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Abstract

Several grassland bird species have been shown to be area sensitive. This area sensitivity occurs when a species' frequency of occurrence, or relative abundance, tends to be lower in smaller fields. The detection of area sensitivity, however, is not consistent among studies because a species may exhibit area sensitivity in one study, but not in another. We tested the hypothesis that a species' area sensitivity varies depending on the amount of grassland in the landscape. The study took place in central North Dakota during the 1996 and 1997 breeding seasons on 46 fields enrolled in the Conservation Reserve Program (CRP). One species, the bobolink (*Dolichonyx oryzivorus*), displayed variable area-sensitivity consistent with our predictions. In landscapes with greater amounts of grassland, the species' relative abundance in smaller fields was higher. Thus, the species' area sensitivity decreased in landscapes with greater amounts of nesting habitat. This finding suggests that use of small prairie remnants by area-sensitive species may be enhanced by increasing the amount of grassland in the surrounding landscape.

Keywords: Abundance, area-sensitive birds, bobolink, *Dolichonyx oryzivorus*, field size, grassland birds, landscape composition, North Dakota

Introduction

In recent decades, several grassland bird species have experienced declines in population size in the United States (Igl and Johnson 1997, Peterjohn and Sauer 1999). As a group, birds nesting in grasslands have experienced greater declines in population size than any other group of birds (Droege and Sauer 1994, Knopf 1994, Herkert 1995). On the breeding grounds, declines of grassland bird populations have been attributed to loss or fragmentation of grassland habitats (Herkert 1994, Vickery and others 1994, Warner 1994), changes in land use and degradation of habitat (Knopf 1994, Igl and Johnson 1997, Johnson and Igl 2001), and mowing of grassland fields during the breeding season (Bollinger and others 1990, Frawley and Best 1991).

Loss or fragmentation of grassland habitat results in a landscape of smaller grassland fields within a matrix of unsuitable habitat. Size of grassland fields may be a determinant of bird-community composition, with larger fields having higher species richness and abundance of individual species (Herkert 1994, Vickery and others 1994). Bird species that are found more often in larger fields than smaller fields are termed "area sensitive" (Whitcomb and others 1981). Many species of grassland birds are considered area sensitive, including northern harrier (*Circus cyaneus*), greater prairie-chicken (*Tympanuchus cupido*), upland sandpiper (*Bartramia longicauda*), sedge wren (*Cistothorus platensis*), clay-colored sparrow (*Spizella pallida*), vesper sparrow (*Pooecetes gramineus*), lark sparrow (*Chondestes grammacus*), savannah sparrow (*Passerculus sandwichensis*), Baird's sparrow (*Ammodramus bairdii*), grasshopper sparrow (*Ammodramus savannarum*), Henslow's sparrow (*Ammodramus henslowii*), Le Conte's sparrow (*Ammodramus leconteii*), bobolink (*Dolichonyx oryzivorus*), eastern meadowlark (*Sturnella magna*), and western meadowlark (*Sturnella neglecta*) (e.g., Herkert 1994, Vickery and others 1994, Helzer and Jelinski 1999, Winter and Faaborg 1999, Johnson and Igl 2001, Horn and others 2002).

However, not all studies of these species have detected area sensitivity. Herkert (1994) detected a positive relationship between eastern meadowlark occurrence and field size in Illinois, whereas Walk and Warner (1999) observed this species in all of their fields in Illinois, regardless of size. In the northern Great Plains, Johnson and Igl (2001) found inconsistent evidence of area sensitivity of grassland birds among the counties they studied. For example, common yellowthroat (*Geothlypis trichas*), grasshopper sparrow, and red-winged blackbird (*Agelaius phoeniceus*) had higher occurrence or density in larger patches in some counties and smaller patches in other counties. Some of the variability in area-sensitivity studies may be due to investigators defining area sensitivity differently (Horn and others 2000, Johnson and Igl 2001). We define an area-sensitive species as one that exhibits nonrandom avoidance (that is, lower probability of occurrence or relative abundance) of small fields that are larger than its territory size (Askins and others 1990, Horn and others 2000). The biological mechanism(s) underlying avoidance of small fields and the reasons for variability are poorly understood,

