

Grassland songbird occurrence on remnant prairie patches is primarily determined by landscape characteristics

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Abstract

Context North American grassland songbird populations have declined significantly due to habitat loss and fragmentation. Understanding the influence of the surrounding landscape on prairie fragment occupancy is vital for predicting the fate of grassland birds in these heavily altered landscapes.

Objectives We examined the relative importance of local and landscape variables on grassland bird occupancy of prairie fragments using a focal-patch study. We also investigated the spatial scale at which landscape variables were most influential.

Methods We surveyed birds on 29 unplowed prairie fragments in western Minnesota and eastern North and South Dakota. We quantified local habitat on the fragment using vegetation surveys and aerial photographs and the landscape surrounding the fragment out to 4 km using aerial photographs. We analyzed occupancy using multi-model approaches applied to multiple logistic regression.

Results Of 38 species encountered, nine were neither too rare nor too abundant to be analyzed. Predictors of

patch occupancy were unique for each bird species, yet general patterns emerged. For eight species, landscape variables were more important than local variables. Mostly, those landscape variables measured configuration (e.g., edge density) and not composition (e.g., percent cover of a particular matrix element). Landscape effects were mostly from variables measured at the greatest extents from the prairie fragment. **Conclusions** Using a focal-patch study design we demonstrated the importance of the surrounding landscape, often out to 4 km from the fragment edge, on prairie occupancy by grassland birds. Effective management of grassland songbirds will require attention to the landscape context of prairie fragments.

Keywords Grassland birds · Landscape context · Prairie fragments · Matrix configuration · Matrix composition

Introduction

Globally, grasslands are among the most threatened biomes (Hoekstra et al. 2005). Grasslands across the globe face habitat loss and fragmentation due to habitat conversion (Askins et al. 2007) and habitat degradation due to increasing grazing pressure and fire suppression (Fuhlendorf et al. 2008). In grasslands around the world, habitat loss and degradation has negatively impacted biota including plants (Piqueray

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et al. 2011; Deák et al. 2016), insects (Moranz et al. 2014; Otto et al. 2016; Poniatowski et al. 2016), herptiles (Gebauer et al. 2013; Rotem et al. 2016), and mammals (Duggan et al. 2011). Grassland birds have been particularly well studied with effects of grassland conversion and degradation documented broadly, such as in Spain (Reino et al. 2012), Brazil (Fontana et al. 2016), and Australia (Baker-Gabb et al. 2016). Overall, grassland bird populations are declining in Europe and North America (Reif 2013).

North America's grasslands have experienced substantial impacts from agricultural expansion and increasing urbanization. In the Great Plains, almost 70% of historic grassland cover has been lost (Samson et al. 2004), with higher losses in the northern tallgrass prairie, where <1% of the original tallgrass prairie remains (Samson and Knopf 1994). Additionally, the current economic climate continues to drive substantial grassland conversion to agriculture (Wright and Wimberly 2013). Such substantial and on-going habitat loss and fragmentation impacts prairie species, including birds. North American grassland songbirds are experiencing the steepest population declines compared to any other group of birds on the continent (North American Bird Conservation Initiative Canada 2012). From 1968 to 2008, 37% of grassland obligate species declined (Sauer and Link 2011). Even common species like Savannah Sparrows (*Passerculus sandwichensis*) and Clay-colored Sparrows (*Spizella pallida*) have declined in at least a part of their range (Igl and Johnson 1997).

In the face of these declines, much research has been done on grassland songbird populations at the habitat patch level including effects of habitat loss and fragmentation (Herkert 1994; Bender et al. 1998; Helzer and Jelinski 1999; Johnson and Igl 2001; Davis and Brittingham 2004; Fletcher 2005) and habitat quality and vegetation structure (O'Leary and Nyberg 2000; Davis 2005; With et al. 2008). Multiple bird species are area- or edge-sensitive (DeLisle and Savidge 1996; Winter et al. 2000; Jensen and Finck 2004; Koper and Manseau 2009) and respond to specific vegetation or structural features (Whitmore 1981; Davis et al. 1999; Winter et al. 2005; Jacobs et al. 2012). These details, while important, tend to ignore that prairie fragments do not exist in isolation, but are embedded in landscapes which vary in terms of the types, amounts, and configuration of matrix (non-habitat) elements. Matrix can provide secondary

habitat (Johnson 2000), alter predation or parasitism rates (Borgmann and Rodewald 2004; Patten et al. 2006), and influence dispersal (Haas 1995), all of which can potentially impact grassland birds on prairie remnants. A recent multi-taxa review found that the type of matrix surrounding a patch influenced species richness or abundance in 95% of the studies reviewed (Prevedello and Viera 2010). Despite this, few studies have analyzed the influence of the surrounding landscape on populations on patches of remnant habitat (Rodewald 2003).

Landscape-level effects may not be identical across all songbirds. Each species has its own specialized suite of resources needed for foraging and reproduction (Ehrlich et al. 1988) that may cause different species to respond differently to landscape elements. Similarly, dispersal, movement, and avoidance behaviors, which can vary between species, could also influence species responses to the surrounding landscape (Eycott et al. 2012), including the spatial scale at which species-landscape interactions manifest. Connecting landscape patterns to life history traits may allow for extrapolation of trends to species with similar resource requirements (such as habitat preferences or functional groups). Identifying such connections between species behaviors and life history traits would permit the development of management techniques that are suitable for more than a single target species making it easier to maximize conservation resources. These patterns could also be used to identify prairies on which particular groups of species are at risk or in need of additional of management attention. A previous study found that it is possible to predict forest bird community responses to landscape changes using species' life history traits (Hansen and Urban 1992), and it makes sense to try incorporating the same kinds of information for grassland songbirds.

Studying landscape-level effects is best done using a focal-patch approach (Brennan et al. 2002) where each habitat patch and surrounding landscape represents an experimental unit in the analysis and replication occurs at the landscape level rather than the habitat patch level. This focal-patch approach allows effects due to the surrounding landscape to be separated from those due to local characteristics of the habitat patch (Thornton et al. 2011) and minimizes the likelihood of spatial autocorrelation influencing the analysis (Brennan et al. 2002). Despite the obvious advantages of the focal-patch approach, many of the

previous landscape studies of grassland songbirds were based on sampling units not focal patches (e.g., Ribic and Sample 2001; Bakker et al. 2002; Kalinowski and Johnson 2010) making it difficult to distinguish habitat and landscape effects in their results.

Most grassland songbirds migrate at least short distances every year (Igl and Johnson 1997) requiring them to choose a prairie patch to establish their breeding territory upon their return. This process is hierarchical, as birds are influenced by different factors at progressively smaller scales as they narrow their range of movement from large (migratory movements) to small (establishing nesting or feeding territories; Hutto 1985). As such, the final occupancy patterns may be influenced by aspects of the landscape at broader scales. To capture this effect, we used a larger spatial extent (4 km) than most of the previous landscape studies of grassland songbirds, most of which looked no farther than 2 km into the landscape (e.g., Bergin et al. 2000; Bajema and Lima 2001; Ribic and Sample 2001; Grant et al. 2004; Jacobs et al. 2012).

