function. We compared support for each model using AIC values, visually inspected the fit of the detection functions, and used the best model to estimate densities of each species in the 6 grassland types by post-stratifying by grassland type in DISTANCE (Buckland et al. 2001).

RESULTS

Regression Models

We detected 206 northern bobwhites, 428 field sparrows, 1,413 grasshopper sparrows, 1,527 Henslow's sparrows, 4,384 dickcissels, 529 bobolinks, 2,029 eastern meadowlarks, and 319 brown-headed cowbirds during 1,612 point counts over 3 yr. Some planned visits to points did not occur so the observed sample size (1,612) was less than the potential number of point-visits (1,680, based on 70 grassland patches $\times$ 4 points $\times$ 2 visits $\times$ 3 yr). The tolerance values for our continuous independent variables were >0.90 so multicollinearity was not a problem. There was model selection uncertainty for some species; model support (Akaike weight [w_i]) for the top model of each species ranged from 0.196 to 0.945 (Table 1).

The global model for northern bobwhite had a $\hat{c} = 0.56$ and the correlation between observed and predicted counts was 0.34. The grassland type + structure model was the top supported model for northern bobwhite. However, there was great model selection uncertainty and the confidence set included the null model (Table 1). Given competing support by the null model, and that model-averaged coefficients had confidence intervals that overlapped 0 (Appendix 1), we concluded we had no support for grassland type, structure, or landscape effects on northern bobwhite.

The global model for field sparrow had a $\hat{c} = 0.67$ and the correlation between observed and predicted counts was 0.53. The structure model, followed by landscape + structure and grassland type + structure models were in the confidence set of models (Table 1). Predicted count increased 65% over the increasing range of shrub cover (Fig. 2, Appendix 1).

The global model for grasshopper sparrow had a $\hat{c} = 0.79$ and the correlation between observed and predicted counts was 0.65. The grassland type + structure model and grassland type + landscape + structure models were in the confidence set (Table 1). Predicted counts were greater in the 2 grassland and hayed grassland types than the CRP grassland types (Fig. 3, Appendix 1). Predicted counts decreased 70%, 24%, and 79% over the range of increasing litter depth, shrub cover, and vegetation height-density, respectively (Fig. 2, Appendix 1). Predicted counts increased 21% over the increasing range of percent grassland, but the confidence interval for this effect overlapped 0 (Fig. 4, Appendix 1).

The global model for Henslow's sparrow had a $\hat{c} = 0.75$ and the correlation between observed and predicted counts was 0.57. The grassland type + landscape + structure model was the only model in the confidence set (Table 1). Predicted counts were greatest in native-prairie hayed grassland (Fig. 3, Appendix 1). We surveyed all NPH patches before haying in all 3 yr. Predicted counts increased 68% and 50% over the increasing range of litter depth and vegetation height-density, respectively, and decreased 78% and 20%

