Patterns of Area Sensitivity in Grassland-Nesting Birds

MAIKEN WINTER* AND JOHN FAABORG

Division of Biological Sciences, University of Missouri, 110 Tucker Hall, Columbia, MO 65211, U.S.A.

Abstract: *Between 1995 and 1997, we studied breeding birds in fragments of native tallgrass prairie in southwestern Missouri to determine the effect of habitat fragmentation on grassland bird populations. Data on density and nesting success collected in 13 prairie fragments of various sizes revealed three levels of area sensitivity. The most area-sensitive species, Greater Prairie-Chicken (*Tympanuchus cupido*), was absent from small prairie fragments. An intermediate form of area sensitivity was apparent in only one species, Henslow's Sparrow (*Ammodramus henslowii*), which occurred in lower densities in small than in large prairie fragments. Based on census (i.e., distributional) data, only those two species were area-sensitive (i.e., negatively affected by habitat fragmentation) in southwestern Missouri. A species can be sensitive not only on a distributional level, however, but also by having lower nesting success in small than in large prairie fragments. The Dickcissel (*Spiza americana*) was the only species that was area-sensitive on such a demographic level. These data indicate that we cannot rely solely on census data to describe the sensitivity of grassland-nesting species to habitat fragmentation, but that we also need to investigate demographic data (e.g., nesting success). Whereas it has previously been shown that density measures of forest-nesting birds do not reliably reflect nesting success in habitat fragments of various sizes, ours is the first study that describes this pattern for grassland-nesting species.*

Patrones de Sensitividad de Area en Aves que Nidan en Pastizales

Resumen: *Entre 1995 y 1997 estudiamos aves anidando en fragmentos de praderas de pastos altos nativos en el Suroeste de Missouri para determinar el efecto de la fragmentación del hábitat en poblaciones de aves de pastizal. Los datos de densidad y éxito de nidada colectados en 13 fragmentos de pradera de varios tamaños revela tres niveles de senstividad de área. Las especies más sensitivas al área, la gallineta de pradera (*Tympanuchus cupido*), estuvo ausente de los fragmentos de pradera pequeños. Una forma intermedia de sensitividad de área fue aparente en solo una especie, la paloma de Henslow (*Ammodramus henslowii*), la cual presentó densidades mas bajas en fragmentos pequeños de pradera que en los fragmentos grandes. En base a datos de censos (i.e., distribucionales), solo estas dos especies fueron sensitivas al área (i.e., afectadas negativamente por la fragmentación del hábitat) en el Suroeste de Missouri. Una especie puede ser sensitiva no solamente a nivel distribucional, sino tambien al tener un éxito de nidación mas bajo en los fragmentos pequeños de pradera que en los grandes. Spiza americana fue la única especie que fue sensitiva al área a nivel demográfico. Estos datos indican que no podemos basarnos únicamente en datos de censos para describir la sensibilidad a la fragmentación del hábitat de las especies que nidan en pastizales, sino que también debemos investigar los datos demográficos (e.g., éxito de nidación). Se ha demostrado que las mediciones de densidad de aves que nidan en bosques no reflejan de una manera confiable el éxito de nidación en fragmentos de hábitat de varios tamaños, nuestro estudio es el primero que describe este patrón en especies que nidan en pastizales.*

*Current address: 611 Winston Court, Apartment 4, Ithaca, NY 14850–1953, U.S.A., email mwinte02@syr.edu

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Introduction

Among the most important results of the many studies on habitat fragmentation is the identification of species that occur in higher densities in large than in small fragments of suitable habitat. Such species are negatively affected by habitat fragmentation and are referred to as area sensitive (Robbins 1979). Originally, data on a species' presence or absence were used to determine if a species was area sensitive (N. K. Johnson 1975; Robbins 1979; Whitcomb et al. 1981; Blake & Karr 1984; Hayden et al. 1985; Blake 1986), following the original concept of island biogeography (MacArthur & Wilson 1967). Presence and absence data, however, do not differentiate between species that occur in both small and large fragments but that differ in density among habitat fragments of various sizes. Therefore, later studies investigated the distribution of birds in more detail by measuring bird density (e.g., Blake & Karr 1984; Wenny 1993). Area-sensitivity studies based on abundance or density data assume that species that occur in lower densities in small than in large fragments are more sensitive to habitat fragmentation than species that occur in similar numbers across fragments of various sizes. Several studies on forest- and grassland-nesting birds, however, have shown that density estimates are not always reliable indicators of the quality of a habitat (Van Horne 1983; Maurer 1986; Wiens 1989; Vickery et al. 1992b; Zimmerman 1992); individuals in habitats with high bird density can have lower reproductive success than those in areas with low bird density. Studies on the effect of habitat fragmentation on bird populations therefore have included estimates of pairing success (Gibbs & Faaborg 1990; Villard et al. 1993) and nesting success (e.g., Porneluzi et al. 1993; Donovan et al. 1995a, 1995b). Because area sensitivity can occur on both a distributional and a demographic level, evaluations of area sensitivity must include measures of both abundance and nesting success.

A number of possible reasons for area sensitivity have been suggested, although there is still uncertainty about the extent that local factors (e.g., proximity to edge) or regional factors (e.g., landscape-level habitat cover) may control the expression of these factors (Winter 1998). It has been suggested that birds in small fragments can experience (1) higher rates of nest depredation (Gates & Gysel 1978; Wilcove 1985; Robinson et al. 1995); (2) higher rates of nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Brittingham & Temple 1983; Robinson 1992); (3) increased interspecific competition (Whitcomb et al. 1981; Ambuel & Temple 1983); (4) lower abundance and diversity of insect prey (Whitcomb et al. 1981; Burke & Nol 1998); (5) fewer adequate breeding microhabitats (Wilcove et al. 1986); (6) reduced pairing success (Gibbs & Faaborg 1990; Porneluzi et al. 1993; Villard et al. 1993; Van Horn et al. 1995; Hagan et al. 1996); and (7) low immigration rates of individuals from larger habitats with higher reproductive rates (Lynch & Whigham 1984).