We report on a study investigating grassland songbird occurrence on remnant prairies embedded in heterogeneous landscapes. We used a focal-patch approach, with the focal-patch defined as the extent of the contiguous native prairie for a given remnant prairie patch, allowing us to distinguish between landscape and local effects on songbird occurrence. We quantified the landscape out to 4 km around the focal patch allowing us to incorporate some of the largest scale landscape data investigated thus far for grassland birds. Finally, we compare the bird species responses to landscape structure across habitat guilds.

Methods

Site selection

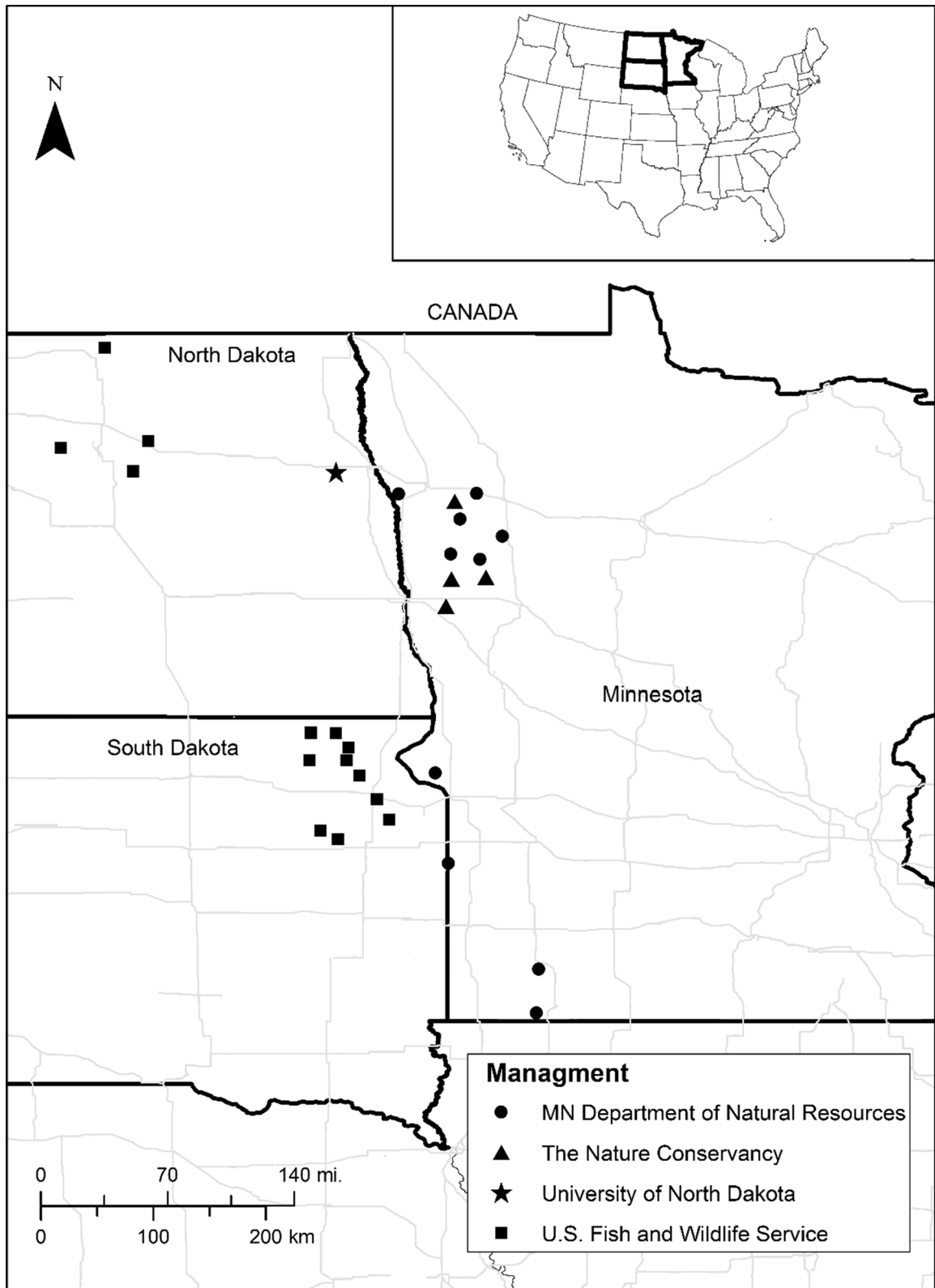
We selected 29 native, unplowed prairie fragments located in western Minnesota and eastern North and South Dakota, owned and/or managed by The Nature Conservancy, Minnesota Department of Natural Resources, U.S. Fish & Wildlife Service, or the University of North Dakota (Median patch size 67.5 ha with a range of 7.1–1180.9 ha; Fig. 1). Prairie fragments are relatively rare in this area with most

being very isolated (15 of the 29 fragments did not have any other native, unplowed prairie within 4 km). Fragments were chosen to maximize the range of sampled fragment sizes and the variation in the surrounding landscape (based on cover of woody vegetation, grass, agriculture, and open water), to exclude patches scheduled for burning or grazing management during the 2-year study period, and to ensure a minimum separation of 8 km to reduce issues with spatial autocorrelation.

Bird counts

We conducted bird counts from mid-May through mid-July, on all 29 sites in 2010 and 2011. Counts occurred when birds were most active and vocal, from dawn until approximately 10:30 to 11:00 am CDT, and on days with weather conditions conducive to hearing and seeing birds (wind speeds less than 32 km/h, minimal precipitation; Bibby et al. 1992). We sampled each site twice during each field season, except when weather conditions and flooding limited access. Seven sites were surveyed twice in 2010, and 26 sites were surveyed twice in 2011.

Each count used a linear transect that allowed sampling of significant portions of each prairie patch while minimizing sampling time (Anderson and Ohmart 1981; Gibbons et al. 1996). Transect length was dictated by prairie fragment size: 400 m in the smallest fragments (7–40 ha), 800 m in the medium fragments (41–161 ha), and 1200 m in the large fragments (>161 ha). These distances were based on the length of transects that would fit within the prairie fragment (on the small and medium fragments) and time available for surveying (on the large fragments). Transects were placed at least 100 m from the edge of the prairie, to avoid edge effects that might influence the bird community (Fletcher 2005). In two cases, prairie fragments were shaped so that a standard-length transect would not fit and still be at least 100 m from the prairie's edges. For these sites, we used shortened transects (700 and 750 m) that extended as far as the shape of the prairie allowed. Transects were a single straight line, unless the size of the prairie or the location of wetlands prevented it. In those cases we broke the transect into multiple smaller transects (Gates 1981) placed at least 300 m apart to avoid double counting birds (Davis and Brittingham 2004; Koper and Schmiegelow 2006).



