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RESEARCH ARTICLE

Multi-scale models of grassland passerine abundance in a fragmented system in Wisconsin

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Abstract Fragmentation of grasslands has been implicated in grassland bird population declines. Multi-scale models are being increasingly used to assess potential factors that influence grassland bird presence, abundance, and productivity. However, studies rarely assess fragmentation metrics, and seldom evaluate more than two scales or interactions among scales. We evaluated the relative importance of characteristics at multiple scales to patterns in relative abundance of Savannah Sparrow (*Passerculus sandwichensis*), Grasshopper Sparrow (*Ammodramus savannarum*), Eastern Meadowlark (*Sturnella magna*), and Bobolink (*Dolichonyx oryzivorus*). We surveyed birds in 74 southwestern Wisconsin pastures from 1997 to 1999 and compared models with explanatory variables from multiple scales: within-patch vegetation structure (microhabitat), patch (macrohabitat), and three landscape extents. We also examined interactions between macrohabitat and landscape factors. Core area of pastures was an important predictor of relative abundance, and composition of the landscape was more important than configuration. Relative abundance was frequently higher in pastures with more core area and in landscapes with more grassland and less wooded area. The direction and strength of the effect of core pasture size on relative abundance changed depending on amount of wooded area in the landscape. Relative abundance of grassland birds was associated with landscape variables more frequently at the 1200-m scale than at smaller scales. To develop better predictive models, parameters at multiple scales and their interactive effects should be included, and results should be evaluated in the context of microhabitat variability, landscape composition, and fragmentation in the study area.

Keywords Fragmentation · Grassland birds · Landscape · Area sensitivity · Patch · Relative abundance · Vegetation · Modeling · AIC

Introduction

In response to the call for a hierarchical approach to bird conservation (e.g., Coppedge et al. 2001; Turner et al. 2001; Bissonette and Storch 2003), a multi-scale approach to assess factors associated with bird

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abundance and nest success has become commonplace. This is especially relevant for studies assessing effects of habitat fragmentation (e.g., Chalfoun et al. 2002), and has been recommended specifically for grassland bird species (Koper and Schmiegelow 2006).

Research indicates that grassland birds select territories using information at more than one scale. Some species are more likely to occur or have higher densities on large patches of suitable habitat (Bollinger and Gavin 1992; Herkert 1994a, b; Vickery et al. 1994; Johnson and Igl 2001). In northeastern and midwestern U.S. grasslands, the landscape matrix surrounding a patch can influence the strength and direction of patch size effects on density or relative abundance (Coppedge et al. 2001; Ribic and Sample 2001; Bakker et al. 2002; Horn and Koford 2006). Furthermore, inter-annual variability of microhabitat attributes could influence the relative importance of patch and landscape factors on grassland bird density or relative abundance (Davis 2004; Winter et al. 2005). In a year when quality habitat is relatively scarce, patch or landscape characteristics may be of secondary importance as suitable nesting microhabitat becomes scarce. To accurately assess effects of patch size on grassland bird abundance, it is important to take into account both microhabitat and landscape scales in the context of inter-annual variation in microhabitat.

Hierarchy theory predicts that birds are selecting landscape characteristics before selecting finer scale attributes (Turner et al. 2001; Hutto 1985; Wiens 1973). Grassland bird studies have assessed importance of patch-scale characteristics in relation to one scale up (landscape) (e.g., Davis et al. 2006; Horn and Koford 2006), or one scale down (microhabitat or vegetation) (e.g., Davis 2004). Few studies have assessed the relative importance of all three scales on grassland bird abundance (Winter et al. 2006).

A multi-scale approach also allows assessment of interactions between the influence of landscape attributes and patch size (Mazerolle and Villard 1999; Andren 1994). A habitat criterion for grassland birds is large, open areas (Bollinger and Gavin 1992; Herkert 1994a; Part and Soderstrom 1999), and the composition of the landscape matrix may influence occupancy or abundance within a given patch size. For example, a small grassland patch within a grassland-dominated matrix may be more likely to be occupied than a similar-sized patch within a matrix dominated by non-grassland habitat (Horn and Koford 2006).

The purpose of this study is to evaluate grassland passerines in southwestern Wisconsin pastures for (1) the relationship between relative bird abundance and microhabitat, macrohabitat, and landscape characteristics, (2) how macrohabitat and landscape parameters interact in predictive models of relative bird abundance over multiple years, and (3) the extent to which landscape features are associated with relative bird abundance in this system.