Most studies on the effects of habitat fragmentation on bird populations have focused on forest-nesting birds (e.g., Wilcove et al. 1986; Askins et al. 1990; Robinson et al. 1995; Donovan et al. 1995a, 1995b). Yet many grassland-nesting birds are declining at even greater rates than forest-nesting birds or any other avian guild in North America (Herkert et al. 1993; Peterjohn & Sauer 1993; Samson & Knopf 1994; Herkert 1995, 1997). The two factors most likely to cause these declines are loss and fragmentation of habitat on the breeding grounds (Herkert 1991; Helzer 1996; reviewed in Swanson 1996). Most of the studies that investigated fragmentation effects on grassland-nesting birds describe the distribution of birds across grassland habitats of various sizes (Herkert 1994). These studies show that density and species diversity are higher in large than in small prairie fragments (Herkert 1994), as shown in many studies on forest-nesting birds (e.g., Hayden et al. 1985). Little, however, is known about how the nesting success of grassland birds is affected by habitat fragmentation (but see R. G. Johnson & Temple 1990; Winter 1996).

We describe area sensitivity of grassland-nesting birds in fragments of native tallgrass prairie in southwestern Missouri. We used both abundance and demographic measures to understand area sensitivity in these species.

Methods

Study Area and Study Plots

We studied the distribution of grassland-nesting birds across native tallgrass prairie fragments in Vernon, Dade, and Barton counties in southwestern Missouri from 1995 through 1997. Size of fragments ranged from 31.2-1084 ha ($\bar{x}$ = 74.8 ha). In 1995 we studied 12 prairie fragments and added 1 small (43.7 ha) prairie fragment in 1996. To reduce variation among plots due to differences in vegetation structure, we selected prairies nonrandomly based on their similarity in vegetation (study plots had <10% woody cover). Further, we chose only those small fragments surrounded by habitat less suitable to grassland-nesting birds, such as roads, agricultural fields, forest, intensively grazed farms, or managed cemetery. Some large fragments were bordered by forest on one side, but the majority were surrounded by pasture, hayfields, or agricultural fields. Most prairie fragments were at least 5 km apart. On all prairies, the most common grasses were big bluestem (*Andropogon gerardii*), little bluestem (*Scizachochyrium scoparius*), and Indiangrass (*Sorghastum nutans*); dominant forbs included sunflowers (*Helianthus* spp.), milkweeds (*Asclepias* spp.), blazing star (*Liatris spicata*), and sensitive briar (*Mimosa quadrivalvis*). All study areas were property of the

Missouri Department of Conservation, the Nature Conservancy, the Missouri Prairie Foundation, or the Missouri Department of Natural Resources and were actively managed with prescribed burning and haying. Typical management regimes were not influenced by our study. The effects of management on grassland bird density and nesting success is discussed elsewhere (Winter 1998).

In each prairie fragment we randomly selected 2 or 3 permanent study plots ($\overline{x} = 2.54$, $n = 33$) ranging from 2 to 6 ha in size ($\overline{x} = 4.35$ ha) that were at least 150 m apart. In relatively large (>50 ha) fragments, study plots were at least 50 m from any edge habitat (forest, field, road, shrub-line), whereas the border of some study plots in small prairies was as close as 10 m to a nonforested edge.

Avian Density

Each study plot contained 1–3 parallel transects 200 m long and 100 m apart (Skinner et al. 1984) that were marked with wooden stakes at 50-m intervals. Along each transect we conducted fixed-distance linear transect censuses 6–8 times during each field season (between 10 May and 6 July 1995, 14 May and 6 July 1996, and 9 May and 11 July 1997). Censuses were conducted between sunrise and 1000 hours in the absence of rain and at wind velocities below 15 km/hour. During each census, we recorded all birds seen and heard within 50 m of either side of a transect and noted the movements of birds during the census to avoid double counting. We did not record birds flying over the study plots. The number of singing males per plot was transformed to the number of singing males per 1000 m of transect (=10 ha); this value is referred to as the density of a species.

We assumed that each species and individual birds have a similar probability of being detected, but the probability of detection can vary with species (Villard et al. 1993; Hagan et al. 1996). Further, unpaired males can sing more frequently than paired males (Gibbs & Faaborg 1990; Porneluzi et al. 1993; McShea and Rappole 1997). This variation can lead to an under- or overestimation of breeding birds in an area. We did not determine the pairing status of the individual birds on our study plots and therefore were unable to investigate how song frequency was related to pairing status. Instead we assumed that a singing male indicated the presence of a breeding pair.

Nesting Success of Grassland Birds

Throughout each field season we located and monitored nests of grassland-nesting birds that we found in any plot or in adjacent similar habitat. We focused our nest search efforts, however, on Henslow's Sparrows and Dickcissels because these species have declined severely, for reasons not well understood (Herkert et al. 1993). We found nests by walking across the study sites and adjacent areas of similar vegetation, paying close attention to the behavior and vocalizations of nearby birds. We also found many nests by chance during other activities such as bird censuses and vegetation measurements. Each nest was marked with a pink flag placed 5 m north of the nest, and nests were checked every 3–4 days to determine their fate. A nest was considered successful if it fledged at least one young of the parental species.

Vegetation Characteristics

Density, species diversity, and nesting success of grassland-nesting birds are highly dependent on vegetation structure (Bowman & Harris 1980; Rotenberry & Wiens 1980; Winter 1994). Area effects might thus be confounded by differences in vegetation characteristics among prairie fragments. To account for these effects, we characterized the vegetation of each study plot and nesting site. All vegetation measurements were made by the same observer (M.W.) in all years to reduce observer bias (Gottfryd & Hansell 1985). We avoided measuring vegetation when it was wet (e.g., after rain or heavy dew) to reduce disturbance to the vegetation.