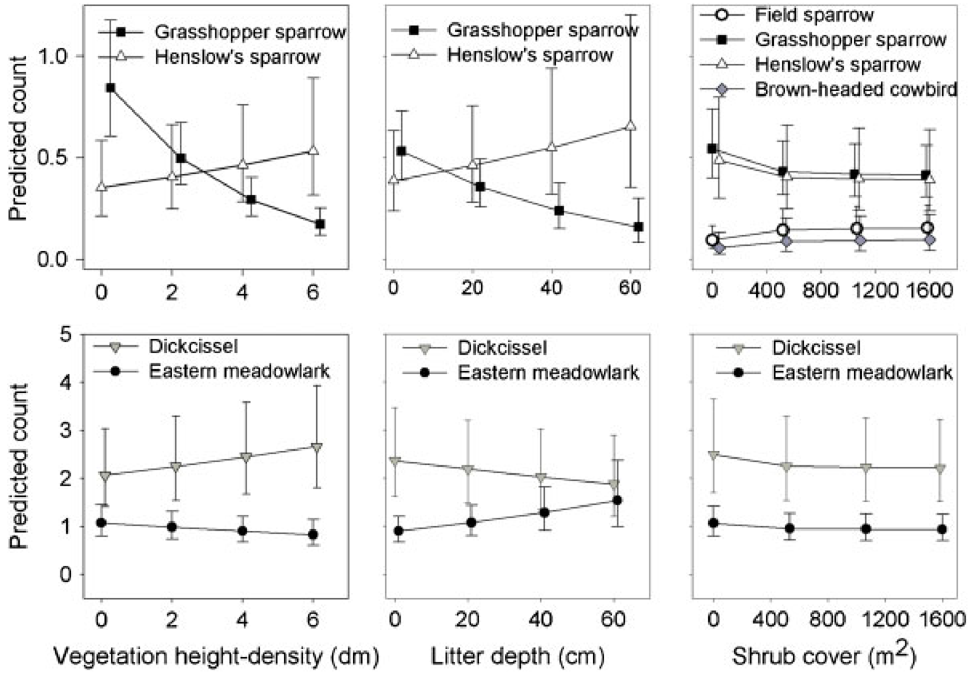

Figure 2. Model-averaged estimates of counts (±95% CI) of grassland birds at different levels of vegetation height-density, litter depth, and shrub cover in Missouri, 2001–2003. Counts represent the mean number of detections in 5-min point count.

over the increasing range of edge density and shrub cover, respectively (Figs. 2 and 4; Appendix 1). Predicted counts increased 109% over the increasing range of percent grassland, but the confidence interval for this effect overlapped 0 (Fig. 4, Appendix 1).

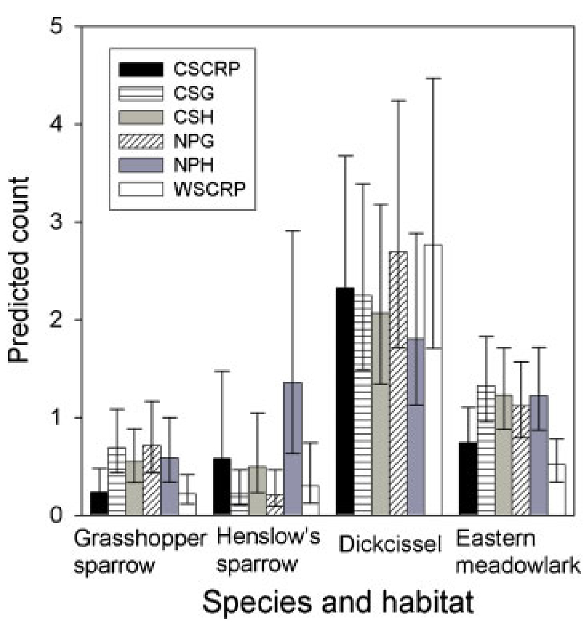

Figure 3. Model-averaged estimates of counts (±95% CI) of grassland birds (grasshopper sparrow, Henslow's sparrow, dickcissel, eastern meadowlark) in 6 grassland types (cool-season Conservation Reserve Program fields [CSCRP], grazed cool-season grasses and forbs [CSG], hayed cool-season grasses and forbs [CSH], grazed native prairie [NPG], hayed native prairie [NPH], warm-season Conservation Reserve Program fields [WSCRP]) in Missouri, 2001–2003. Counts represent the mean number of detections in 5-min point count.

The global model for dickcissel had a $\hat{c} = 0.74$ and the correlation between observed and predicted counts was 0.67. The grassland type + landscape + structure, landscape + structure, and grassland type + structure models were included in the confidence set (Table 1). Predicted counts decreased 21% and 11% over the increasing range of litter depth and shrub cover, respectively; and increased 29% over the increasing range of vegetation height-density (Fig. 2, Appendix 1). Predicted counts decreased 39% and 21% over the increasing range of edge density and percent grassland, but the confidence interval for these effects overlapped 0 (Fig. 4, Appendix 1).