Methods

Study area

We surveyed 74 pastures (mean area = 36.9 ha, median = 22.9 ha, range = 1.5–169.0 ha) from 1997 to 1999 in Crawford, Green, Grant, Iowa, Lafayette and Vernon counties of southwestern Wisconsin, part of the Driftless Area. For May–July 1997, 1998, and 1999, average temperature in Darlington, Wisconsin (located within 100 km of all study sites) was 17.6, 19.3, and 19.9°C, respectively and mean monthly rainfall was 12.8, 4.0, and 16.1 cm, respectively (U.S. Dept. of Commerce N.O.A.A. 2007). Average decadal (1990–1999) May–July temperature was 18.7°C and mean monthly rainfall was 11.7 cm. For our study, 1997 was slightly cooler and wetter than average, 1998 had an average temperature but was extremely dry, and 1999 was slightly warmer but much wetter than average.

We surveyed all pastures we could find (using orthophotos, drive-by, and consulting with farmers and state agricultural agents) that were greater than 1.5 ha and contained <5% woody vegetation. The distribution of size classes was skewed towards smaller pastures because they are more common than large pastures in this region. Pastures were dominated by non-native cool-season grasses such as Kentucky bluegrass (*Poa pratensis* (L.)), quack grass (*Elytrigia repens* (L.)), timothy (*Phleum pratense* (L.)), fescue (*Festuca* spp.), rye grass (*Elymus virginicus* (L.)), and smooth brome (*Bromus inermis* (Leyss.)). Shrubs were rare, but thistle (*Carduus* spp., *Cirsium* spp.) was common. Each pasture contained 0–7 isolated trees (usually Burr Oak (*Quercus* *macrocarpa*)). Study sites reflected the range of cattle stocking densities in the study region. Stocking rates on a subset of pastures used in a related study were 0.61–4.28 animal units/ha (mean = 2.09, SE = 0.37, n = 10) and 0.75–4.33 animal units/ha (mean = 2.19, SE = 0.34, n = 9) in 2000 and 2001, respectively (1 animal unit = 454 kg) (Renfrew et al. 2005).

Bird surveys

Birds were surveyed using 100-m-radius, 5-min point counts. All individuals seen and heard were counted. Points were located so as to fit as many as possible in areas of each site that contained no trees, with the outer edge of each point circle at least 25 m from pasture edges when possible. Points were separated by ≥300 m to avoid double counting birds (Savard and Hooper 1995). Two surveys were conducted at each site: one in late May and one in June, with 3–4 weeks between surveys. Four different observers conducted point counts, one of whom conducted them in all 3 years (i.e., 2 observers per year). To minimize bias, observers conducted practice point counts together for 2–3 d to calibrate to each other. Each of the 2 observers surveyed half of the sites for the first survey, and then the other half for the second survey.

Microhabitat variables

We chose vegetation (microhabitat) variables to measure structural characteristics associated with grassland bird abundance (e.g., Rotenberry and Wiens 1980; Sample 1989). Measurements were made at each site within 5 days of the first bird survey in May, when most nesting birds had established territories. To minimize bias in vegetation measurements, one person conducted measurements in all 3 years, and a second person (different each year) conducted measurements only after calibrating with the first person. Within each point-count circle, we established four random stations. At each station, %bare ground, %live cover, and %live cover composed of forbs were estimated within a standard 0.5-m^2 Daubenmire frame (Daubenmire 1968) to the nearest 5%. Vegetation height-density (cm) was recorded with a Robel pole placed at the center of the frame (Robel et al. 1970); the pole was read from a height of 1.5 m rather than from 3 different heights. Readings of vegetation obstruction were taken by looking at the pole from 4 directions at 90° intervals, and the resulting 4 values were averaged. Measurements for vegetation variables were averaged over all point counts to obtain one value per pasture for each variable. The vegetation variables were not highly correlated ($r < 0.40$).