◀ **Fig. 1** Field sites in North Dakota, South Dakota, and Minnesota, $n = 29$. Agency responsible for managing the site is indicated by symbol on the map

Transects were walked at a steady pace and all birds seen or heard within 50 m of the transect were recorded. We used the same observer at all sites to avoid observer bias. Birds flying over the transect were only recorded if they actually landed on the prairie fragment or were observed foraging aerially above it. For each bird sighted we recorded the species and distance along the transect (determined by a hand-held GPS accurate to 3 m, Garmin eTrex H Handheld Navigator).

Local habitat characteristics

We used a Robel pole to quantify vegetation height and structure (Robel et al. 1970) every 100 m along the transect, with the pole placed 1-m off the transect to avoid the disturbance to the vegetation from walking the transect. We also visually estimated the percent cover of grasses, forbs, trees, shrubs, and bare ground within 5 m along each transect. The estimates were made along 100 m segments of the transect, then averaged over the length of the transect. These measurements were performed once during the study (2010) on the same day as the bird surveys, because the relative amount of each cover type was unlikely to change drastically between the two survey years. In addition, we interpreted and digitized (using Arc GIS 9.3 and 10.0: ESRI 2010; 2011) land cover from digital aerial photographs of each prairie fragment to determine the percent cover of grass, woody vegetation, vegetated wetlands, and open water on each prairie fragment. These images were obtained from the National Agriculture Imagery Program (NAIP), via the Minnesota Department of Natural Resources Data Deli (<http://deli.dnr.state.mn.us>), the North Dakota GIS Hub (<http://www.nd.gov/gis>), and the South Dakota Department of Environment and Natural Resources (<http://www.sdgs.usd.edu>). The most recent images available at the time were from 2009 (Minnesota and North Dakota) and 2008 (South Dakota).

Landscape characteristics

We collected landscape-level data by interpreting and digitizing land cover from the digital aerial

photographs described in the local habitat characteristics section. We verified the aerial photographs by walking the outer perimeter of each prairie fragment, and driving through each landscape and observing the land cover. For each prairie remnant, we used GPS coordinates to locate the site on the aerial photograph and digitized the remnant boundaries based on the extent of native unplowed prairie using site maps provided by the organization managing the site. Multiple sites were surrounded by grasslands of other types [such as Conservation Reserve Program (CRP) plantings or restored prairie], which were excluded from the remnant since bird species might respond differently to these types of grasslands due to differences in vegetation structure (Ahlering and Merkord 2016).

Once the remnant patch was defined, we created a 4-km buffer around the site, to delineate landscape extent. This distance provided greater spatial extent than previously seen in most avian landscape studies (e.g., Bakker et al. 2002; Renfrew and Ribic 2008; Ribic et al. 2009a) while still being manageable for digitizing landscape features. The digitized landscapes varied from 5418 to 10,448 ha (median = 6435.6 ha, IQR: 6160.3–7578.9 ha) and were separated from their closest neighbor by a minimum of 1 km and a maximum of 79 km, with a median of 13 km (IQR: 4–31 km).

We defined land use/land cover categories using a land cover classification scheme (Table 1) adapted from a U.S. Geological Survey classification scheme developed for remotely-sensed data (Anderson et al. 1976). We streamlined this scheme to eliminate matrix elements absent in our study area and more finely subdivided grassland categories (i.e., differentiating between native grasslands, marginal grasslands, restored grasslands, and CRP). We interpreted aerial photographs visually and digitized polygons of like land use/land cover.

To assess the spatial scale of landscape effects, we subdivided each of the 29 landscapes using five different buffers (500 m, 1, 2, 3, and 4 km). For each landscape and at each spatial scale we calculated landscape measures including the amount of each landscape element, the configuration of each landscape element, and overall measures of landscape structure.

We calculated percentage cover for each landscape element from the digitized landscape. The remaining

Table 1 Land cover classification scheme adapted from Anderson et al. (1976). In this adaptation, grassland habitats are more specifically subdivided according to management history. Variable names are indicated in parenthesis

Level 1	Level 2	Matrix element description
Agriculture	Small grains & row crops (Row)	Actively plowed, planted, and harvested fields
	Pasture (Pas)	Grassland used for grazing cattle, horses, and other livestock
	Hay (Hay)	Grasslands that are cut and baled at least once a year, including road margins and similar fragments that are otherwise unused
Forested	High density forest (HDF)	Tree cover of 10% or more, of any tree species assemblage
	Savannah (Sav)	Mixed grassland and trees, with a tree cover of less than 10%
	Forested riparian buffer (FRB)	The area of land under influence of a stream or river, with more than 10% tree canopy cover
	Windbreaks (Win)	Rows of planted trees in a linear arrangement
	Shrubs (Bru)	Areas with greater than 10% shrub cover
Grassland	Native grassland (Nat)	Unplowed prairie that retains at least a partial native prairie plant community
	Restored grassland (Res)	Grasslands currently displaying a prairie plant community, which had been previously used for agricultural purposes and replanted with native species.
	Conservation Reserve Program (CRP)	Fields enrolled in the Conservation Reserve Program, previously agriculture but planted with prescribed grass seed mixes
	Herbaceous riparian buffer (HRB)	The area of land under influence of a stream or river, with less than 10% tree canopy cover
	Marginal grassland (Mar)	Areas of grassland not actively managed or grazed, such as along fences and in between fields. Also fields that have been left to go fallow, but were not enrolled in the Conservation Reserve Program
Water	Open water (Wat)	Ponds, lakes, and portions of wetlands that do not contain emergent vegetation
	Wetlands (Wet)	Submerged or saturated areas covered in emergent vegetation at the time of study. Includes natural and man-made wetlands
Anthropogenic	Urban (Urb)	Land with a high proportion (80% or more) of impermeable surfaces, including roads, residential and commercial areas, and associated land features (parks, lawns, golf courses etc.)
	Rural commercial (RC)	Land occupied by extensive buildings, paved areas, or bare ground, not adjacent to a town or city, including airports
	Rural residential (RR)	Farm homesteads and associated outbuildings, lawns, and windbreaks
	Gravel pit (Grav)	Areas where vegetation and topsoil have been removed to access gravel deposits
	Minor road (Road)	Roads with 1 or 2 lanes, including rural paved and gravel roads
	Major highway (Hwy)	Roads with 4 or more lanes
Barren land	Railroad (Rail)	Railroad tracks and associated gravel beds
	Bare ground (Bare)	Areas lacking in vegetative cover, not associated with mines, agriculture, residences, or commercial sites

landscape variables were calculated from a raster image. We converted each digitized aerial photograph to a raster image using ERDAS Imagine 2011 (Intergraph 2011) and used FRAGSTATS version 3.3 (McGarigal et al. 2002) to calculate landscape indices (Table 2). For each landscape element, we

assessed the structure and arrangement of that element within the landscape using various measures (see Table 2). We also assessed indices of the aggregate landscape to determine if the songbirds were responding to the overall combination of the composition and configuration of the elements in the landscape. The

Table 2 List of variables used in the three-pronged multi-model logistic regression analysis framework. Local variables included vegetation measurements taken along the sampling transects and % cover variables measured using ArcGIS. Aggregate landscape variables were measured using FRAGSTATS, and were divided into composition and configuration classes. Matrix element variables, focusing on specific habitat types found within the overall landscape, were also divided into composition and configuration classes, with composition variables being measured using Arc GIS and configuration classes being measured with FRAGSTATS