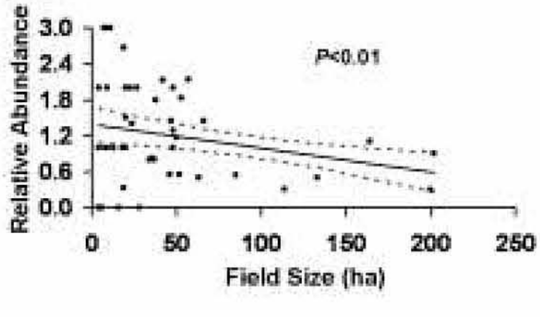

Figure 1. Relation between relative abundance of bobolink in fields and field size in central North Dakota in the 1996 (darkened circles) and 1997 (outlined circles) breeding seasons for moderate-grassland-cover landscapes. Means were weighted by the number of point counts conducted in a field. The dashed lines are the 95% confidence limits of the mean for each field.

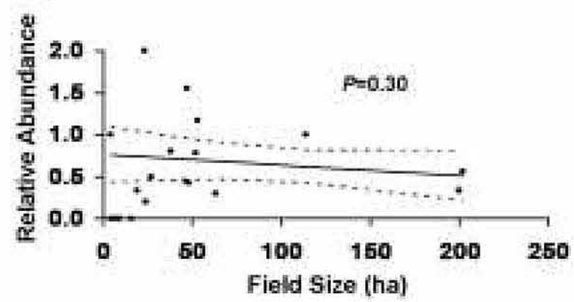

Figure 3. Relation between relative abundance of brown-headed cowbird in fields and field size in central North Dakota in the 1996 and 1997 breeding seasons. Darkened and outlined circles are from fields in moderate-grassland-cover landscapes in 1996 and 1997, respectively. Darkened and outlined squares are from fields in greater-grassland-cover landscapes in 1996 and 1997, respectively. See legend of Figure 1 for more explanation.

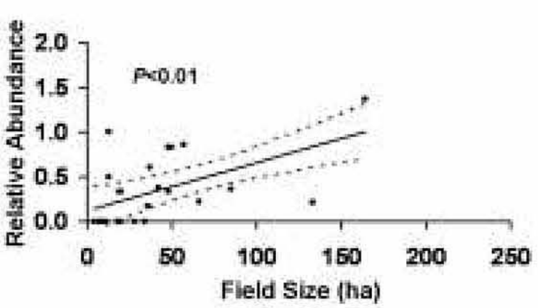

Figure 2. Relation between relative abundance of bobolink in fields and field size in central North Dakota in the 1996 (darkened squares) and 1997 (outlined squares) breeding seasons for greater-grassland-cover landscapes. See legend of Figure 1 for more explanation.

however, and determining why species might display variable area-sensitivity is a major conservation need (Vickery and Herkert 2001). Johnson and Igl (2001) suggested that variable area-sensitivity may be due to differences in study design, analytical methods, geographic location, or the landscape in which the study takes place.

Landscape composition can affect species composition, abundance, and possibly area sensitivity (Askins and others 1987, Freemark and others 1995, Andrén 1996, Herkert and others 1996, Venier and Fahrig 1996, Söderström and Pärt 2000, Coppedge and others 2001, Johnson and Igl 2001, Ribic and Sample 2001). In Missouri, McCoy (1996) observed that landscape features within 1 and 5 km of a grass field influenced both the occurrence and abundance of several grassland-bird species. Ribic and Sample (2001) observed greater grassland bird density in transects surrounded by greater amounts of grassland, pasture and hay, and lesser amounts in transects surrounded by other habitat types.

How might differences in landscape composition, specifically the amount of grassland, affect area sensitivity of grassland birds? One possible mechanism may involve competition and a despotic distribution (Fretwell and Lucas 1969, Horn 2000, Renfrew 2002). If landscapes with more grassland attract higher densities of breeding birds in the grassland habitat, for example, then intraspecific competition might be greater there than in landscapes with less grassland. Area-sensitive species that can avoid the smaller fields in the less densely populated, low-grassland landscape might be forced to use them in the more densely populated, greater-grassland landscape. Two predictions follow from this hypothesized mechanism. First, area sensitivity will vary with landscape composition. In landscapes with low to moderate amounts of nesting habitat, there will be positive relationships between probability of occurrence and field size, or between relative abundance and field size, indicating area sensitivity. In landscapes with greater amounts of grassland, the relationship between probability of occurrence and field size will be weak or nonexistent. A relationship between relative abundance and field size may or may not be evident in these landscapes. The second prediction—and a key one—is that abundance within nesting habitat will be higher in landscapes with more grassland.