Macrohabitat and landscape variables

All land use 1200 m beyond the boundaries of each pasture was digitized from 1995 1:20,000 black-and-white orthophotos (Southeastern Wisconsin Regional Planning Commission GIS Division) using ArcInfo (Environmental Systems Research Institute 1998). Pasture sites were delineated by the contiguous grassland that was under active grazing management during the study. Any adjacent land use that was grassland but was managed for purposes other than grazing was not part of the pasture site. Nest density declined dramatically within approximately 25 m of pasture edges (Renfrew et al. 2005), so we considered core pasture habitat to be total area of pasture >25 m from the pasture edge. We used natural log of core habitat area (ha) (macrohabitat) in all analyses. Land cover was assigned to one of the following categories: suitable grassland (pasture, grass hay, alfalfa, CRP, idle grass), developed (included urban or suburban areas, farmsteads and roads), wooded, and crop (corn, grain, soybean, and rotations of any combination of these crops). Land cover type was determined by ground-truthing in 1998 and 1999; during the growing season we accessed every polygon, and noted attributes of each polygon on a hard copy of the image. Changes in land use between years were minimal. Contiguous patch area was the area of the pasture site plus the area of any contiguous grassy cover adjacent to the pasture (grass hay, idle grassland, alfalfa or CRP). We did not use the core of the contiguous area because the proportion of edge in these large areas and relative difference in area between pastures with different shapes were small. A boundary was drawn where adjacent grasslands bordered <3% of the contiguous patch to prevent the inclusion of grasslands that were connected to the contiguous patch only by small “bottlenecks.”

To evaluate how the landscape may influence bird abundance at different scales, we created 3 landscape buffers, 0–200 m, 0–700 m, and 0–1200 m, from the outer edge of each pasture (i.e., larger buffers included smaller buffers). We transformed ArcInfo vector coverages into raster grids with 20-m pixels. We chose this pixel size because it smoothed differences between coverages due to digitizing accuracy without losing the smallest polygons.

We were interested in the percentage, fragmentation, and shape of suitable grassland and wooded patches in the landscape surrounding each pasture site. We calculated landscape metrics from raster data using FRAGSTATS (McGarigal and Marks 1994) and APACK (Mladenoff and DeZonia 2001). For all three buffer sizes, we calculated the percentage of the landscape that was suitable grassland and wooded areas. Percentage cropland was not used in analyses because, as the third most common land use, it would have been correlated with suitable grassland and wooded areas. Additional metrics were calculated for the 1200-m buffer based on their ability to succinctly and meaningfully quantify fragmentation. To quantify the degree of fragmentation of grasslands and wooded areas, we calculated the centroid connectivity index for each land cover type (Forman and Godron 1986), which indicates whether the landscape is composed of many small patches that are far apart versus large patches that are relatively close together (Mladenoff and DeZonia 2001). Mean core area index of grasslands was calculated to evaluate the proportion of grassland area composed of core area (>25 m from the edge of a patch). This metric was a proxy for a shape index.

Analysis

Relative bird abundance estimates for each species were calculated for each pasture and within each year from point counts. Relative abundance per point count was the average of the two surveys.

We tested for differences in vegetation structure using repeated measures analysis of variance using sites that were surveyed in all 3 years ($n = 51$). We checked for interactions between vegetation variables and year for the most abundant species, Savannah Sparrow (*Passerculus sandwichensis*). There were interactions with year ($P < 0.05$) for height density and forb cover. In particular, the relationship between forb cover and height density in 1997 and 1999 was positive and negative, respectively. Therefore, we modeled relative abundance of each species for each year separately.

We modeled relative abundance as functions of microhabitat, macrohabitat and landscape variables at different scales using a priori models (Burnham and Anderson 2002). Core area, percent suitable grassland, and percent wooded areas were included for all buffers but contiguous patch area and the fragmentation metrics were only included in the 1200-m buffer models. We included interactions between vegetation variables and the interactions between patch core area and landscape variables. Buffers were modeled separately. Exploratory analyses indicated no non-linear relationships. For each year, we modeled ln (relative abundance) of each species in a generalized linear model framework with a Gaussian error structure (McCullagh and Nelder 1989). We adjusted for spatial autocorrelation by fitting spherical variograms to residuals and using spatial parameters (nugget and range) to adjust the covariance matrix (Cressie 1993). Model selection was done using Akaike Information Criteria adjusted for sample size (AICc) (Burnham and Anderson 2002).

We modeled relative abundance in three ways: as a function of microhabitat variables, macrohabitat and landscape variables, and combinations of microhabitat, macrohabitat, and landscape variables. For combination models, we used the microhabitat model with the minimum AICc as the base model for adding macrohabitat and landscape variables (Fletcher and Koford 2002).

We used the model with the minimum AICc from all three sets of models as the best model for each species/year combination. Models with an AICc value within 4.0 of the minimum AICc were considered plausible models (Burnham and Anderson 2002). To assess the relative importance of variables at different scales, we summed the weights of plausible models in which a variable was present (ω_i) (Burnham and Anderson 2002). Variables with weights >0.20 are reported. Adjusted R^2 values were calculated for the best models. Analyses were run in S-PLUS 2000 (MathSoft 1999).