Variable type	Units	Calculated with	Variable name
Local variables			
Transect variables			
Forb cover	%	Visual estimate	Forb
Grass cover	%	Visual estimate	Grass
Shrub cover	%	Visual estimate	Brush
VOR	decimeter	Robel pole	Robel
Patch variables			
Patch size	hectare	ArcGIS	Patch
Tree cover	%	ArcGIS	HDF
Open water	%	ArcGIS	Water
Wetland	%	ArcGIS	Wetland
Aggregate landscape variables			
Composition			
Matrix element richness	n/a	Fragstats	PR
Matrix element diversity	n/a	Fragstats	SHDI
Configuration			
Total edge density	meters/hectare	Fragstats	EDL
Contagion	%	Fragstats	Contag
Matrix element variables ^a			
Composition			
Area	%	ArcGIS	A
Configuration			
Number of patches	n/a	Fragstats	NP
Median patch area	ha	Fragstats	MD
Patch density	#/100 hectares	Fragstats	PD
Edge density	meters/hectare	Fragstats	ED
Euclidean nearest neighbor distance	meters	Fragstats	ENN

^a Each of these variables are calculated for each land cover type (see list in Table 1)

aggregate landscape variables were divided into those associated with the composition of the landscape (types of land cover elements present: Habitat Richness, Habitat Diversity) and with the configuration of those different landscape element patches (the arrangement of patches within the landscape: Total Edge Density, Contagion). As the landscape sampled changed size with different sized focal patches, we normalized all landscape variables to avoid any potential bias.

Data analysis

We used multiple logistic regression in R 2.14.2 (R Development Core Team 2015) to relate species presence/absence to landscape and habitat characteristics. We only analyzed species found on 11–20 of the

29 sites (Table 3) to ensure that there was enough variability in the data to allow the model-fitting algorithm to be successful. The logistic regressions were completed within a multi-model framework (Burnham and Anderson 2002). Because of the large number of potential explanatory variables involved, we took a multi-pronged (local variables, matrix elements, and aggregate landscape variables) and multi-stage approach to the multi-model multiple logistic regression analysis (Fig. 2). Due to the fact that we had longer transects on larger prairie fragments there was a potential for the passive sampling effect to bias the presence data (Johnson and Igl 2001; Ribic et al. 2009b). We corrected for this by using transect length as an offset in all the logistic regression models (Faraway 2006). This process was repeated for each bird species analyzed.

Table 3 Bird species (common name, alpha code, scientific name) observed on the focal patches organized by habitat preference status (based on feeding and breeding habitats, Ehrlich et al. 1988). Species used in the logistic regression analyses are identified by **

Species	Scientific Name	Number of sites
Grassland Obligates		29
Bobolink (BOBO)	<i>Dolichonyx oryzivorus</i>	28
Chestnut-collared Longspur (CCLO)	<i>Calcarius ornatus</i>	4
Dickcissel (DICK)	<i>Spiza americana</i>	7
Grasshopper Sparrow (GRSP)**	<i>Ammodramus savannarum</i>	12
Savannah Sparrow (SAVS)	<i>Passerculus sandwichensis</i>	26
Upland Sandpiper (UPSA)**	<i>Bartramia longicauda</i>	13
Western Meadowlark (WEME)**	<i>Sturnella neglecta</i>	19
Wilson's Snipe (WISN)	<i>Gallinago gallinago</i>	1
Grassland Users		29
Brown-headed Cowbird (BHCO)	<i>Molothrus ater</i>	21
Clay-colored Sparrow (CCSP)	<i>Spizella pallida</i>	27
Cliff Swallow (CLSW)**	<i>Hirundo pyrrhonota</i>	14
Eastern Kingbird (EAKI)	<i>Tyrannus tyrannus</i>	25
Field Sparrow (FISP)	<i>Spizella pusilla</i>	4
Killdeer (KILL)	<i>Charadrius vociferous</i>	1
LeConte's Sparrow (LCSP)**	<i>Ammodramus leconteii</i>	12
Vesper Sparrow (VESP)	<i>Pooecetes gramineus</i>	5
Western Kingbird (WEKI)	<i>Tyrannus verticalis</i>	1
Wetlands		27
Common Yellowthroat (COYE)	<i>Geothlypis trichas</i>	23
Marsh Wren (MAWR)**	<i>Cistothorus palustris</i>	14
Red-winged Blackbird (RWBL)	<i>Agelaius phoeniceus</i>	25
Sedge Wren (SEWR)**	<i>Cistothorus platensis</i>	13
Yellow-headed Blackbird (YHBL)	<i>Xanthocephalus xanthocephalus</i>	6
Tree		17
American Goldfinch (AMGO)**	<i>Carduelis tristis</i>	12
Black-billed Magpie (BBMA)	<i>Pica pica</i>	1
Orchard Oriole (OROR)	<i>Icterus spurius</i>	1
Tree Swallow (TRES)	<i>Tachycineta bicolor</i>	8
Yellow Warbler (YEWA)	<i>Dendroica petechia</i>	6
Shrub		11
Alder Flycatcher (ALFL)	<i>Empidonax alnorum</i>	1
Brown Thrasher (BRTH)	<i>Toxostoma rufum</i>	1
Gray Catbird (GRCA)	<i>Dumetella carolinensis</i>	4
Song Sparrow (SOSP)	<i>Melospiza melodia</i>	1
Willow Flycatcher (WIFL)	<i>Empidonax traillii</i>	8
Human		9
Barn Swallow (BARS)**	<i>Hirundo rustica</i>	12
Eastern Phoebe (EAPH)	<i>Sayornis phoebe</i>	1
Mourning Dove (MODO)	<i>Zenaida macroura</i>	1
Rock Pigeon (ROPI)	<i>Columba livia</i>	1
Generalist		20
American Robin (AMRO)	<i>Turdus migratorius</i>	7
Common Grackle (COGR)	<i>Quiscalus quiscula</i>	24