Plot vegetation was characterized along a 200-m transect, which was placed through the middle of each study plot. We located a sampling point in each 10-m interval of the transect by taking a randomly chosen number of steps along the transect interval and then stepping a random distance to the left or right (selected by coin-toss), perpendicular to the transect (Noon 1981; Winter 1999). At each sampling point we used a 30 × 50 cm Daubenmire (1959) frame to estimate percent coverage of standing dead plants, dead plants lying horizontally, grasses, forbs, woody vegetation, and soil. Standing and lying dead plants were combined into the category of litter. The grass category included sedges (*Carex* spp.) because the growth structure of both is similar. We also counted the number of woody stems within each frame. Vegetation height and litter depth were measured to the nearest centimeter at each corner of the Daubenmire frame. Visual obstruction was determined by placing a Robel pole (Robel et al. 1970) in the middle of each Daubenmire frame and estimating the cover of the pole by vegetation to the nearest 0.5 decimeter in each cardinal direction at a 4-m distance. Plot vegetation was measured twice during each field season, at the end of May and the end of July. Vegetation measurements between those periods were highly correlated. Because vegetation measurements in July explained more of the variation in density than those measured in May (M.W., unpublished data), we used only the latter measurements for analysis. For each measuring point, we calculated the mean from the four measurements of height, litter depth, and visual obstruction. Because vegetation measurements within one plot were not

independent of one another, data were pooled for each plot, and the mean was used for all further calculations.

Vegetation at nests of Henslow's Sparrows and Dickcissels was characterized within 1 week after activity at a nest had ceased. Vegetation was characterized in the same manner as described above at five areas around the nest site: directly at the nest and at a distance of 0.5 m from the nest in each cardinal direction. For each nest we calculated the mean for each of the five measuring points and then used that mean in further analyses. Further, we estimated percent cover of the nest by vegetation when viewed directly from above and the distance of each nest to the nearest change in vegetation structure (i.e., edge; see Winter 1998). Because nest parasitism by Brown-headed Cowbirds was low and did not affect nesting success (see Winter 1998), we do not describe the data on cowbird parasitism.

Analysis

General

In all analyses of size effects, we used log-transformed fragment size. To assess vegetation effects and to avoid problems associated with multicollinearity (Neter et al. 1990), we combined vegetation variables into independent linear combinations of the original variables using principal component analysis (PCA; James 1971). The principal components that explained more than 70% of the variation in vegetation characteristics were used for analyses. In all analyses on vegetation and fragment-size effects, we used linear regression analysis (proc reg or proc logistic; SAS Institute 1995) with the following explanatory variables: log-size, principal component scores, all one-way interactions between log-size and principal components (size × PC1, size × PC2, size × PC3), and all one-way interactions among principal components (PC1 × PC2, PC1 × PC3, PC2 × PC3). Principal components and their interactions among themselves will be referred to as "vegetation variables." To determine which model best predicted the dependent variable, we used Akaike's information criterion (AIC; Akaike 1969; Lebreton et al. 1992). The AIC computes the maximum log-likelihood L for a given model, plus the number of variables n in the model using the formula AIC = $-2\ln L \times 2n$. The model in which AIC is smallest was then selected as the best predictor.

Distribution of Grassland-Nesting Birds

In all analyses of bird density we excluded one large prairie fragment (113.0 ha). This prairie fragment differed from all other large prairies by its intense management with annual haying that caused the vegetation structure to differ greatly from all other areas. Intensive

haying was probably the reason density and species diversity in this prairie were unusually low (Winter 1998), causing this prairie to be an outlier in all analyses.

Only two species of grassland-nesting birds were not seen on the entire range of fragment sizes: Upland Sandpiper and Greater Prairie-Chicken (Appendix). We investigated whether the presence of these two species was affected by the size of prairie fragments. We used logistic regression (proc catmod, SAS Institute 1995) with year (categorical), number of 200-m transect censuses in each prairie, and fragment size as independent variables; the dependent variable was whether any birds of the two species in question were observed on at least one census transect in that year.

We analyzed density data for only the four most common species (Grasshopper Sparrow, Henslow's Sparrow, Dickcissel, and Eastern Meadowlark) because sample sizes for the remaining species were too small for statistical analysis. Variation in bird density among years was analyzed by analysis of variance (ANOVA; proc glm, SAS Institute 1995). Because the density of each species differed significantly among years ($p \leq 0.0001$) and there was a significant interaction between prairie and year ($p \leq 0.0001$), further analyses were conducted separately for each year. Using the density of the 6–8 bird censuses per plot in each year as dependent variables, we compared bird density among plots within a prairie and among prairies with nested ANOVA. We identified the influence of prairie fragments on density, independent of the variation among plots, by using plot as an error term in testing for variation among prairies (Zar 1984).

To investigate how density was related to fragment size, we performed separate linear regression analyses for each species and each year. Differences in vegetation characteristics among prairie fragments, however, could confound the effect of fragment size on bird density; in turn, differences in fragment size could confound vegetation effects. To determine the influence of fragment size on bird density independent of vegetation variables, we excluded the influence of vegetation variables on bird density by regressing bird density on vegetation variables. We then investigated if any additional variation in bird density could be explained by the size of a prairie fragment, with the residuals as the dependent variable in a linear regression against fragment size. In turn, to determine how much variation in bird density was explained by vegetation variables independent of fragment size, we estimated the residuals from the relation between bird density and fragment size and used those residuals as the dependent variable in regression analysis with vegetation variables. A comparison between the size of the R^2 values of these two residual regressions then indicated whether fragment size or vegetation characteristics were more important in determining bird density on each plot.