Results

Attributes of the bird community, microhabitat and landscape characteristics

Savannah Sparrow was the most abundant species in the pastures with relative abundance between 1.59 (SE = 0.12, $n = 66$) in 1997 and 2.16 birds/ha (SE = 0.17, $n = 60$) in 1999. Bobolink relative abundance ranged between 0.30 (SE = 0.06, $n = 66$) in 1997 and 0.69 birds/ha (SE = 0.11, $n = 60$) in 1999, and Eastern Meadowlark relative abundance varied between 0.17 (SE = 0.03, $n = 60$) in 1999 and 0.23 birds/ha (SE = 0.04, $n = 66$) in 1997. The least abundant species, Grasshopper Sparrow, had relative abundance values between 0.14 (SE = 0.03, $n = 66$) in 1997 and 0.19 birds/ha (SE = 0.04, $n = 64$) in 1998.

Vegetation was shorter, less dense, and had lower percent live cover in 1997 compared to 1998 and 1999 ($P < 0.01$, all tests, Table 1). Percent bare ground was higher in 1998 and 1999 compared to 1997. Differences in pasture vegetation between 1997 and the other 2 years are likely due to cooler temperatures in 1997.

Within the 1200-m buffer surrounding the pastures, there was proportionately more grassland area than wooded area (Table 2). Among the buffers, there was less grass and more wood in the 200-m buffer than in the larger buffers. Grassland patches were larger and closer together while wooded patches were smaller and more fragmented in the 1200-m buffer.

Microhabitat (vegetation), macrohabitat (patch), and landscape effects

For all four passerines, microhabitat variables were present in the majority of minAIC models (Table 3) and relative variable importance was high (>0.50) for most years (Table 4). For each species, specific microhabitat variables in the minAIC vegetation models varied among years (Table 3). However, in all 3 years, best models for Grasshopper Sparrow included %live, and best models for Bobolink included height density and %bare ground (Table 3).

Among all species and all years, core area of the pasture (macrohabitat) was consistently important. Core area was included in all but two of the minAIC models for all species—year combinations (Table 3). Relative importance of pasture core area was high (range = 0.75–1.0) in all but one species-year combination (Table 4). When core pasture was a main effect, bird abundance increased with increasing core pasture area in all cases.

The composition of the landscape was associated with grassland bird abundance. Of the landscape variables, %grass and %wood were most likely to be

Table 1 Summary of vegetation structure in Wisconsin pastures

Variable	Description	Mean	SE	Min	Max
LIVE	Percent of vegetation that is live				
1997		62.77	1.38	32.50	82.92
1998		77.19	1.53	40.0	98.13
1999		76.29	1.22	47.50	98.75
FORB	Percent of live vegetation composed of forbs				
1997		27.85	1.74	0.31	58.13
1998		35.31	2.51	0	80.63
1999		32.11	2.59	0	68.75
BARE	Percent of ground that is bare				
1997		16.95	1.66	0	58.75
1998		41.78	2.86	1.25	97.50
1999		54.04	2.78	3.75	98.75
HD	Vegetation height-density (cm)				
1997		5.44	0.42	0.63	17.81
1998		13.03	1.04	0.78	52.19
1999		8.38	0.62	0.75	25.95

Values were averaged over plots within pastures, and then averaged over pastures. $n = 66$ for 1997, 64 for 1998, and 60 for 1999

Table 2 Summary of metrics included in landscape models of grassland bird abundance in Wisconsin pastures 1997–1999

Metric	Description	200 m buffer			700 m buffer			1200 m buffer		
		Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
GRASS	Proportion of landscape that is suitable grassland	0.35	0.02	0.00–0.88	0.38	0.02	0.09–0.70	0.38	0.02	0.14–0.74
WOOD	Proportion of landscape that is wooded	0.30	0.03	0.00–0.87	0.25	0.02	0.01–0.79	0.26	0.02	0.01–0.75
CORE	Core area of pasture (ha)	28.41	3.98	0.19–148.27	28.41	3.98	0.19–148.27	28.41	3.98	0.19–148.27
CONTIG	Suitable grassland area contiguous with and including pasture (ha)							188.37	21.22	2.56–999.16
CCEGRASS	Connectivity of suitable grasslands							88.39	18.22	5.56–1124.10
CCEWOOD	Connectivity of wooded areas							30.11	5.70	0.54–322.66
MCAI	Mean core area index of suitable grassland patches							49.02	1.48	20.58–83.55