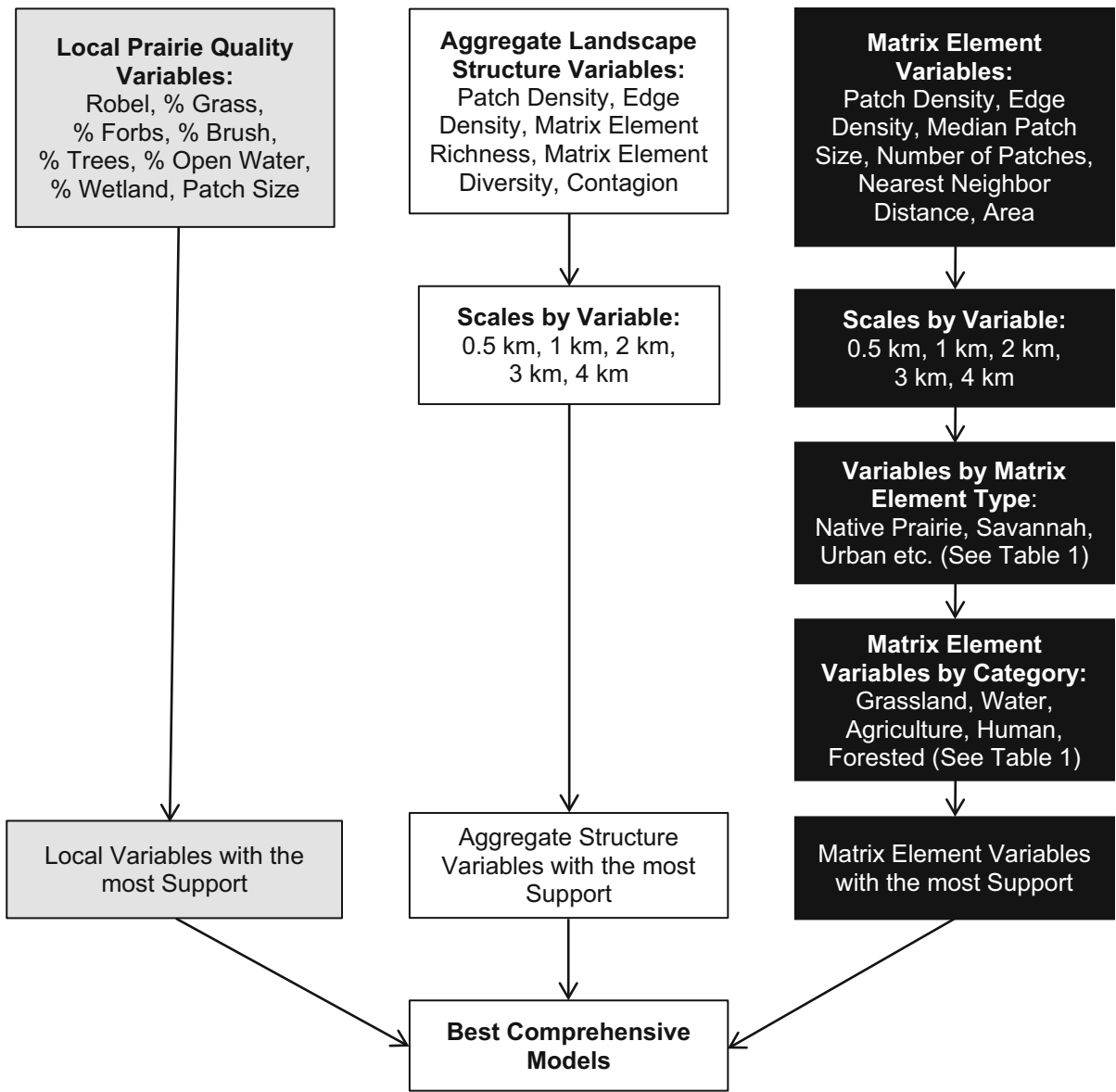


Fig. 2 For each species, occurrence was analyzed using multiple rounds of multi-model logistic regression analysis to identify the variables with the most statistical support at each

level of measurement. For each round of analysis, variables with strong support ($\Delta AIC < 2$) were retained and moved to the next round of analysis

The local variable branch of the analysis consisted of a single multi-model logistic regression analysis to identify the local variables with strong statistical support (defined throughout as those with $\Delta AICc < 2$). The aggregate landscape branch of the analysis focused on those variables associated with overall landscape diversity and structural complexity and was conducted in two steps (Fig. 2). First, for each aggregate landscape variable we identified the spatial scale(s) with the most

statistical support which were retained for the next step. Second, that pool of variables was combined in a multi-model multiple logistic regression analysis to determine the final set of aggregate landscape variables with the most statistical support. The third branch of the analysis (Fig. 2) focused on matrix element variables associated with the structure and amount of those individual matrix elements within the landscape. Because of the large number of variables in this branch, we used multiple

Table 4 The number of models produced for each bird species analyzed (species alpha codes in Table 3) using the multi-pronged multi-model logistic regression approach. The range in deviance explained by the supported models and the range of model weights are indicated

Bird species	Number of models	Range of deviance explained (%)	Range of model weights
GRSP	14	34–46	0.05–0.12
UPSA	5	35–65	0.13–0.33
WEME	13	38–60	0.06–0.14
CLSW	7	28–57	0.11–0.25
LCSP	3	43–47	0.24–0.50
MAWR	6	39–51	0.11–0.24
SEWR	2	63–69	0.37–0.63
AMGO	3	65–77	0.19–0.52
BARS	23	40–72	0.03–0.08

rounds of analysis to narrow the pool of variables. As with the aggregate landscape variables, the first round was used to identify the important scale(s) for each variable. The most important variables were then identified for each matrix element, then for groupings of similar matrix elements (based on Level 1 classifications described in Table 1). We then used the variables from this round to build final matrix element models consisting of the best supported variables from all matrix element types.

We then incorporated the top variables from the local, aggregate landscape, and matrix element analyses into a single analysis to produce the set of best ($\Delta AICc < 2$) logistic regression models including both landscape and local features. Finally, for each bird species we used the entire set of top models to calculate the deviances associated with each specific variable to determine their relative importance. For each variable within a model, the variable deviance was weighted by that of the model itself. Those weighted deviances were then averaged across all models for each variable to assess the relative importance of that variable.

Results

Of the 38 species encountered, nine—American Goldfinch (*Carduelis tristis*), Barn Swallow (*Hirundo rustica*), Grasshopper Sparrow (*Ammodramus sava-narum*), Le Conte’s Sparrow (*Ammodramus leconteii*), Sedge Wren (*Cistothorus platensis*), Upland Sandpiper (*Bartramia longicauda*), Cliff Swallow (*Hirundo pyrrhonota*), Marsh Wren (*Cistothorus palustris*), and Western Meadowlark (*Sturnella*

neglecta)—were found on between 11 and 20 field sites (Table 3) allowing for statistical analysis. The multi-model, logistic regression analysis resulted in multiple models for each bird species that explained 28–77% of patch occupancy deviance (Table 4).

Grasshopper Sparrows were more likely to be found on smaller remnant prairies with less brush cover and in landscapes with fewer CRP edges, greater herbaceous riparian patch density, higher matrix richness and diversity, and lower matrix contagion (Fig. 3A). Upland Sandpipers were more likely to be found on remnant prairies with less grass cover and more brush cover, and in landscapes with more CRP, larger patches of rural commercial land cover, more brush at 1 and 3 km and less brush at 2 and 4 km (Fig. 3B). Western Meadowlarks were more likely to be found on remnant prairies with fewer trees and in landscapes with greater matrix diversity, less matrix contagion, more dispersed CRP patches, and larger windbreak patches (Fig. 3C). Cliff Swallows were more likely to be found on larger remnant prairies with less forb cover, and in landscapes with lower matrix richness, lower matrix contagion, fewer brush patch edges, and lower hay patch density (Fig. 3D). Le Conte’s Sparrows were more likely to be found on prairie remnants with sparser vegetation and less open water, and in landscapes with higher matrix contagion, and more CRP edges (Fig. 3E). Marsh Wrens were more likely to be found on prairie remnants with more wetlands and trees, and in landscapes with lower CRP edge density, more wetland cover, fewer wetland patches, and smaller patches of open water (Fig. 3F). Sedge Wrens were more likely to be found on prairie remnants with less wetlands and less open water, and in landscapes with more total edge density, higher hay