We examined whether landscape composition influenced area sensitivity by comparing the relations between species' probabilities of occurrence, and relative abundances, and field size in landscapes (study-area types) that differed in their amount of perennial grassland.

Methods

Study Areas

We conducted the study in the Prairie Pothole Region of central North Dakota (Barnes, Stutsman, and Wells counties) in the 1996 and 1997 breeding seasons. Two types of 6.4-km x 6.4-km landscapes were selected according to the amount of perennial grassland they contained: moderate grassland cover and greater grassland cover. Moderate- and greater-grassland-cover landscapes contained 15–20% perennial grassland and 51–55% grassland, respectively (Table 1).

The major differences between the moderate- and greater-grassland-cover landscapes were the approximate doubling of U.S. Department of Agriculture Conservation Reserve Program (CRP) and Water Bank Program (WBP) lands, and the increase in other types of grassland, particularly pastureland, in greater-grassland-cover landscapes. Surveyed fields in moderate-grassland-cover landscapes tended to be surrounded by cropland. Fields in greater-grassland-cover landscapes were likely to be surrounded by pastureland, creating a landscape of almost continuous nesting habitat and less isolated fields. Habitat maps of the four study areas can be found in Phillips (2001).

Study areas were selected using digital land cover data from Landsat Thematic Mapper images, which were incorporated into a Geographic Information System (GIS). We also considered logistics, road access, and landowner cooperation.

Field Definition

Field sizes were determined with the GIS. A field was defined as a distinct unit of hayland or reseeded grassland enrolled in the CRP or WBP that was surrounded by roads or other habitat classes such as cropland, pastureland, and/or wetland (Horn and others 2002). For example, 20 ha of CRP land that was adjacent to 5 ha of hayland was considered a single field of 25 ha unless the CRP land and hayland were separated by hard edges, such as roads, that can cause decreased densities of grassland birds (Reijnen and others 1996, Sutter and others 2000). Conservation Reserve Program, WBP, and hay fields were combined when making field size calculations because many of the CRP fields used had undergone emergency haying the previous year making the habitat types more similar (Horn and Koford 2000). Pastureland was considered a different habitat class because many grassland bird species have considerable differences in abundance in pastures compared to CRP and hayland (Kantrud 1981, Renken and Dinsmore 1987, Best and others 1995).

We recognize that no single field definition may be applicable to all grassland birds. Our definition is most applicable for species such as bobolink and sedge wren that avoid short grass. Using a definition that did not distinguish between CRP land and pastureland would have resulted in very few fields in the greater-grassland-cover landscapes. Like pasture, grassland birds may also use small grain fields during the breeding season (Best and others 1995, Patterson and Best 1996). However, the quality of these crops varies, and at the time of bird settlement these habitats may have no vegetation. Fields smaller than 4 ha (10 acres) were not used to avoid confounding territory size requirements of grassland songbirds with area sensitivity (Renfrew 2002).

In the four study areas, we sampled 46 fields comprising 2,013 ha (4,972 acres, median = 28 ha or 69 acres, Table 1). In the moderate-grassland-cover landscapes, 25 fields comprising 1,001 ha (2,472 acres) were sampled (median = 28 ha or 69 acres, Table 1). Twenty-one fields comprising 1,012 ha (2,501 acres) were sampled in greater-grassland-cover landscapes (median = 27 ha or 67 acres, Table 1).

Bird Data Collection

In all study areas, we surveyed birds in all planted cover enrolled in the CRP and WBP except two parcels in one of the greater-grassland-cover landscapes that were surrounded by predator exclosure fences and three parcels in greater-grassland-cover landscapes for which we did not have permission to sample. Birds were only sampled in the CRP or WBP portion of each field even if the field included adjacent hayland.