To determine how much variation in bird density was explained by fragment size and vegetation variables together, we also performed regression analysis with fragment size, vegetation variables, and the interactions between fragment size and principal components as explanatory variables in the regression model. Density of Henslow's Sparrows in Prairie State Park, the largest (1084 ha) prairie in this study, was unusually low in 1996, probably due to intensive fire management in this park (S. R. Swengel, personal communication; Winter 1998). Therefore, we also conducted the same analysis for Henslow's Sparrows without this plot in 1996.

Nesting Success

To calculate nesting success and its dependence on fragment size, we excluded (1) nests that were found with an incomplete clutch and that were depredated the next time they were checked and (2) nests of species for which we found fewer than five nests in a given prairie. When investigating the dependence of nesting success on both fragment size and vegetation variables, we also excluded nests that had been destroyed by haying and that had not been followed to the end of nesting because vegetation data on those nests were not obtained. We estimated species-specific probabilities of daily Mayfield nest survival for each species (Mayfield 1975; D. H. Johnson 1979), with the total probability of nesting success defined as the probability that a nest successfully survived both incubation and nestling periods and fledged at least one young of the parental species. Standard errors for daily nest survival rates were calculated with the formula for binomial populations (Zar 1984:377). We used daily probabilities of nest survival rates for the combined periods of incubation and nestling stages in all calculations.

We used two separate regression analyses (proc glm and proc logistic; SAS Institute 1995) to determine the effect of fragment size and vegetation variables on the probability of daily nesting success. The success of a nest might not be independent of the success of another nest in the same prairie because nests are exposed to some of the same local factors. To avoid pseudoreplication by using each nest as an independent data point (as it is done in logistic regression), we combined all nests of a species in each prairie to calculate the mean daily survival probability per prairie, separately for each year. Year was included as a categorical variable in the analysis. These mean values were then entered in a linear regression analysis to determine if daily nesting success varied with fragment size. Because the number of nests in different prairies, and thus the reliability of the estimate of nesting success, was not equal among prairies, we used the inverse of the standard error of the survival estimates plus one as a weighting factor in each regres-

sion (Freund & Littell 1991). Prairies in which we had found fewer than five nests for one species were excluded from this analysis. Therefore, sample sizes for Dickcissels in 1995 and for Grasshopper Sparrows and Eastern Meadowlarks during each year were too small for this analysis. To increase sample size, we combined data for Henslow's Sparrow, Grasshopper Sparrow, and Eastern Meadowlark over all 3 years to a new category of "ground-nesting species" and used regression analysis with these combined data. Because interaction between year and size did not have a significant effect on nesting success in either Henslow's Sparrow or Dickcissel, we did not include the interactive effect in the linear regression model.

To investigate the magnitude of the effect of fragment size on nesting success, we calculated 95% confidence intervals for the slope of the regression equation. We determined the worst possible effect of a reduction of fragment size from 100 to 50 ha on daily rates of nest success by multiplying the upper confidence interval by the logarithm of 100 and 50 respectively. The difference in the resulting rates of daily nest survival was the amount by which daily rates of nest success were expected to change with a reduction of size from 100 to 50 ha.

We used stepwise logistic regression (proc logistic, SAS Institute 1995; Hosmer & Lemeshow 1989) for all years combined to determine if fragment size was more important in determining nesting success of Dickcissels and Henslow's Sparrows than other nest characteristics, including proximity to edge, percent nest cover, or nest vegetation variables summarized in principal components. Residuals were used to determine the effect of fragment size independent of vegetation variables. These analyses resulted in a misleadingly low p value for size effect due to the effect of pseudoreplication. The results of this analysis, however, do allow a comparison between the relative importance of fragment size and other variables on nesting success. We used correlation analysis (proc corr, SAS Institute 1995) to determine if nesting success and density were correlated.

Results

Distribution of Grassland-Nesting Birds

During each of the 3 years, Henslow's Sparrow was the most common species in our study area, followed by Dickcissels, Grasshopper Sparrows, and Eastern Meadowlarks (Table 1; Appendix). Greater Prairie-Chickens and Upland Sandpipers were the only grassland-nesting species that did not occur in prairie fragments smaller than 77 ha. The probability of seeing Greater Prairie-Chickens on at least one transect during at least one census was higher in large than in small prairie fragments ($\chi^2 = 12.38$, $p < 0.001$, df = 30; Appendix). This size ef-

Table 1. Mean bird density (male birds/10 ha) and standard error in 31 (1995) and 33 (1996, 1997) study plots in prairie fragments of southwestern Missouri, 1995–1997.

Species	1995 (SE)	1996 (SE)	1997 (SE)
Henslow's Sparrow	6.34 (0.97)	5.56 (0.77)	9.19 (1.48)
Grasshopper Sparrow	4.32 (0.32)	3.54 (0.45)	3.25 (0.66)
Dickcissel	3.82 (0.27)	2.80 (0.28)	2.36 (0.26)
Eastern Meadowlark	2.80 (0.65)	4.59 (0.67)	3.10 (0.76)
Red-winged Blackbird	0.38 (0.28)	0.04 (0.03)	0.08 (0.05)
Eastern Kingbird	0.21 (0.09)	0.05 (0.02)	0.11 (0.04)
Greater Prairie-Chicken	0.13 (0.09)	0.04 (0.03)	0.04 (0.02)
American Goldfinch	0.09 (0.06)	0.05 (0.02)	0.05 (0.02)
Common Yellowthroat	0.04 (0.02)	0.04 (0.02)	0.05 (0.03)
Brown-headed Cowbird	0.04 (0.02)	0.03 (0.01)	0.02 (0.02)
Northern Bobwhite	0.05 (0.02)	0.02 (0.01)	0.01 (0.01)
Field Sparrow	0.05 (0.04)	0.01 (0.01)	0
Upland Sandpiper	0.01 (0.01)	0	0.01 (0.01)
Scissor-tailed Flycatcher	0.01 (0.01)	0	0.03 (0.02)
Ruby-throated Hummingbird	0	0	0.07 (0.03)
American Crow	0	0.01 (0.01)	0
Mourning Dove	0.01 (0.01)	0	0
Bell's Vireo	0	0	0.05 (0.05)

fect was not due to a larger number of transects in large prairie fragments because the effect of the number of transects on the probability of occurrence was not significant ($\chi^2 = 0.58$, $p = 2.80$, df = 30). Year also did not have an effect on the probability of the occurrence of Greater Prairie-Chickens ($\chi^2 = 1.14$, $p = 0.56$, df = 30). The frequency of occurrence in Upland Sandpipers ($n = 3$) was too low for statistical analysis.