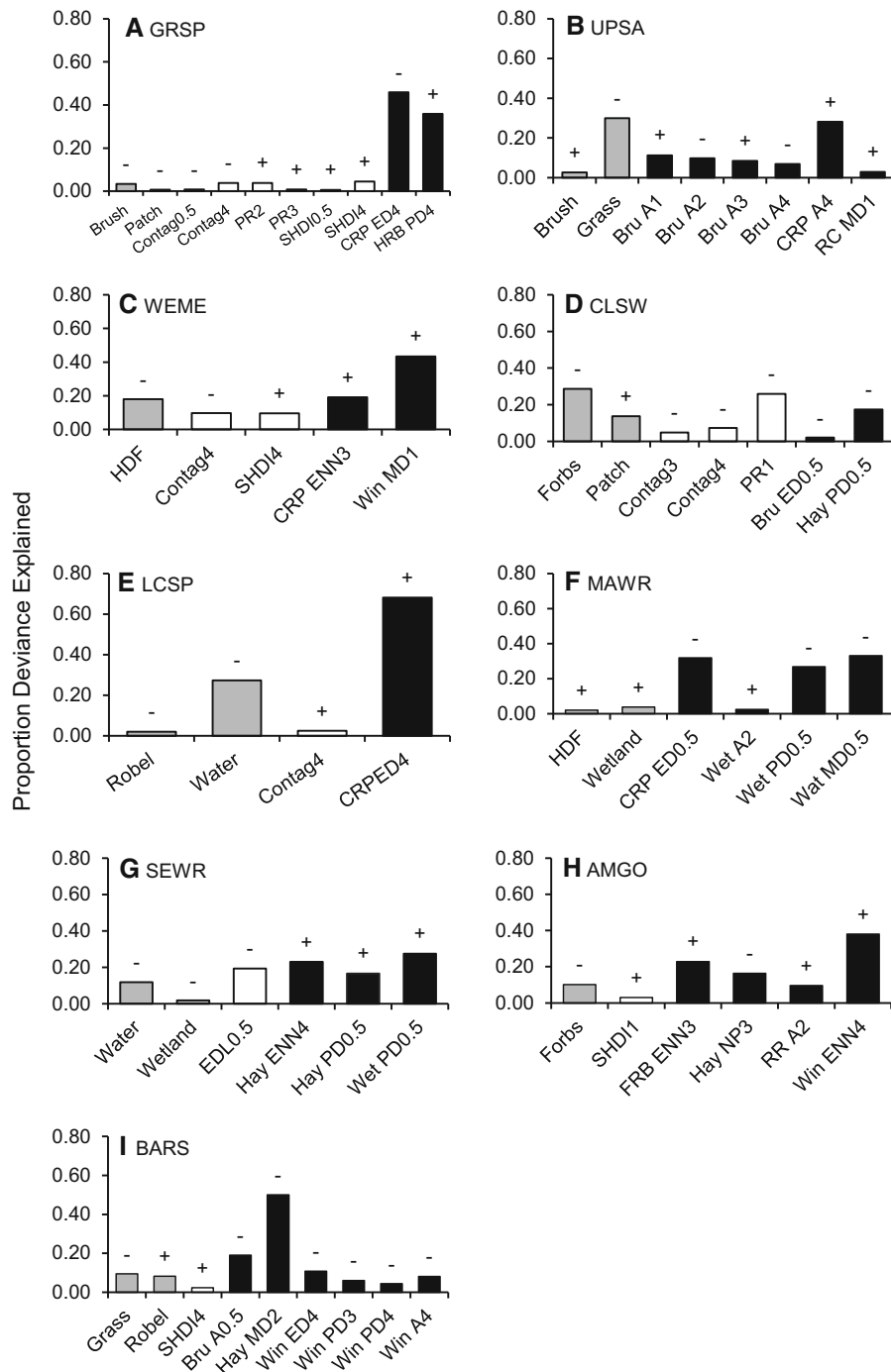


Fig. 3 Proportion of deviance explained by the components of the average model constructed from all top models (those with $\Delta AIC > 2$) for each bird species (Panels A–I). The \pm above each bar indicates if the term had a positive or negative effect on species presence. Model components are grouped into those associated with the prairie patch (grey bars), those associated with aggregate landscape measures (white bars), and those associated with specific landscape matrix elements (black bars).

Variable names are from Table 2. For all landscape variables measurement scale (in km) is indicated by the number at the end of the variable name. For the matrix element variables, the matrix element variable name is from Table 1 and measurement variable name is from Table 2; for example, Pas ED 0.5 refers to edge density of pasture patches within 0.5 km of the prairie patch edge

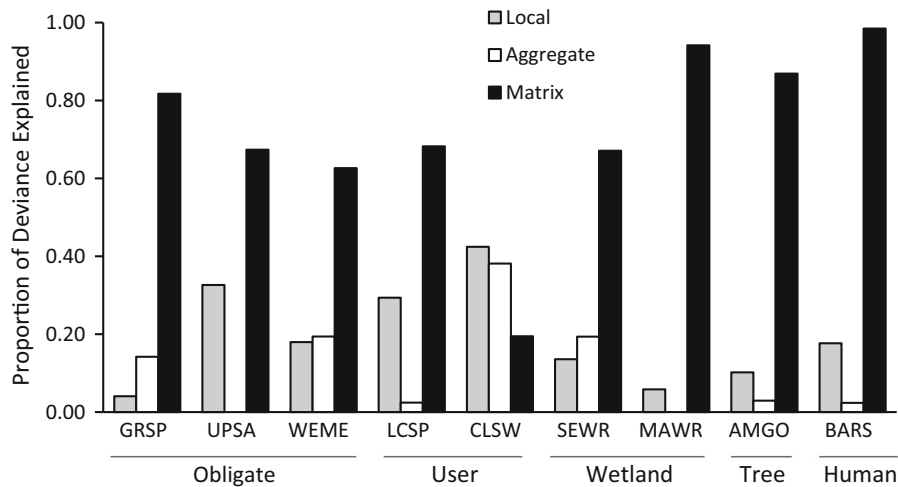
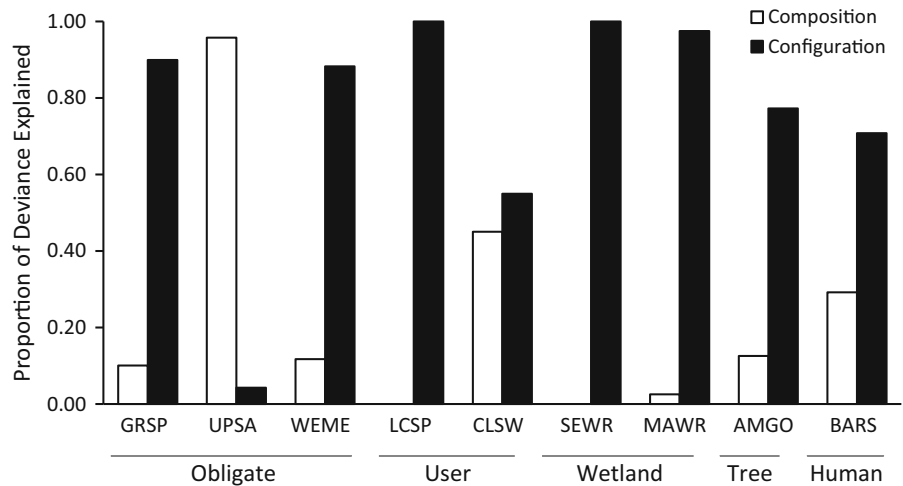