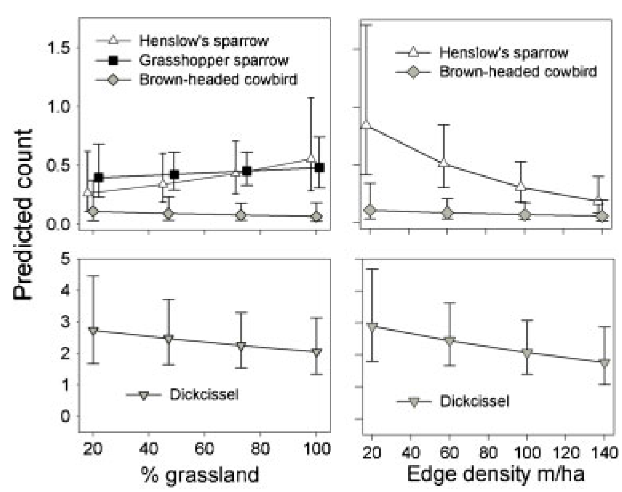

Figure 4. Model-averaged estimates of counts (±95% CI) of Henslow's sparrow, grasshopper sparrow, brown-headed cowbird, and dickcissel at different levels of percent grassland and grassland–non-grassland edge density in a 1-km radius of bird-survey points in Missouri, 2001–2003. Counts represent the mean number of detections in 5-min point count.

The global model for bobolink had a $\hat{c} = 0.58$ and the correlation between observed and predicted counts was 0.61. The confidence set for the bobolink included the grassland type + structure, structure, null, and grassland type + landscape + structure models, in decreasing order of importance (Table 1). As a result of strong model selection uncertainty and support for the null model, no effects had confidence intervals that did not overlap 0 (Appendix 1); therefore we concluded we had no meaningful support for grassland type, landscape, or structure effects.

The global model for eastern meadowlark had a $\hat{c} = 0.88$ and the correlation between observed and predicted counts was 0.28. The grassland type + structure and grassland type + landscape + structure models were supported (Table 1). Predicted counts were greater in CSG, CSH, NPG, and NPH grassland types than in WSCRP (Fig. 3, Appendix 1). Predicted counts decreased 23% and 12% over the increasing range of vegetation height-density and shrub cover, respectively, and increased 71% over the increasing range of litter depth (Fig. 2, Appendix 1).

The global model for brown-headed cowbird had a $\hat{c} = 0.90$ and the correlation between observed and predicted counts was 0.31. The structure and landscape + structure models were supported for the brown-headed cowbird (Table 1). Predicted counts increased 71% over the increasing range of shrub cover (Fig. 2, Appendix 1). Predicted count decreased 40% and 48% over the increasing range of percent grassland and edge density, respectively; however, the confidence interval for these effects overlapped 0 (Fig. 4, Appendix 1).

Distance-Based Density Estimates

We fit DISTANCE models using 114 northern bobwhite, 319 field sparrow, 1,011 grasshopper sparrow, 1,022 Henslow's sparrow, 2,959 dickcissel, 406 bobolink, 1,542 eastern meadowlark, and 247 brown-headed cowbird detections from 2002 to 2003. We could only fit distance models and estimate densities for grasshopper sparrow, Henslow's sparrow, and dickcissel; these were 3 of the 4 most abundant species. The remaining species did not meet a basic assumption of the distance-modeling approach, that detections decline with distance from the observer (Buckland et al. 2001). The models with year, grassland type, and year + grassland type as covariates were the best-supported models for grasshopper sparrow, Henslow's sparrow, and dickcissel, respectively. Visual inspection of the detection function indicated the models fit the data. Overall detection probabilities (SE) were 0.213 (0.0073), 0.118 (0.0044), and 0.237 (0.0048) for grasshopper sparrow, Henslow's sparrow, and dickcissel, respectively. Using the best model for each species, we post-stratified observations in DISTANCE by grassland type to estimate density in each grassland type (Fig. 5).