We used 5-minute, 100-m radius point counts to estimate the probability of occurrence and relative abundance of grassland songbirds. During each count, we recorded the number of individuals of each species seen or heard. Counts were conducted between 6:25 and 9:30 in the morning from 4 June to 16 July 1996 and from 28 May to 18 June 1997. The same individual (D. Horn) performed all the point counts. The location and number of counts in the CRP or WBP portion of each field was predetermined and based on two criteria: 1) count locations were at least 100 m from any field edge (with the exception of fields that had a diameter less than 200 m), and 2) counts were placed at least 250 m from other count points. The number of counts in the CRP or WBP portion of each field was the maximum number of points in a grid-like pattern that could fit within a field and meet these criteria. Thus, the number of point counts conducted on a field was

Table 1. Habitat composition (%) and field information of study areas, two of moderate-grassland cover and two of greater-grassland cover, in central North Dakota used during the 1996 and 1997 grassland-songbird nesting seasons.

Study area and Year	Planted cover[a]	Hay	Pasture	Wetland	Cropland[b]	Other	# of fields and size range (ha)		# of point counts /counts per field	
Moderate-grassland cover										
1996	11.9	0.1	2.8	7.0	76.2	2.1	11	13–133	66	1–14
1997	14.8	2.4	3.0	14.7	63.3	1.9	14	4–164	66	1–19
Greater-grassland cover										
1996	25.9	4.6	20.6	7.8	39.4	1.7	10	4–200	75	1–27
1997	23.5	1.6	29.9	17.6	25.7	1.7	11	4–202	74	1–32

[a] Planted cover comprised primarily Conservation Reserve Program and Water Bank Program fields.

[b] Cropland comprised primarily wheat, sunflower, canola, corn, and soybeans

proportional to field size. Each of those points was visited once during the season, but care was taken to distribute the counting across study areas and across the range of field sizes as the season progressed. A total of 281 point counts were conducted (Table 1). The number of point counts in a field ranged from 1 to 32 with a median of 4.5.

Statistical Analyses

We used logistic regression to determine if a species' occurrence (binary response) in a field was influenced by the following explanatory variables: year (1996 or 1997), study-area type (moderate- or greater-grassland cover), field size (continuous variable), and the interaction between study-area type and field size. Species exhibiting an interaction effect between study-area type and field size were considered to display variable area-sensitivity. Because sampling fields proportional to size can result in a positive relationship between probability of occurrence and field size that is a sampling artifact (Connor and McCoy 1979, Horn and others 2000), we randomly selected a single point count from each field, regardless of size, to be used in occurrence analyses (for example, Vickery and others 1994, Renfrew 2002).

We used linear regression to determine if a species' relative abundance in a field was influenced by the following explanatory variables: year, study-area type, field size, and the interaction between study-area type and field size. Relative abundance was determined by calculating the mean number of birds per point count within a field. To stabilize the variance in the regressions, means were weighted by the number of point counts conducted in a field, such that each field's contribution in the analysis was equal to the number of points counts conducted in that field divided by the total number of point counts conducted in all fields. We did not conduct a nested analysis examining the effect of field size within study areas because such an analysis would have had limited statistical power. We did, however, distinguish the study areas on the figures showing abundance as a function of field size in an effort to determine whether large differences in abundance between study areas, compared to within study areas, could be responsible for the statistical effects we observed.

Although occurrence and abundance data are correlated (Wright 1991), our occurrence analysis used a single point count per field, whereas the abundance analysis used all point counts per field. Moreover, both occurrence and abundance data are used for determining if a species is area sensitive (Johnson and Igl 2001). We selected logistic and linear regression models with the fewest variables that fit the data based on Akaike's information criterion values (Akaike 1973, Akaike 1985). We did not examine the year *x* study-area type interaction because finding such an effect would not be readily interpretable; it could be due to different responses in the two years or to the fact that we had different study areas in the two years. Data were analyzed using the Logistic and Reg Procedures of the SAS statistical package (version 6.12; DiIorio 1991, Stokes and others 1995, SAS Institute 1997).