Table 3 Minimum AIC models for grassland passerine abudance on pastures in Wisconsin 1997–1999

Species	Year	Model	Akaike weight	Adj-R^2
Savannah Sparrow	1997	[%live] + %forb + height-density + core area × %wood-1200 m + [core area × grass connectivity] + %grass-1200 m × %wood-1200 m	0.65	0.48
	1998	core area + [%grass-1200 m] + %wood-1200 m + [wood connectivity]	0.15	0.27
	1999	[%bare] + core area	0.05	0.33
Grasshopper Sparrow	1997	[%bare] + [%live × height-density] + contiguous area	0.22	0.37
	1998	%live + %forb × %bare + core area + %grass-1200 m	0.09	0.22
	1999	[%live] + core area	0.09	0.21
Eastern Meadowlark	1997	[%live × height-density] + %bare × height-density + %live × %bare + [%wood-200 m] + [core area × %grass-200 m]	0.36	0.36
	1998	%bare × %live + %live × height-density	0.13	0.28
	1999	core area + [%wood-1200 m] + [mean core area index (grass)]	0.12	0.16
Bobolink	1997	height-		

Brackets indicate a negative relationship with bird abundance. Variables are defined in Methods. Numbers after dashes are buffer sizes

found in the minAIC models (Table 3). Percent grass had moderate to high relative variable importance for Savannah Sparrow, Grasshopper Sparrow, and Bobolink (Table 4). Percent wood was found in two of the three minAIC models for Savannah Sparrow and Eastern Meadowlark (Table 3) and had relatively high variable importance, particularly for Savannah Sparrow (Table 4). The percentage of grass and wood habitat in the landscape, as well as all landscape parameters in general, were important most frequently at the 1200 m scale (Table 4). For Savannah Sparrow and Grasshopper Sparrow, landscape composition at this scale was important in all three years of the study.

Table 4 Relative variable importance (≥ 0.20 only) for microhabitat (vegetation) and macrohabitat variables and landscape variables in 200, 700, and 1200-m buffers used to model the abundance of grassland passerines on pastures in Wisconsin 1997–1999

Species	Year	Micro-habitat (veg.)	Macro-habitat (core area)	Landscape														
				%grass buffer size			%wood buffer size			Core area × %grass buffer size			Core area × %wood buffer size			%grass × %wood buffer size		
				2	7	12	2	7	12	2	7	12	2	7	12	2	7	12
Savannah Sparrow	1997					0.91			0.91			0.27			0.91			0.91
	1998	0.22	1	0.35		0.38	0.40		0.24	0.29			0.36					
	1999	0.65	1			0.25		0.20	0.50									
Grasshopper Sparrow	1997	1	0.79			0.67												
	1998	0.75	0.94	0.20	0.22	0.41												
	1999	0.93	0.94	0.21		0.30												
Eastern Meadowlark	1997	0.63	0.99	0.97			0.73			0.97								
	1998	1	0.22															
	1999	0.93	0.79						0.50									
Bobolink	1997	1	0.98						0.88						0.51			
	1998	1	0.96			0.38												
	1999	0.99	0.75		0.49	0.26												

Specific microhabitat variables are from Table 1. Variables are defined in the Methods. Buffer sizes are coded as 2 for 200 m, 7 for 700 m, and 12 for 1200 m

Fragmentation metrics were sometimes included in best models, and relative variable importance was as high as 0.96 (Table 5). Grass connectivity and mean core area index of grass frequently each had a relative variable importance >0.20 (Table 5). In all but one case, fragmentation metrics occurred as interactions when they were included in minAIC models (Table 3).

Macrohabitat—landscape interactions

Pasture core area effects on bird abundance sometimes depended on landscape composition, and in one case depended on a landscape fragmentation metric (Tables 4, 5). Interactions between core area and landscape composition were particularly important in 1997 for three of the four species (all but Grasshopper Sparrow) (Tables 3, 4). Two of the interactions involved wooded areas. In 1997, the interaction between core area and %wood in the 1200 m buffer affected relative abundance in the pastures for Savannah Sparrow and Bobolink. For both species, when percentage of wood in the landscape was low (mean = 4.9%, SE = 0.7%, $n = 17$), there was no relationship between relative bird abundance and core area ($P > 0.25$). In contrast, when percentage of wood was high (mean = 47.2%, SE = 2.5%, $n = 17$), relative bird abundance had a positive relationship with core area ($P < 0.05$) (Fig. 1).