DISCUSSION

We found support for effects of grassland type, vegetation structure, or landscape on 6 of 8 species. Vegetation structure effects were most often supported (6 of 8 species), followed by landscape effects (4 species) and grassland type (3 species).

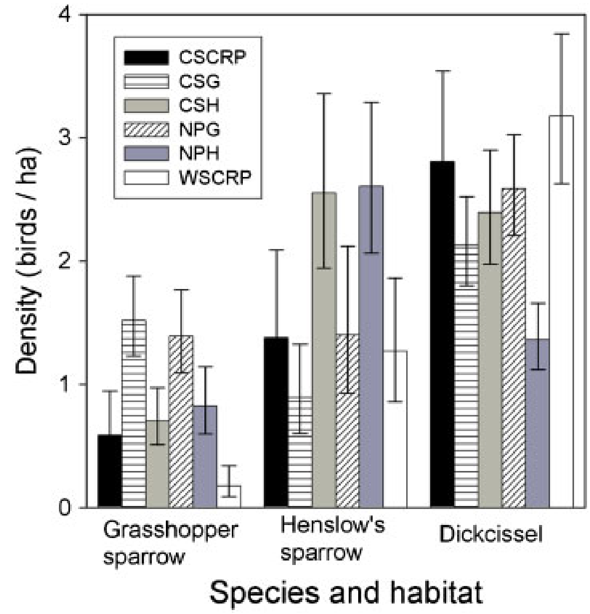

Figure 5. Estimated density of grassland birds in 6 grassland types in Missouri, 2002–2003. Estimates were made with the best-supported model and with separate detection probabilities estimated by year, grassland type, and year and grassland type for grasshopper sparrow, Henslow's sparrow, and dickcissel, respectively. Grassland types were cool-season Conservation Reserve Program fields (CSCRP), grazed cool-season grasses and forbs (CSG), hayed cool-season grasses and forbs (CSH), grazed native prairie (NPG), hayed native prairie (NPH), and warm-season Conservation Reserve Program fields (WSCRP).

The 6 common grassland types, and measures of vegetation and landscape structure we used, were useful for explaining abundance patterns. Similarly, or to an even greater extent, other studies of grassland birds have found support for landscape factors (Ribic and Sample 2001, Fletcher and Koford 2002, Ribic et al. 2009*a*). We found only weak to moderate support for effects of percent grassland and edge density on bird abundance, probably because our BCA-based study sites were selected to have a high percentage of grassland and a low percentage (<5%) of forest. Although we used predicted counts and density estimates as indicators of which grassland types might support the highest population numbers, further investigation of reproductive success in these types or structures would provide greater confidence in predicted response to management. We found, as have others (e.g., Bakker et al. 2002, Fuhlendorf et al. 2006, Ribic et al. 2009*a*), that responses to vegetation structure and landscape composition varied among species.

Field sparrow abundance was most affected by vegetation structure. As shrub cover increased, the relative abundance of field sparrows increased. This species inhabits old fields throughout Missouri and its presence is usually coincident with shrubs. Grasshopper sparrow abundance was affected by grassland type, vegetation structure, and landscape effects and density was highest in grazed areas (CSG and NPG). In northern Oklahoma, Fuhlendorf et al. (2006) also found grasshopper sparrows to be abundant under traditional stocking rates of 1.2 ha/270-kg steer. However, Saab et al. (1995) identified studies wherein grasshopper sparrows responded positively to moderate grazing on tallgrass sites but negatively to heavy grazing. Relative abundance of the grasshopper sparrow increased as the vegetation height-density, litter depth, and shrub cover decreased. Winter (1998) found vegetation height-density to be the most important variable determining densities of this species, with higher numbers at sites with lower vegetation height-densities. Grasshopper sparrows in Winter's (1998) study were not affected by landscape structure at any radius.