Fig. 4 Proportion of deviance explained in the top models partitioned between local, aggregate landscape, and matrix element variables. Species codes as in Table 3. Habitat

preference for species indicated: grassland obligates, grassland users, wetland users, tree associated, and human associated

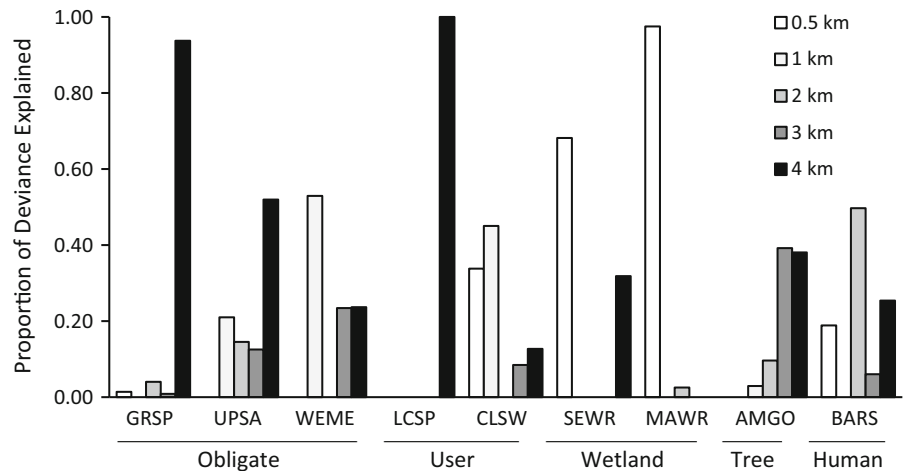
Fig. 5 Proportion of deviance explained by landscape variables (both aggregate landscape and matrix elements) in the top models partitioned between measures of landscape composition and configuration (see Table 2 for lists of variables in each group). Species codes as in Table 3. Habitat preference for species indicated: grassland obligates, grassland users, wetland users, tree associated, and human associated



patch density and more dispersed hay patches, and greater wetland patch density (Fig. 3G). American Goldfinches were more likely to be found on prairie remnants with less forb cover, and in landscapes with higher matrix diversity, more dispersed forested riparian and windbreak patches, fewer hay patches, and more rural residential cover (Fig. 3H). Finally, Barn Swallows were more likely to be found on prairie remnants with less grass cover and denser vegetation, and in landscapes with higher matrix diversity, less brush cover, smaller hay patches, and less windbreak cover arranged with lower patch density and fewer patch edges (Fig. 3I).

Presence of eight of the nine species was most strongly influenced by landscape matrix element variables, while Cliff Swallow responded most strongly to local variables (Fig. 4). Among landscape variables, measures of configuration explained substantially more deviance in presence than measures of composition for seven species, while measures of composition and configuration were about equal for Cliff Swallow and measures of composition explained more deviance in presence for Upland Sandpiper (Fig. 5). Five out of nine species had the largest amount of deviance in presence explained by landscape variables measured at the highest spatial scales

Fig. 6 Proportion of deviance explained by landscape variables (both aggregate landscape and matrix elements) in the top models partitioned between the spatial scales investigated. Species codes as in Table 3. Habitat preference for species indicated: grassland obligates, grassland users, wetland users, tree associated, and human associated



(3 and 4 km), the Western Meadowlark had an equal amount of deviance explained by large and small spatial scales, and the three remaining species (Cliff Swallow, Sedge Wren, and Marsh Wren) had the most deviance in presence explained by landscape variables measured at the smallest spatial scales (0.5 and 1 km; Fig. 6).

There was no clear relationship between the relative importance of local vs landscape variables and habitat guild, although the species with the strongest influences of local variables were all grassland obligates or users. Two grassland obligate species and one of the two grassland users responded most strongly to landscape variables measured at the 4 km scale. The type of variables that had the biggest effect on presence varied by habitat guild. Grassland obligates and grassland users responded primarily to CRP, hay, and brush with most species responding to patch arrangement (e.g., measures of edge, spacing, or patch density) as opposed to amount. The wetland users responded most strongly to patch density of water-based matrix elements.

Discussion

Individual species responses

The presence of Grasshopper Sparrows on a focal patch was strongly influenced by landscape edges. Edge sensitivity has been documented in this species (DeLisle and Savidge 1996; Helzer and Jelinski 1999),

including a negative effect of shrubs (Whitmore 1981; Grant et al. 2004; Sutter and Ritchison 2005).

Local patch variables that influence nesting and foraging abilities played the largest role in predicting prairie remnant use by Upland Sandpipers. This species requires bare ground for nesting and feeding (Houston et al. 2011) explaining the negative effect of grass cover on sandpiper presence. Remnant prairie patches are more likely to be used by sandpipers only in landscapes with large enough grassland areas to provide both the bare ground and the dense vegetation needed for birds to feed and nest (Fritcher et al. 2004) which seem to be provided by CRP grasslands.

Western Meadowlarks were strongly influenced by the amount of edge in the landscape surrounding remnant prairies (as indicated by patch size and contagion measures). Western Meadowlarks are both edge (Bock et al. 1999) and area sensitive (Helzer and Jelinski 1999; Johnson and Igl 2001), although area sensitivity may be due to edge sensitivities (Johnson and Igl 2001; Fletcher 2005), and this edge sensitivity likely explains the importance of edges in the landscape for meadowlark occurrence. Locally, the amount of tree cover on the prairie fragment decreased the probability of Meadowlark occurrence, probably due to increased predation risk (Johnson and Temple 1990; Conover et al. 2011).

Unlike most other species in this study, deviance in Cliff Swallow presence was almost entirely explained by local variables. This species prefers open spaces conducive to aerial foraging (Ehrlich et al. 1988; Brown and Brown 1995) which are more likely to

occur on larger prairie patches with less forb coverage. Further, insect prey availability seems to be an important determinant of Cliff Swallow colony location and size (Brown et al. 2002) and is likely affected by the size and quality of the prairie patch.

We found Le Conte's Sparrow were more likely to be present on prairie patches embedded in landscapes with more CRP edges. This species breeds in both native prairie and CRP fields (Igl and Johnson 1995, 1999; Lowther 2005) though is potentially edge avoiding (Johnson and Igl 2001). Interestingly, Le Conte's Sparrow responded positively to CRP edge density in the surrounding landscape, suggesting that habitat patch edge sensitivity may not extend to the overall landscape structure.