Results

Occurrence Analyses

Twelve species of grassland songbirds were found (Table 2). In the analysis of probability of occurrence, no species had an interaction between field size and study-area type (Table 3). However, R^2 values were low in general, indicating that our modeling probably failed to capture important influences on variation in presence/absence. Field size influenced the occurrence of two species (Table 3). Bobolink occurrence was positively related to field size and, thus, was area sensitive. Its probability of occurrence ranged from 0.24 in 4-ha (10-acre) fields to 0.92 in 202-ha (499-acre) fields, and reached 50% of maximum at a field size of 59 ha (146 acres). Brown-headed cowbird occurrence was negatively related to field size. Its probability of occurrence ranged from 0.78 in 4-ha (10-acre) fields to 0.22 in 202-ha (499-acre) fields.

Abundance Analyses

If landscape composition influences area sensitivity, our first prediction was that there would be an interaction between the effects of field size and study-area type. We detected relationships between relative abundance in fields and the interaction between field size and study-area type for three species: bobolink, red-winged blackbird, and grasshopper sparrow (Table 4). Bobolink and red-winged blackbird abundance were positively related to field size in moderate-grassland-cover landscapes, but no relationship was detected in greater-grassland-cover landscapes (bobolink data shown in Figures 1 and 2). Although we did not test this relationship within study areas, Figures 1 and 2 distinguish the study areas and indicate that large differences in abundance between study areas, compared to within study areas, was

Table 2. Relative abundance of 12 grassland bird species in 46 CRP and WBP fields in central North Dakota during the 1996 and 1997 breeding seasons.

Species	Mean[a]	Var
Sedge wren (*Cistothorus platensis*)	0.78	0.98
Common yellowthroat (*Geothlypis trichas*)	0.57	0.39
Clay-colored sparrow (*Spizella pallida*)	0.91	0.86
Savannah sparrow (*Passerculus sandwichensis*)	0.59	0.51
Grasshopper sparrow (*Ammodramus savannarum*)	0.05	0.08
Le Conte's sparrow (*Ammodramus leconteii*)	0.67	0.56
Song sparrow (*Melospiza melodia*)	0.11	0.12
Bobolink (*Dolichonyx oryzivorus*)	0.57	0.59
Red-winged blackbird (*Agelaius phoeniceus*)	0.52	0.92
Western meadowlark (*Sturnella neglecta*)	0.05	0.04
Brown-headed cowbird (*Molothrus ater*)	1.02	1.85
American goldfinch (*Carduelis tristis*)	0.17	0.25

[a] n = 281 point counts.

not responsible for the relationships we observed. Grasshopper sparrow had no relationship between abundance and field size in moderate-grassland-cover study-area types, but was positively related to field size in greater-grassland-cover study-area types. However, grasshopper sparrows were only observed in two fields in moderate-grassland-cover landscapes and three fields in greater-grassland-cover landscapes. Thus, statistical significance may not reflect biological significance. Brown-headed cowbird abundance was negatively related to field size (Table 4, Figure 3).

If landscape composition influenced area sensitivity, our second prediction was that we would detect differences in abundance between landscape types. Savannah sparrow and American goldfinch were more abundant within greater-grassland-cover landscapes (Table 4). On average, when field size was ignored, bobolink abundance was higher in greater-grassland-cover landscapes (Figures 1 and 2). Savannah sparrow, bobolink, and American goldfinch relative abundances were 0.46, 0.50, and 0.08 (variances = 0.70, 1.05, and 0.20), respectively, in moderate-grassland cover fields and 0.71, 0.62, and 0.24 in greater-grassland cover fields (variances = 0.29, 1.26, and 0.38).

Discussion

Only one grassland bird species—the bobolink—exhibited relationships that were consistent with both our predictions. Specifically, the bobolink's area sensitivity was influenced in a predictable manner by the amount of perennial grassland in the landscape. The species' abundance in smaller fields was greater, relative to large fields, in the landscapes with greater grassland cover. Furthermore, the relative abundance of bobolink was higher in those landscapes. Other studies have also found that the abundance of this species appears to be affected by landscape variables such as the density of grassland-agriculture edge (negative effect; Fletcher, Jr. and Koford 2002), cover type diversity, area of woodlots, and number of habitat patches (all negative; Ribic and Sample 2001).

Johnson and Igl (2001) reported variable area-sensitivity of grassland birds in the northern Great Plains, but did not collect data on landscape composition. Species, such as grasshopper sparrow and bobolink, had higher occurrence and abundance in large patches in many, but not all, counties.