Density of each of the four species analyzed varied significantly among plots within prairies ($p < 0.05$ for each species). Therefore, we could use density estimates of each plot as independent data in the analysis. Density also differed among prairies for Henslow's Sparrows in 1996 ($F = 3.4$, $p = 0.01$, df = 11) and 1997 ($F = 3.9$, $p = 0.005$; df = 11); Dickcissels in 1995 ($F = 11.0$, $p < 0.001$, df = 10), 1996 ($F = 17.4$, $p < 0.001$, df = 11), and 1997 ($F = 4.6$, $p < 0.002$, df = 11); and Grasshopper Sparrows in 1997 ($F = 3.0$, $p = 0.02$, df = 11). This variation among prairies might be due to differences in fragment size, vegetation characteristics, or characteristics of the surrounding landscape (Winter 1998).

Variation in density of all four species was better explained by vegetation variables than by fragment size (Table 2). In each year, the first three principal components explained more than 80% of the variation in vegetation characteristics (Table 3). These components represented a continuum from low to high litter, low to high vegetation, and low to high woody cover. The only species that was significantly affected by fragment size after taking variation due to vegetation variables into account was the Henslow's Sparrow (Table 2). The extent to which fragment size influenced Henslow's Sparrow density varied greatly among years (Fig. 1), however, and vegetation characteristics generally were more important in determining its density. Fragment size did not influence the density of Grasshopper Sparrows. Rather, its density was highly dependent on vegetation characteristics. Both fragment size and vegetation characteristics had little influence on densities of Dickcissel (Fig. 1) and Eastern Meadowlark. The models that best predicted bird density always included vegetation variables, whereas fragment size was consistently part of the AIC model in Henslow's Sparrows only. Considering the results on distribution and density of grassland-nesting birds, it appeared that the only species with consistent area sensitivity in southwestern Missouri were the Greater Prairie-Chicken and Henslow's Sparrow.

Nesting Success

Contrary to our expectations based on distributional area sensitivity, the daily probability of nesting success of Henslow's Sparrows was higher than in any other species (Table 4), and its nesting success was not significantly related to fragment size (slope = -0.40 ± 0.44; Fig. 2a). The 95% confidence intervals for the effect of fragment size on Henslow's Sparrow nesting success was between -1.28 and 0.48. Although our sample size was too small to determine if fragment size had an effect on the nesting success of Henslow's Sparrows, the confidence intervals indicate that at worst a decrease in fragment size from 100 to 50 ha would result in a 14% decrease in daily rates of nest survival. The nesting success of all ground-nesting species as a group also was not significantly affected by fragment size (slope = 0.004 ± 0.03; Fig. 2c). The 95% confidence interval for the effect of fragment size on daily nest survival ranged between -0.056 and 0.064. The worst possible effect of a decrease in fragment size from 100 to 50 ha on rates of daily nest success was 1.9% less strong than for Henslow's Sparrows. Only the nesting success of Dickcissels was significantly affected by fragment size (slope: 0.02 ± 0.008; Fig. 2b). At worst, its daily nesting success decreased by 1% with a decrease in fragment size from 100 to 50 ha. Nesting success was not correlated with bird density in Dickcissels ($r = -0.05$, $p = 0.83$, $n = 23$) or Henslow's Sparrows ($r = 0.40$, $p = 0.20$, $n = 12$).

Table 2.   Regression models describing the relation between bird density, vegetation variables, and fragment size.

Species		Full model[a]				Vegetation model[b]				Size model[c]				Akaike's information criterion (AIC) model[d]			
		F	p	R²	df	F	p	R²	df	F	p	R²	df	variables entered[e]	F	p	R²
Henslow's																	
Sparrow	1995	12.6	0.000	0.88	27, 10	5.2	0.002	0.60	27, 6	8.3	0.008	0.24	27, 1	all but p2p3	14.8	0.000	0.88
	1996	2.8	0.025	0.60	29, 10	2.5	0.048	0.40	29, 6	2.6	0.119[f]	0.08	29, 1	size, sp1, sp3	9.2	0.000	0.51
	1997	14.4	0.000	0.89	28, 10	12.	0.000	0.77	28, 6	6.7	0.015	0.20	28, 1	all but p1 and sp2	19.8	0.000	0.89
Dickcissel	1995	2.6	0.041	0.60	27, 10	3.0	0.028	0.46	27, 6	0.3	0.582	0.01	27, 1	p2, sp1, sp2, sp3	7.4	0.000	0.56
	1996	3.0	0.017	0.62	29, 10	1.6	0.190	0.29	29, 6	2.7	0.111	0.09	29, 1	p1, sp1, sp2, p1p2	8.8	0.000	0.58
	1997	1.2	0.331	0.41	28, 10	2.1	0.067	0.39	28, 6	0.9	0.346	0.03	28, 1	size, sp3, p1p3	4.1	0.016	0.33
Grasshopper																	
Sparrow	1995	3.8	0.008	0.69	27, 10	7.0	0.000	0.67	27, 6	1.7	0.209	0.06	27, 1	size, p1, p2, p3	12.2	0.000	0.68
	1996	2.7	0.028	0.59	29, 10	4.1	0.006	0.52	29, 6	1.3	0.257	0.04	29, 1	size, p3, sp2, sp3, p2p3	6.0	0.000	0.56
	1997	8.2	0.000	0.82	28, 10	11.8	0.000	0.76	28, 6	0.0	0.838	0.00	28, 1	p1, p2, sp1, p2p3	25.7	0.000	0.81
Eastern																	
Meadowlark	1995	1.2	0.349	0.42	27, 10	1.2	0.334	0.26	27, 6	0.1	0.737	0.00	27, 1	p1, p2, p1p2	4.5	0.012	0.36
	1996	1.5	0.203	0.45	29, 10	1.6	0.193	0.29	29, 6	0.0	0.948	0.00	29, 1	sp1, sp2, sp3, p1p2, p2p3	2.7	0.048	0.36
	1997	0.9	0.527	0.34	28, 10	1.3	0.283	0.27	28, 6	0.7	0.412	0.02	28, 1	p2, p3, p1p2	3.1	0.042	0.27