Other interactions involved suitable grassland. In 1997, the relationship of Eastern Meadowlark relative abundance with core pasture area depended on %grass in the 200 m buffer. When %grass in the 200 m buffer was low, relative abundance increased with increasing core area; mean abundance was 0.06 birds/ha and 0.2 birds/ha for pastures with small and large core areas, respectively. When pastures were in landscapes with higher %grass in the 200 m buffer, the pattern reversed itself; mean abundance was 0.6 birds/ha and 0.2 birds/ha for pastures with small and large core areas, respectively. In 1997, the interaction of %grass and %wood in the 1200 m buffer was important for Savannah Sparrow relative abundance. When pastures were in landscapes with low %wood, relative densities decreased with increasing %grass in the landscape; mean abundance was 2.2 birds/ha when %grass was low and dropped to an average of 1.1 birds/ha when %grass was high.

Table 5 Relative variable importance (≥0.20 only) of landscape fragmentation metrics that were calculated only for 1200 m buffers used to model the abundance of grassland passerines on pastures in Wisconsin 1997–1999

Species	Year	Contiguous patch area	Mean grass connectivity	Mean wood connectivity	Mean core area index (grass)	Core area × grass connectivity	%grass × centroid grass connectivity	%grass × mean core area index (grass)	Core area × mean core area index (grass)
Savannah Sparrow	1997		0.91			0.91			
	1998			0.24					
	1999			0.27					
Grasshopper Sparrow	1997	0.22	0.56		0.20		0.25	0.20	
	1998								
	1999		0.24		0.36		0.22		
Eastern Meadowlark	1997								
	1998				0.23				
	1999				0.96				
Bobolink	1997				0.39				0.25
	1998		0.33						
	1999	0.25							

Variables are defined in the Methods

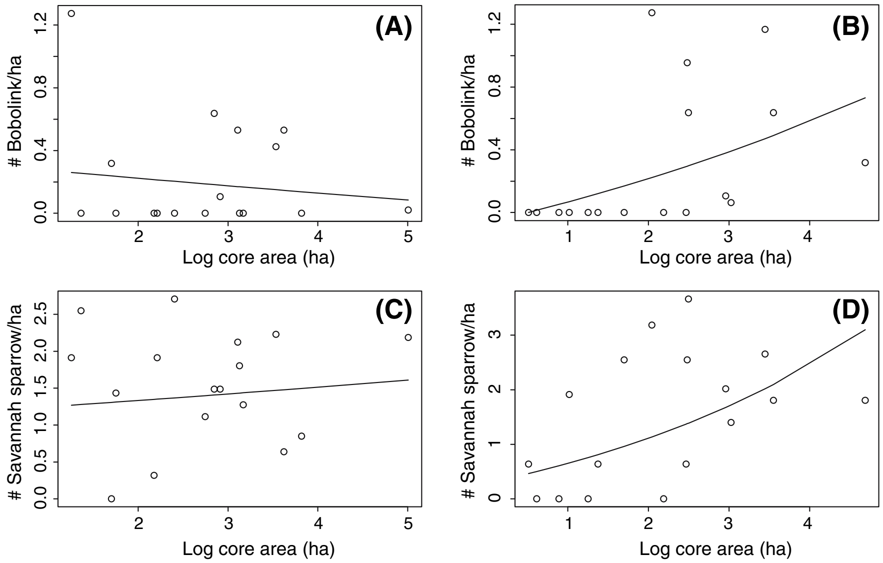

Fig. 1 Bobolink and Savannah sparrow relative abundance (#birds/ha) in relation to log of the core area (ha) of Wisconsin pastures in 1997 in landscapes with low (**a, c**) and high percentage (**b, d**) of wooded area in 1200 m buffers surrounding the pastures

In contrast, in landscapes with higher %wood, relative abundance in pastures had little association with %grass in the landscape; densities were 1.3 birds/ha and 1.2/ha when %grass in the 1200 m buffer was low and high, respectively.

Discussion

Importance of microhabitat, macrohabitat, and landscape characteristics

Vegetation structure was an important predictor of bird abundance for all species in our study. However, vegetation structure varied inter-annually, as did responses of grassland bird abundance to measured vegetation variables. Two of the 4 species in our study were consistently associated with specific microhabitat variables in all 3 years. Variation in response to microhabitat has also been found by Winter et al. (2005, 2006) in tallgrass prairies of North Dakota and Minnesota.