Few studies have examined the effect of landscape composition on area sensitivity of grassland birds. Renfrew (2002) examined four species in Wisconsin pastures and found that the extent of wooded habitat in the landscape affected density of bobolink and savannah sparrow because these species responded more strongly to pasture core-area in landscapes with greater coverage of woods. Bakker and others (2002) examined five species in the mixed grass and tallgrass regions of South Dakota and found some indication that the amount of grassland in the landscape positively affected occupancy of small, suitable patches by sedge wren, clay-colored sparrow, and grasshopper sparrow, but not savannah sparrow or western meadowlark. Horn and others (2002) did not detect an effect of landscape composition in their study of grassland songbirds in south-central Iowa. Among the possible reasons for their unusual finding is their atypical study area that had more woody vegetation in greater-grassland-cover landscapes. This caused species, such as bobolink, to actually be less abundant in the landscape with greater grassland-cover.

One unexpected result from our study was that, other than the bobolink, few species even showed evidence of positive area sensitivity. Johnson and Igl (2001) found bobolink to be area sensitive more consistently than the other species they examined. Six other species previously considered area sensitive occurred in our study areas, but we did not detect area sensitivity. Two of these, grasshopper sparrow and western

Table 3. Parameters of logistic regression models of the probability of occurrence of grassland bird species in fields in central North Dakota during the 1996 and 1997 breeding seasons and the explanatory variables: year, study-area type, field size, and the interaction between study-area type and field size. Only final species models with a significant explanatory variable are shown.

Species and Variable	Parameter estimate	SE	p	R^{2a}
Sedge wren				
Intercept	1.3433	0.9914	0.1754	0.08
Year	–1.2480	0.6405	0.0514	
Common yellowthroat				
Intercept	1.7280	0.9985	0.0835	0.11
Year	–1.4404	0.6432	0.0251	
Clay-colored sparrow				
Intercept	–1.7280	0.9985	0.0835	0.11
Year	1.4404	0.6432	0.0251	
Savannah sparrow				
Intercept	–2.1401	1.0203	0.0359	0.11
Year	1.4469	0.6310	0.0218	
Le Conte's sparrow				
Intercept	0.7538	0.4287	0.0787	0.22
Study-area type	–2.2007	0.7019	0.0017	
Bobolink				
Intercept	–1.2150	0.4735	0.0103	0.12
Field size	0.0179	0.0088	0.0410	
Red-winged blackbird				
Intercept	–1.8627	0.6220	0.0027	0.13
Study-area type	1.2713	0.6833	0.0628	
Field size	0.0107	0.0074	0.1476	
Brown-headed cowbird				
Intercept	–1.2412	1.1009	0.2596	0.19
Year	1.7291	0.7279	0.0175	
Field size	–0.0121	0.0073	0.0988	

[a] R^2 is derived from SAS Institute Inc. (1997)

Table 4. Parameters of linear regression models of the relative abundance of grassland bird species in fields in central North Dakota during the 1996 and 1997 breeding seasons and the explanatory variables: year, study-area type, field size, and the interaction between study-area type and field size. Only final species models with a significant explanatory variable are shown. Where an interaction was found, no parameter estimates are reported.

Species and Variable	Parameter estimate	SE	P	F	R^2
Sedge wren					
Intercept	1.4353	0.3035	0.0001	5.25	0.11
Year	–0.4423	0.1930	0.0268		
Common yellowthroat					
Intercept	0.9498	0.1563	0.0001	6.72	0.13
Year	–0.2575	0.0994	0.0129		
Clay-colored sparrow					
Intercept	0.4453	0.2074	0.0373	5.53	0.11
Year	0.3100	0.1319	0.0233		
Savannah sparrow					
Intercept	0.1020	0.1284	0.4314	9.35	0.40
Year	0.2824	0.0739	0.0004		
Study-area type	0.2798	0.0775	0.0008		
Field size	–0.0008	0.0006	0.1444		
Grasshopper sparrow					
Intercept	–0.0617	0.0473	0.1993	7.49	0.42
Year	0.0679	0.0247	0.0089		
Study-area type					
Field size					
Interaction	0.0012	0.0004	0.0093		
Bobolink					
Intercept	–0.3227	0.2036	0.1206	5.91	0.37
Year	0.3069	0.1066	0.0063		
Study-area type					
Field size					
Interaction	–0.0064	0.0018	0.0010		
Red-winged blackbird					
Intercept	–0.0312	0.2223	0.8892	3.24	0.24
Year	0.1670	0.1164	0.1590		
Study-area type					
Field size					
Interaction	–0.0057	0.0020	0.0060		
Brown-headed cowbird					
Intercept	0.4904	0.2552	0.0613	14.77	0.41
Year	0.6042	0.1498	0.0002		
Field size	–0.0040	0.0011	0.0006		
American goldfinch					
Intercept	0.0833	0.0460	0.0767	6.29	0.13
Study-area type	0.1583	0.0631	0.0159		