[a] *Full model with fragment size and vegetation variables as independent variables.*
[b] *Vegetation variables as independent variables, independent of variation due to fragment size.*
[c] *Fragment size as independent variable, independent of variation due to vegetation variables.*
[d] *Model that best predicts variation in species richness or density after the AIC (Akaike 1969; Lebreton et al. 1992).*
[e] *Size, fragment size; p1, p2, p3, principal components; sp1/sp2/sp3, interaction between fragment size and principal component; p1p2/p1p3/p2p3, interactions between principal components.*
[f] *When Prairie State Park is excluded, then F = 9.3, p = 0.05, R² = 0.26.*

Stepwise logistic regression indicated that fragment size, an interaction between fragment size and the first principal component, and year significantly affected Dickcissel nesting success (Table 5). The first principal component explained >74% of the variation in nest vegetation variables and summarized a continuum from low to high litter cover, low to high vegetation and visual obstruction measurements, and high to low soil cover

Table 3.   Principal components for vegetation characteristics measured within study plots in fragments of native tallgrass prairie in southwestern Missouri, 1995–1997.

| Output of principal components analysis	1995			1996			1997		
	PCI	PCII	PCIII	PCI	PCII	PCIII	PCI	PCII	PCIII
Eigenvalue	3.1	2.5	1.8	3.3	2.8	1.6	3.9	2.1	1.5
Percentage explained	35.0	27.8	20.4	36.5	30.9	18.2	43.6	23.4	16.2
Cumulative percentage explained	35.0	62.9	83.3	36.5	67.3	85.6	43.6	67.0	83.2
Correlation to original variables									
litter depth	−0.24	0.52	−0.07	0.44	0.06	−0.35	0.37	−0.32	0.16
vegetation height	0.40	0.39	0.06	−0.01	0.55	−0.23	0.41	0.21	0.25
visual obstruction	0.42	0.36	0.15	−0.01	0.53	−0.25	0.37	0.28	0.32
number of woody stems	−0.42	0.00	0.67	0.33	0.07	0.54	−0.38	−0.24	0.32
litter cover	−0.45	0.33	−0.18	0.45	−0.23	−0.30	0.22	−0.55	−0.29
grass cover	0.46	−0.01	0.03	−0.43	−0.26	−0.09	0.27	0.08	0.49
forb cover	0.37	0.07	−0.03	−0.04	0.50	0.08	0.01	0.50	−0.46
woody cover	−0.12	−0.03	0.69	0.33	0.13	0.54	−0.40	−0.16	0.37
soil cover	0.10	−0.57	−0.08	−0.44	0.13	0.25	−0.36	0.36	0.20
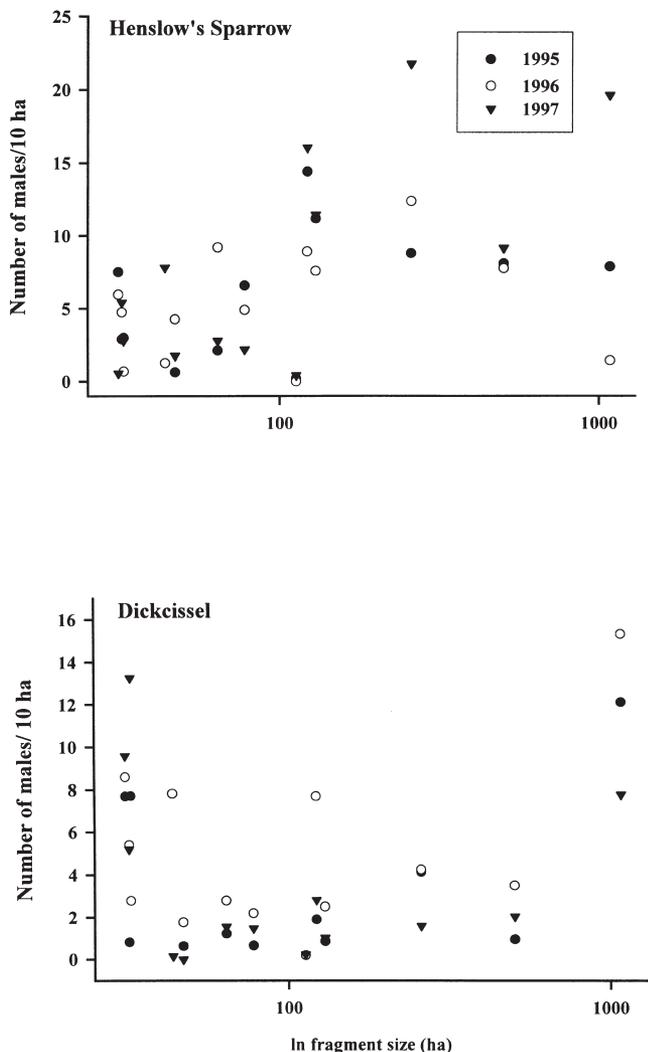
Figure 1. Density of Henslow's Sparrows and Dickcissels in prairie fragments of various sizes in southwestern Missouri, 1995–1997.