Reasons for variability in response to microhabitat are likely due to the nature of grasslands in which the birds evolved. Historically, grasslands were a “changing mosaic” frequently disturbed via natural and human influence (Collins and Glenn 1995). Species that have low site fidelity such as Henslow’s Sparrow and Dickcissel (Herkert et al. 2002; Temple 2002) as well as more site faithful species (e.g., Bobolinks (Bollinger and Gavin 1989)) are responsive to inter-annual fluctuations (Winter et al. 2005) as an adaptation to this dynamic system. Our results suggest that in southwestern Wisconsin pastures, grassland bird species are selecting structural attributes within their known range of preferences (Sample and Mossman 1997), and responding to inter-annual changes in vegetation structure created by weather and grazing.

The influence of factors at macrohabitat and landscape scales are expected to be more consistent among and within studies compared to effects of microhabitat factors. Within our study, core area (macrohabitat) was consistently important, and our results concur with studies that found higher grassland bird densities on larger patches (e.g., Herkert 1994a, b; Bakker et al. 2002; Davis 2004). Other studies have found no relationship or inconsistent relationships (e.g., Johnson and Igl 2001; Davis et al. 2006; Winter et al. 2006). Such discrepancies may be due in part to landscape context (which was not measured by the researchers). For example, patch size may be more influential in more fragmented landscapes.

In our study, landscape composition, specifically suitable grass and woody habitats, was important for all species. Species’ relative abundances were positively associated with %grass in the landscape. Types of grass adjacent and in proximity to grass patches are just beginning to be recognized as features that may influence occurrence and abundance of some species in a patch (e.g., Niemuth 2000; Ribic and

Sample 2001; Bakker et al. 2002). Similar to our study, other studies have found presence of woody patches (even solitary trees) in the surrounding landscape to be associated with lowered occurrence or densities of grassland birds in the focal patch (e.g., Coppedge et al. 2001; Ribic and Sample 2001; Bakker et al. 2002; Grant et al. 2004; Cunningham and Johnson 2006, Winter et al. 2006). These patterns are presumed to be caused by effects of wooded edges on productivity (e.g., Herkert et al. 2003; but see Grant et al. 2006), although these effects may not be detectable in highly fragmented landscapes such as ours (Renfrew et al. 2005).

That composition of the landscape explained more variance in bird abundance than fragmentation metrics in our study supports the modeling work of Fahrig (2001, 2002) who posited that the amount of habitat on the landscape is more important than how it is distributed. Studies that found landscape composition factors to be important to grassland bird abundance did not simultaneously investigate the importance of fragmentation metrics. For edge-sensitive forest birds, models developed by With and King (2001) suggest that lifetime reproductive output was affected by habitat clumping. Forest fragmentation usually entails a loss of forest in the landscape, so that changes in both composition and fragmentation of the landscape are confounded. In contrast, grassland fragmentation often entails a reduction in habitat quality (lower quality surrogate grasslands replace higher quality grasslands), and increased fragmentation does not necessarily imply a concurrent loss in the proportion of grassland. Hence, landscape composition may be more important than fragmentation for grassland birds.

Interactions of macrohabitat and landscape characteristics

Grassland bird ecologists are just beginning to investigate the importance of interactions in explaining patterns of abundance across a landscape. Of the few studies that have investigated interactions, some have not found support (Johnson and Winter 2004; Winter et al. 2006) while others have (Horn and Koford 2006). Our results support the idea that interactions between macrohabitat and landscape factors may be important. In more wooded landscapes, Savannah Sparrows and Bobolinks avoided smaller pastures and were more abundant in larger pastures. Although interactions between patch core area and the amount of woodlands might be expected from what we understand about grassland bird ecology, interactions between core area and amount of grassland in the landscape is only beginning to be investigated. Similar to our results in 1997 for Eastern Meadowlarks in pastures, Horn and Koford (2006) found that Bobolink abundance was positively associated with field size only when Conservation Reserve Program fields were located in a landscape with a low amount of perennial grassland; when fields were located in a landscape with large amounts of perennial grassland, the relationship reversed. The mechanism for this interaction is unknown. Horn and Koford (2006) present an argument based on interspecific competition when habitat is not available, and Sample et al. (2003) explain such patterns in terms of how birds perceive boundaries among the different surrogate grassy habitats.