Henslow's sparrows had the most complex response to grassland type, structure, and landscape factors. Our results were consistent with other midwestern studies that found positive associations between Henslow's sparrow abundance and vegetation height-density and litter depth (Zimmerman 1988, Herkert 1994, Winter 1998, Herkert 2007). Both Herkert (1994) and Winter (1998) found densities of this species to be lower in hayfields mowed within the previous 12 months, which contrasts with the apparent affinity shown by the species for hayed grasslands in this study. Relatively late haying dates on NPH in Missouri could contribute to making this grassland type attractive to Henslow's sparrows, although hayfields would not be expected to have much litter. Swengel and Swengel (2001) reported native-prairie haying in late June to late July in southwestern Missouri. Henslow's sparrows can initiate nests in that region until mid-July (Winter 1999), so mowing could cause some nest destruction (Winter 1998), and hayfields can act as ecological traps for some species (Perlut and Strong 2011). Henslow's sparrows responded positively to increased amounts of grassland and decreased amounts of edge habitat in the surrounding landscape, which is consistent with Winter's (1998) findings that numbers increased with total area of grass and mean patch size within a 5-km radius of study sites (Winter 1998).

Dickcissels responded to grassland type, structure, and landscape factors, and responded strongly to shrub cover (negative) and vegetation height-density (positive). High densities of dickcissels in CSCRP and WSCRP were likely because of robust weeds that are often present in these plantings. Winter (1998) also found that dickcissel density increased with vegetation height-density, time since haying, and the percentage of grass cover in a 5-km radius of study sites, but the effects of within-patch management and the surrounding landscape were ameliorated in prairies of larger size. As litter depth and shrub cover increased, the relative abundance of dickcissel decreased. Dickcissel densities were only slightly lower in the other grassland types except for NPH, where it was about half that of WSCRP.

Eastern meadowlarks responded to grassland type, structure, and landscape factors and were more abundant in the CSG, CSH, NPG, and NPH grassland types than the 2 CRP types that had a tall, weedy structure. Warren and Anderson (2005) found more meadowlark nests in habitat with a greater amount of standing dead vegetation, but McCoy et al. (2001) reported higher abundances in CRP fields planted with cool-season grasses, which had lower vegetation height-density compared to fields planted with warm-season grasses. Their relative abundance was similar in the 4 other grassland types.

There was support for vegetation structure and landscape effects on brown-headed cowbirds. However all confidence intervals overlapped 0 except for shrub cover; counts increased about 18% over the range of shrub cover. This finding is consistent with their responding to host densities rather than specific grassland types. Barber and Martin (1997) reported that cowbirds may be attracted to individual host species of high densities and that rate of parasitism on other host species in the habitat may increase as a result.

A notable aspect of our results was the variation in abundance within grassland types, as indicated by the large confidence intervals (Figs. 1 and 5). Although we examined many factors that affect grassland-bird abundance, we may have missed some important factors (haying vs. burning, Swengel and Swengel 2001; macro- and micro-habitat features and bird behavior, Johnson and Winter 2005; availability of prey, Hamer et al. 2006). Although our study areas were at least 16 ha, area sensitivity could have been responsible for some of the variability (Ribic et al. 2009*b*). Weather and annual differences in reproductive output could affect spatial and temporal variability (e.g., Wiens 1974, Niemuth et al. 2008). Landscape factors can also affect avian responses to particular grassland types (Ribic and Sample 2001; Bakker et al. 2002; Fletcher and Koford 2002; Ribic et al. 2009*a*, *b*). This variability makes it difficult to predict population responses to specific habitat changes. Creation of a variety of vegetation structures, though, results in habitat for a variety of species (e.g., Bakker et al. 2002, Fuhlendorf et al. 2006, Ribic et al. 2009*a*).