(Winter 1998). Once the variation in vegetation variables among prairie fragments was taken into account, year and fragment size (e.g., "residual") were the only significant factors influencing Dickcissel nesting success

(Table 5). In contrast, Henslow's Sparrow nesting success was not influenced by either fragment size or vegetation characteristics. The only variable that entered the stepwise logistic regression model for this species was distance to edge; the nesting success of Henslow's Sparrows decreased with increasing proximity to edge (Table 5). Once differences in vegetation among prairies of various sizes were taken into account, fragment size and nest cover also entered the Henslow's Sparrow model, but with high p values ($p > 0.1$). Thus, Dickcissels seemed to be the only species that showed demographic area sensitivity. Sample size for Henslow's Sparrows was, however, too small to reliably determine the effect of fragment size on its nesting success.

Discussion

Our study showed that habitat fragmentation can negatively affect grassland-nesting birds at different levels. Presence and absence data identified only the largest grassland-nesting species (Greater Prairie-Chicken) as area sensitive in southwestern Missouri. This species has been described previously as highly sensitive to habitat fragmentation (Cannon & Christisen 1984; Westemeier 1985). A less conspicuous form of area sensitivity can be seen in species that have lower densities in small than in large habitat fragments. In our study, such an intermediate level of area sensitivity was found only in Henslow's Sparrows, a species of great conservation concern (Pruitt 1996). Census (i.e., distributional) data thus implied that only these two grassland-nesting species were negatively affected by habitat fragmentation in southwestern Missouri.

Nesting data revealed yet another species that was negatively affected by habitat fragmentation: the Dickcissel. This species has been described as relatively insensitive to habitat fragmentation because its density does not differ among fragments of various sizes (Herkert et al. 1993). Our study revealed, however, that its nesting success declined with decreasing fragment size,

Table 4. Nesting data for four grassland-nesting birds in prairie fragments of southwestern Missouri.

Species	Total nests[a]	Depredated nests[b]	Exposure days[c]	Daily survival rate (SE)[d]	Nesting success[e]
Henslow's Sparrow	59	25	550.5	0.95 (0.009)	39.47
Dickcissel	242	128	2251.5	0.94 (0.005)	29.25
Grasshopper Sparrow	23	15	206.0	0.93 (0.018)	22.04
Eastern Meadowlark	47	33	521.0	0.94 (0.011)	19.48

[a]Total number of nests monitored.
[b]Total number of depredated nests.
[c]Total number of exposure days (Mayfield 1975).
[d]Probability of daily Mayfield nesting success ("day") = −(no. depredated nests/no. Mayfield days) + 1. SE = sqrt (day × (no. depredated nests/no. Mayfield days)/no. Mayfield days).
[e]Percentage of nests that are successful over the entire interval = day$^{interval\ length}$. Interval length was 20 days for Henslow's and Grasshopper Sparrows, 21 for Dickcissels, and 25 for Eastern Meadowlarks (Ehrlich et al. 1988).

a)

Year effect: $F= 11.28$, $p= 0.009$
Size effect: $F= 1.18$, $p= 0.31$
Model-$R^2= 0.80$, df= 9

b)

Year effect: $F= 7.49$, $p= 0.01$
Size effect: $F= 4.68$, $p= 0.05$
Model-$R^2= 0.46$, df= 16

c)