Variability within scales and patch definition

The amount of variability in a factor within any given scale could influence its importance relative to factors at other scales (Winter et al. 2006). If between-site vegetation (microhabitat) structure is homogenous, variation in bird occurrence or abundance caused by landscape factors would be more easily detected. However, the quality and availability of suitable habitat must also be considered. If the microhabitat is all suitable but quality is poor, landscape factors may be irrelevant. Alternatively, if the microhabitat is variable so that only a small proportion of sites contain suitable habitat, birds will select sites with suitable habitat, and vegetation structure will be an important explanatory variable in bird occurrence or abundance. For example, in our study Bobolink abundance was predicted by microhabitat as well as landscape variables. However, Ribic and Sample (2001) found that in the same region of Wisconsin, only landscape variables were important predictors of Bobolink abundance. Bobolinks prefer vegetation that is at the taller, denser end of the spectrum in terms of grassland structure (Sample and Mossman 1997). Our sites consisted of grazed pastures with a relatively low proportion of habitat suitable for Bobolinks, whereas sites in Ribic and Sample (2001) spanned a variety of grasslands with, presumably, a greater proportion of suitable habitat. Limited availability of suitable habitat among sites in our study likely enhanced the importance of microhabitat in our models. Habitat availability among sites may also explain why Koper and Schmiegelow (2006) found little evidence that grass in the southern Alberta landscape influenced Savannah Sparrow abundance, in contrast to our findings. Our pasture sites may have shorter, more suitable habitat for Savannah Sparrows than prairies in Alberta, where birds may occupy existing suitable habitat with less regard to landscape features. Furthermore, their study area consists of more grassland (22–95%, mean not provided) than ours, perhaps above some threshold at which effects of grass in the landscape can be detected. Although preferences for vegetation structure could overshadow the influence of landscape characteristics, this does not mean that landscape is not influencing settling decisions.

Patch definition in grassland studies varies depending on species' habitat requirements (Horn and Koford 2006). In our study, defining the patch as the pasture plus all grasslands contiguous with the pasture did not improve models of grassland bird abundance. Our landscapes had a high proportion of non-grassland land use types, and the addition of grasslands that happened to be adjacent to the pasture sites may not have increased patch size enough to have a quantifiable effect. Using multiple definitions of the patch boundaries in different landscapes may shed some light on how birds perceive the landscape (Sample et al. 2003).

Extent of landscape effects

Dunning et al. (1992) suggested that neighborhood or "small-scale landscape" effects on abundance are affected more by adjacent patches than patches farther away. However, we found landscape variables at the largest scale investigated (1200 m) were most frequently included in best models and had higher variable importance than variables at smaller scales. These findings indicate that birds may be responding, in part, to the landscape at a broader scale as they make settling decisions. This idea is supported by Cunningham and Johnson (2006), who found that for most grassland bird species, tree cover at larger landscape scales (800–1,600 m) provided better models than smaller scales. Studies that looked at effects of landscape up to 800 m found the 800-m scale better predicted bird abundance than smaller scales (Best et al. 2001; Ribic and Sample 2001). Studies that evaluated the influence of landscape at broader scales than our study (McCoy 1996) found landscape effects at about 1 km. Although it is difficult to draw a general conclusion for different regions, landscapes, and species (Winter et al. 2006), landscape influences in grassland systems may be more extensive than envisioned by Dunning et al. (1992).

Conclusions

Evidence of associations between landscape features and grassland bird occurrence or abundance is accumulating (McCoy 1996; Best et al. 2001; Ribic and Sample 2001; Bakker et al. 2002; Johnson and Winter 2004; Horn and Koford 2006; Koper and Schmiegelow 2006; Winter et al. 2006), regardless of differences in terms of methodology used, avian species studied, and landscape context. Two of the seven grassland passerine species in Koper and Schmiegelow (2006) responded to factors at several scales, consistent with what we found for all four of the species we evaluated. Although Koper and Schmiegelow (2006) argue that mechanisms occur on a local scale, Stephens et al. (2003) found that fragmentation at the landscape scale better predicts avian nest success than patch or edge characteristics.

We recommend that future research incorporate a multi-scale, multi-year approach, and include patch-landscape interactions. It remains unclear to what extent results may be driven by the inherent variability of microhabitat and characteristics of the landscape in a given system. The landscape and vegetation context of a study may be driving models, and it is important to clearly describe the study area and assess whether patterns are consistent among years. Replicating this study in other regions of the Midwest or comparing landscape effects for sites with different types of grassland would help evaluate consistency of landscape effects on grassland bird abundance, both geographically and among different microhabitats. Evaluating the effect of landscape characteristics at sites within versus at the edge of a species' range of habitat requirements may also help to tease out the relative importance of landscape.

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