We could only fit distance models for 3 of the most abundant species. The remaining species did not meet the assumption that detections decline with distance, perhaps as a result of birds moving away from the observer or too few detections or distance intervals to fit detection functions. For example, northern bobwhites may be best monitored by a different technique. Most bobwhite individuals were calling outside the 100-m radius and therefore were not included within our counts. Moreover, radio-collared northern bobwhites have been observed moving away from the observer before they call (A. R. Forbes, Missouri Department of Conservation, personal communication).

Like other studies that estimated detectability of grassland birds (Diefenbach et al. 2003), we found that detectability varied as a function of covariates. Patterns in abundance among grassland types were very similar between predicted counts (Fig. 3) and distance-based density estimates (Fig. 5). The only notable difference between methods was a greater relative abundance for Henslow's sparrow in cool-season hayed grassland based on density estimates compared to predicted counts. Because we conducted most surveys before haying, it is possible counts were biased low in this habitat because of lower detectability there and the distance model corrected for this. Other biases in counts might have been evident relative to vegetation structure, but we did not consider more complex distance models with these covariates. Newer modeling approaches that simultaneously address detectability and habitat effects on abundance can better address these issues, but our surveys were not designed for these methods (Royle 2004, Kéry 2008).

MANAGEMENT IMPLICATIONS

We suggest different grassland types and vegetation structure (height-density, litter depth, shrub cover) will be needed to support abundant populations of priority grassland-bird species in Missouri. Managers can use the habitat relationships documented here to select appropriate management practices for individual species. Litter and shrub cover in grassland patches benefits Henslow's sparrows and field sparrows. However, in Missouri, increased shrub cover is rarely a management priority, as an overabundance of shrubs is often perceived as a management problem within grasslands. Both cool- and warm-season CRP provide important habitat for dickcissels, likely due to the tall weedy vegetation. Fall grazing can be used to manage habitat for grasshopper sparrows but previous studies indicate that heavy stocking rates can reduce abundance of this species. Haying can be used to manage habitats for Henslow's sparrows, especially on NPH, although this link needs further testing. Haying reduces litter and nests are vulnerable if fields are cut too early.

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Appendix 1. Model-averaged parameter estimates for generalized linear mixed models with a Poisson distribution used to estimate landscape and habitat effects on number of bird detections during a 5-min point count in Missouri, 2001–2003. Parameters were model averaged from a confidence set of models with ΔAIC_c (change in Akaike's Information Criterion adjusted for small sample size) ≤ 4.

			95% Confidence interval	
Species and effect[a]	**Estimate**	**SE**	**Lower**	**Upper**
Northern bobwhite				
Intercept	−2.126	0.924	−3.938	−0.314
CSCRP	−0.995	0.830	−2.622	0.632
CSG	−0.525	0.517	−1.538	0.488
CSH	−0.252	0.409	−1.054	0.550
NPG	0.126	0.348	−0.556	0.808
NPH	−0.058	0.320	−0.686	0.570
WSCRP				
edgrass	−0.003	0.005	−0.012	0.006
lmean	−0.005	0.008	−0.021	0.011
lshrub	0.023	0.033	−0.042	0.088
pctgrass	−0.005	0.007	−0.019	0.009
rmean	0.025	0.043	−0.059	0.109
Field sparrow				
Intercept	−2.239	0.511	−3.241	−1.237
CSCRP	−0.044	0.143	−0.324	0.236
CSG	−0.207	0.350	−0.892	0.478
CSH	−0.203	0.344	−0.878	0.472
NPG	−0.140	0.253	−0.636	0.356
NPH	−0.183	0.314	−0.799	0.433
WSCRP				
edgrass	0.000	0.001	−0.002	0.002
lmean	0.012	0.006	0.000	0.024
lshrub	0.156	0.024	0.108	0.204
pctgrass	−0.001	0.002	−0.005	0.003
rmean	−0.015	0.046	−0.106	0.076
Grasshopper sparrow				
Intercept	−0.672	0.454	−1.563	0.219
CSCRP	0.079	0.437	−0.777	0.935
CSG	1.149	0.361	0.442	1.856
CSH	0.913	0.371	0.185	1.641
NPG	1.179	0.385	0.425	1.933
NPH	0.984	0.394	0.212	1.756
WSCRP				
edgrass	0.000	0.001	−0.002	0.002
lmean	−0.020	0.005	−0.031	−0.009
lshrub	−0.086	0.014	−0.114	−0.058
pctgrass	0.002	0.004	−0.006	0.010
rmean	−0.264	0.030	−0.323	−0.205
Henslow's sparrow				