meadowlark, may have been too rare in our study fields (Table 2) for us to detect area sensitivity. These species may have been more abundant in pastureland, which had the shorter vegetation they prefer, but which we did not sample. Two others have distinct habitat requirements that may override area sensitivity— clay-colored sparrow which commonly nests in brush and sedge wren which prefers tall, dense grass. Le Conte's sparrow, associated with wetlands in parts of its range, may be similarly constrained. Savannah sparrow, the sixth species, has been reported to be area sensitive (Herkert 1994, Vickery and others 1994, Renfrew 2002), whereas Johnson and Igl (2001) and our study found no evidence of area sensitivity for this species. The discrepancy might be explained by differences in densities among studies (Horn and others 2000, Johnson and Igl 2001, Renfrew 2002). Herkert (1994) found 6.4 savannah sparrows per 100 ha (247 acres) and the species was area sensitive, whereas in North Dakota, the mean number of savannah sparrows per 100 ha of CRP or WBP land was about 4 times greater, and we did not detect area sensitivity. Herkert (1994) did not report the landscape composition, but his references to the "highly fragmented" grassland indicates that there was probably little, if any, grass cover surrounding the public areas he examined. Thus, the differences in abundance between studies could have been related to the amount of grassland in the landscapes. Alternatively, differences in densities may be related to the location of a study within a species' range (Johnson and Igl 2001). Whatever the cause of the differences in abundance, the resulting pattern of variable area-sensitivity among studies is consistent with the hypothesized mechanism outlined in this paper. That is, landscapes with more grassland attract higher densities of breeding birds that are forced to use smaller fields that could be avoided in less densely populated, lower-grassland-composition landscapes. If savannah sparrow responds to grassland cover, the response may occur at percent cover values below those examined in our study.

The study design we used had several problems. First, although the start date for point counts was similar between years, sampling ended earlier in 1997. This difference in time periods could bias our results if the species we studied had significant differences in detection rates between the middle of June and the middle of July (Best 1981). Our attempt to distribute counts across field sizes as the season progressed makes it unlikely that the patterns we observed were due to detectability differences. Second, some study areas were separated by large distances (about 190 km) and, thus, there may have been differences in the regional abundance of birds (Johnson and Schwartz 1993). The landscape immediately surrounding a field, as well as within-field characteristics such as presence of forbs, shrubs, and other woody vegetation, also influence grassland bird species (McCoy 1996, Winter and others 2000). At least for bobolinks, there is not much evidence for differences in abundance between study areas within study-area types (Figures 1 and 2). Finally, grassland bird species may vary in their response to different kinds of grassland in the landscape. We did not assess the extent of use of pastureland as nesting habitat. Because of low sample size, however, we were not able to investigate all factors that could influence species occurrence and abundance. Future studies covering larger scales, more landscape types, and longer time periods are needed to fully understand patterns of area sensitivity.

We conclude that a species' area sensitivity can be influenced by landscape composition in a predictable manner. As the amount of suitable habitat in the landscape increases, the abundance of birds in smaller fields increases. Thus, land managers may be able to increase use of small fields and prairie remnants by area-sensitive grassland birds by increasing the amount of suitable habitat in the landscape. Furthermore, differing results of other habitat fragmentation studies may be due to differences in the amount and arrangement of suitable habitat in the landscape (Villard and others 1993, Andrén 1994, McGarigal and McComb 1995). However, further studies on how landscape composition influences the area sensitivity of grassland songbirds and other avian species are needed to understand the mechanisms involved.

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