The probability of Marsh Wrens occurring on a prairie patch increased with greater wetland area in the surrounding landscape, as would be expected from a wetland associated species (Cunningham and Johnson 2006; Spautz et al. 2006; Kroodsma and Verner 2014). However, the probability of being present decreased with increasing wetland patch density suggesting that landscapes with highly fragmented wetlands were not as attractive to Marsh Wrens. This is likely due to edge sensitivities (Fairbairn and Dinsmore 2001; Spautz et al. 2006). High edge sensitivity also explains our finding that high CRP edge density close to the prairie patch also decreased the probability of Marsh Wren being present.

In contrast to Marsh Wrens, Sedge Wrens were more likely to be present if the landscape had higher densities of wetland and hay patches. Sedge Wrens rely on wet meadows and seasonal wetlands to provide preferred sedge and grass seeds (Herkert et al. 2001). More wetland patches in the landscape likely increases the availability of wet meadow habitat (Fairbairn and Dinsmore 2001; Riffell et al. 2001; Bakker et al. 2002).

As an edge species, American Goldfinch (Herkert 1994; Horn et al. 2002) rely on shrubs and trees for nesting and cover (Stokes 1950; Middleton 1979; McGraw and Middleton 2009; personal observations). At our study sites, trees and shrubs were mostly found in the windbreaks between fields and, to a lesser extent, in riparian buffers, and landscapes with more evenly spaced windbreaks and forested riparian buffers were more likely to have goldfinches. Monotypic hayfields do not contain enough seeds for foraging (McGraw and Middleton 2009) and the

presence of hay fields actually reduces the probability of goldfinch occurrence.

Similar to the American Goldfinch, Barn Swallow presence was driven almost entirely by landscape variables. This species is considered a generalist, using a wide variety of habitats and feeding on many different types of prey (Turner 2006), and preferentially uses edges that concentrate or increase prey availability (Evans et al. 2003). Landscapes with smaller hay patches were more likely to provide such foraging opportunities. The tall vertical structure of windrows can interfere with foraging (Henderson et al. 2007) and so landscapes with more windrows were less likely to have swallows.

Landscape effects

For eight of the nine species studied, the landscape variables explained much more of the deviation in patch occupancy than the local patch characters did. Prior studies of grassland birds have had mixed results with some detecting landscape effects (Söderström and Pärt 2000; Ribic and Sample 2001; Bakker et al. 2002; Hamer et al. 2006; Winter et al. 2006; Renfrew and Ribic 2008), others finding little to no effect of the landscape (Bajema and Lima 2001; Horn et al. 2002; Koper and Schmiegelow 2006; Jacobs et al. 2012), and yet others finding the combination of local and landscape variables having the greatest explanatory power (Fletcher and Koford 2002; Cunningham and Johnson 2006; Quamen 2007). Reviews of landscape studies have found landscape effects in less than 80% of bird-focused studies (Mazerolle and Villard 1999) and that bird studies were least likely to demonstrate landscape effects, even though birds were one of the most frequently studied taxa (Thornton et al. 2011). Some of the ambiguity in the importance of landscape variables is likely due to methodological approaches, particularly how the landscape data were gathered. Studies that simply buffer from the bird sampling points (e.g., Best et al. 2001; Coppedge et al. 2001; Bakker et al. 2002; Fletcher and Koford 2002; Winter et al. 2006) would potentially mix local and landscape data together obscuring the importance of the landscape. Furthermore, many studies tended to measure landscape data on smaller scales (2 km or less) than we did (e.g., Bergin et al. 2000; Bajema and Lima 2001; Ribic and Sample 2001; Grant et al. 2004; Jacobs et al. 2012) and we saw strong bird responses to

landscape variables measured 3–4 km beyond the edge of the prairie patch, suggesting studies measuring landscape variables at smaller scales might miss landscape effects on bird occurrence. The design of our study (a focal patch approach that clearly delineated local vs landscape effects and a large extent for the landscape data) allowed us to detect landscape influences on bird occupancy of remnant prairie patches.

Most of the species we analyzed seemed more sensitive to the configuration of elements in the surrounding landscape, rather than the composition of the landscape. One of the striking patterns across the species in this study is the prevalence of responses to habitat edges. Seven of the nine species responded to at least one edge measurement (either edge density or contagion), and three species (Grasshopper Sparrow, LeConte's Sparrow, Cliff Swallow) responded to more than one edge variable, although the type and magnitude varied significantly between species. Interestingly, only one species responded to total edge density (Sedge Wren), indicating that the specific edge type might be much more important than estimated by previous research (DeLisle and Savidge 1996; Winter et al. 2000; Jensen and Finck 2004; Koper et al. 2009).

The importance of the surrounding landscape, particularly at the larger scales that we observed, match with the hierarchical approach that many bird species use to choose breeding territories (Reed et al. 1999). As birds return in the spring to find new nesting grounds for the year, they first look for specific matrix elements at broad scales. These matrix elements can either be avoided, as Grasshopper Sparrows avoid areas with high CRP edge density, or targeted, as is seen with Upland Sandpipers that choose regions with higher amounts of CRP. Once the migrating birds have selected a region they are going to settle in, focal-patch level characteristics become important, including the relationships with woody vegetation and vegetation structure that have been well documented previously (Whitmore 1981; Davis et al. 1999; Winter et al. 2005; Jacobs et al. 2012).

There was little influence of habitat preference of the bird on relationships between patch occupancy and landscape characters. Grassland obligates and grassland users were slightly more likely to have some influence from local variables, with one grassland user (Cliff Swallow) being the only species to have local

variables as important as landscape variables. Given the demonstrated importance of habitat characteristics for these grassland users (Whitmore 1981; Davis et al. 1999; Winter et al. 2005; Jacobs et al. 2012) it is not surprising that these two groups of birds are more likely to have a stronger influence of local variables. It is worth pointing out that even so, for 4 of the 5 species in these two groups, landscape variables were more important than local variables. The only other pattern with guild was that the wetland users responded to landscape variables at shorter distances than birds from all the other guilds, with the exception of the grassland user the Cliff Swallow. Despite these weak patterns across habitat preference groups, it seems that each species responds to the landscape in a unique manner dictated by the specifics of its life history, behavioral responses to landscape elements, and movement capabilities.

Our findings have implications for conservation management for grassland songbirds. While it is true that songbird management can only occur on specific parcels of land (like the focal patch) rather than at the entire landscape scale, understanding the landscape context around the focal patch can help to identify songbird populations located in less-hospitable landscapes, which may be in need of local habitat improvements that would provide population support. As such, future species management plans should include an understanding of the landscape context out to at least 4 km, if not further. Efforts should also be made to include details about matrix element configuration and edge type rather than area only (particularly for those matrix elements that provide sharp contrasts to grassland structure). Plans targeted at species with very specific or limiting habitat requirements should also include information about landscape composition, with specific attention being paid to matrix elements that either complement those requirements or make them harder to be met.

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