Appendix 1. (*continued*)

Species and effect[a]	Estimate	SE	95% Confidence interval Lower	Upper
Intercept	−0.972	0.750	−2.442	0.498
CSCRP	0.659	0.590	−0.498	1.816
CSG	−0.311	0.514	−1.319	0.697
CSH	0.498	0.524	−0.529	1.525
NPG	−0.354	0.535	−1.403	0.695
NPH	1.514	0.522	0.490	2.538
WSCRP				
edgrass	−0.013	0.005	−0.022	−0.004
lmean	0.009	0.004	0.002	0.016
lshrub	−0.069	0.014	−0.096	−0.042
pctgrass	0.009	0.007	−0.005	0.023
rmean	0.068	0.024	0.021	0.115
Dickcissel				
Intercept	1.599	0.416	0.783	2.415
CSCRP	−0.173	0.198	−0.560	0.214
CSG	−0.207	0.181	−0.562	0.148
CSH	−0.291	0.208	−0.699	0.117
NPG	−0.025	0.152	−0.323	0.273
NPH	−0.427	0.244	−0.906	0.052
WSCRP				
edgrass	−0.004	0.003	−0.009	0.001
lmean	−0.004	0.002	−0.008	0.000
lshrub	−0.037	0.008	−0.052	−0.022
pctgrass	−0.004	0.003	−0.010	0.002
rmean	0.042	0.013	0.017	0.067
Bobolink				
Intercept	−4.771	1.624	−7.954	−1.588
CSCRP	0.966	0.965	−0.926	2.858
CSG	0.732	0.862	−0.957	2.421
CSH	1.609	1.248	−0.838	4.056
NPG	0.197	0.773	−1.318	1.712
NPH	1.274	1.227	−1.131	3.679
WSCRP				
edgrass	−0.001	0.002	−0.006	0.004
lmean	−0.001	0.004	−0.009	0.007
lshrub	−0.039	0.039	−0.115	0.037
pctgrass	−0.001	0.003	−0.007	0.005
rmean	−0.033	0.040	−0.111	0.045
Eastern meadowlark				
Intercept	−0.650	0.266	−1.171	−0.129
CSCRP	0.362	0.202	−0.034	0.758
CSG	0.940	0.177	0.593	1.287
CSH	0.865	0.186	0.501	1.229
NPG	0.772	0.195	0.390	1.154
NPH	0.862	0.185	0.500	1.224
WSCRP				
edgrass	0.000	0.001	−0.002	0.002
lmean	0.009	0.003	0.003	0.015
lshrub	−0.039	0.011	−0.061	−0.017
pctgrass	0.002	0.003	−0.003	0.007
rmean	−0.043	0.019	−0.080	−0.006
Brown-headed cowbird				
Intercept	−1.888	1.164	−4.169	0.393
edgrass	−0.005	0.007	−0.019	0.009
lmean	−0.005	0.008	−0.022	0.012
lshrub	0.167	0.030	0.109	0.225
pctgrass	−0.006	0.009	−0.024	0.012
rmean	−0.045	0.050	−0.142	0.052

[a] Effects were cool-season Conservation Reserve Program fields (CSCRP), grazed cool-season grasses and forbs (CSG), hayed cool-season grasses and forbs (CSH), grazed native prairie (NPG), hayed native prairie (NPH), warm-season Conservation Reserve Program fields (WSCRP), edge density (edgrass), litter depth (lmean), area of shrub cover (lshrub), percent of grassland (pctgrass), and vegetation height-density (rmean).