$F= 0.02$, $p= 0.89$
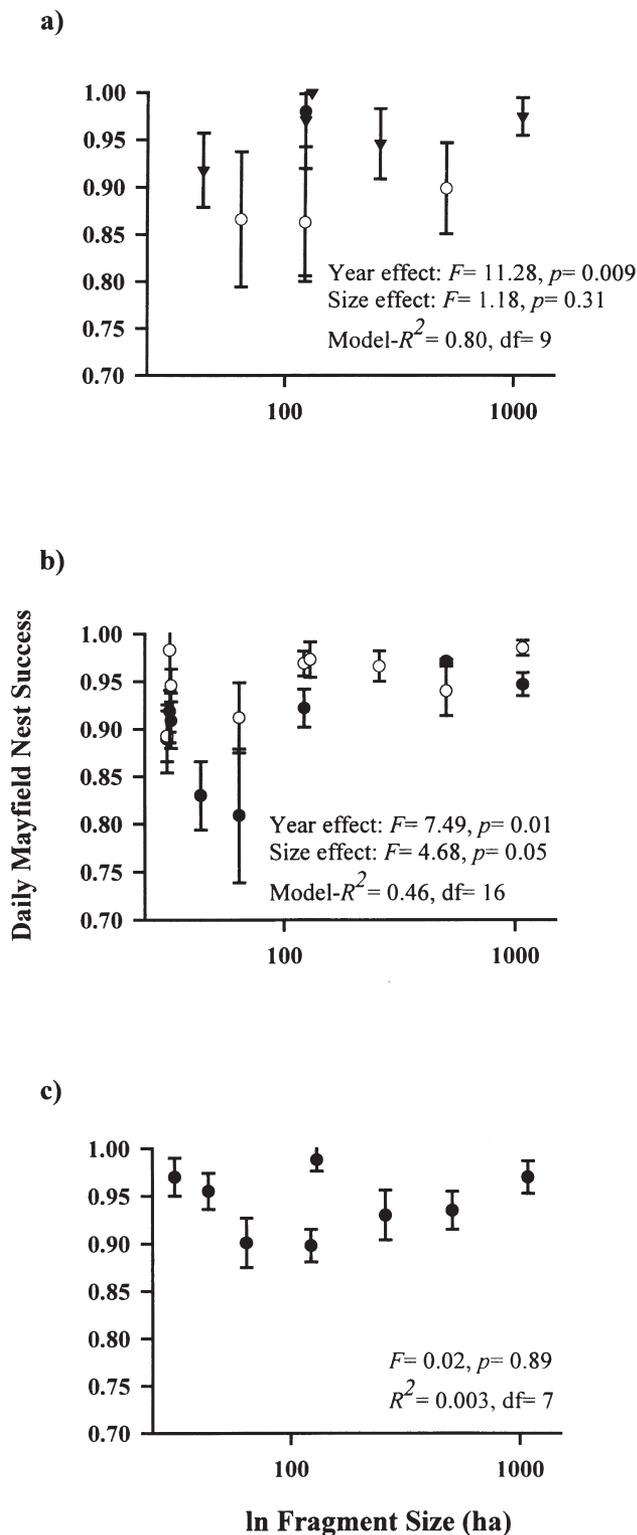$R^2= 0.003$, df= 7

ln Fragment Size (ha)

Figure 2. Mean daily Mayfield nesting success of (a) Henslow's Sparrow, (b) Dickcissel, and (c) ground-nesting birds in prairie fragments of various sizes in southwestern Missouri, 1995–1997. Standard errors are truncated at 1.0 because larger estimates of daily nest success are biologically impossible.

even though its density did not differ among prairie fragments of various sizes. Hence, census data alone did not reflect the sensitivity of Dickcissels to habitat fragmentation. Van Horne (1983) warned that density is a poor indicator for nesting success. Only a few studies of grassland-nesting birds have described such lack of correlation between density and nesting success. Johnson and Temple (1990) studied the nest density and nesting success of three species of sparrows, Bobolinks (*Dolichonyx oryzivorous*), and Western Meadowlarks (*Sturnella neglecta*) in small and large tallgrass prairie fragments in Minnesota. They found that nest density and nesting success were not correlated. A lack of correlation between bird density and nesting success also was reported by Vickery et al. (1992*b*) for three grassland sparrows in Maine and by Zimmerman (1984) for Dickcissels in old fields and prairies in Kansas. Zimmerman (1984), suggested that nesting success in grassland-nesting birds generally might not be dependent on density because the main nest predators, such as striped skunks (*Mephitis mephitis*; Vickery et al. 1992*a*), find nests of grassland-nesting birds incidentally. In prairie fragments in southwestern Missouri, mid-sized carnivores seem to be common nest predators and might be partly responsible for the lack of correlation between density and nesting success in Dickcissels (Winter 1998).

A lack of a relationship between grassland bird density and nesting success in fragments of various sizes, as shown in our study, has not been described previously for grassland-nesting birds. These data illustrate the need to investigate all levels of area sensitivity to better understand the response of grassland-nesting birds to habitat fragmentation. If a species avoids small habitat fragments, there is no doubt that habitat fragmentation does have a negative effect on such extremely area-sensitive species. When census data indicate, however, that a species is intermediately area sensitive or not area sensitive at all, one also needs to investigate demographic data (e.g., nesting success) to get an overall estimate of the sensitivity of a species to habitat fragmentation.

Henslow's Sparrows, which are highly area sensitive based on census data (Herkert et al. 1993; Pruitt 1996), seemed to be less area sensitive on a demographic level than Dickcissels, a species that was not previously considered to be negatively affected by habitat fragmentation (Herkert et al. 1993, but see Swengel 1996). Sample size was too low for a reliable estimate of Henslow's Sparrow nest success in prairie fragments of various sizes. The negative response of Henslow's Sparrow nest success to close proximity to edge, however, does indicate that this species also is somewhat negatively affected by habitat fragmentation (Winter 1998). The reason Dickcissels and Henslow's Sparrows might express area sensitivity on such different levels is possibly directly related to nest placement and predator abundance in relation to edge (Winter 1998).

Table 5. Stepwise logistic regression testing the null hypothesis that nest predation is not related to any of the variables tested for Henslow's Sparrows (*n* = 59 nests) and Dickcissels (*n* = 233 nests), 1995–1997.

Species	Variable entered[a]	Slope[b]	SE	Wald χ^2	p
Original data					
Henslow's Sparrow	proximity to edge	−0.20	0.10	4.74	0.035
Dickcissel	fragment size	−0.42	0.11	14.83	0.000
	prin1 × fragment size	−0.06	0.02	10.00	0.002
	year	−0.74	0.30	6.08	0.014
Residuals (size effects independent of vegetation variables)					
Henslow's Sparrow	residual	−0.47	0.34	1.94	0.164
	nest cover	0.00	0.01	0.02	0.796
	proximity to edge	−0.20	0.10	4.25	0.039
Dickcissel	year	−0.97	0.29	11.62	0.000
	residual	−0.39	0.11	12.86	0.000

[a] *Variables used in the analysis were fragment size (log-transformed), proximity to edge (m), nest cover, and nest vegetation variables (see Methods). Year was included as a categorical variable.*

[b] *Logistic regression calculated the probability that a nest fails. Thus a negative parameter indicates that the probability that a nest fails decreases with increasing fragment size or vegetation variables.*

Grasshopper Sparrows and Eastern Meadowlarks were not area-sensitive on a distributional level, whereas in Illinois both species have been reported to be moderately sensitive to habitat fragmentation because they did not occur in fragments smaller than 10 ha (Herkert 1991). Fragments in our study were too large to detect such moderate area sensitivity.

Conclusion

This is the first study to demonstrate that census data do not reliably reflect the demographic effects of habitat fragmentation on grassland-nesting birds. Other studies have shown that density is not a reliable indicator for nesting success (i.e., Van Horne 1983; Zimmerman 1984; Maurer 1986; Vickery et al. 1992*b*). This concept, however, had not yet been used to assess the effect of habitat fragmentation on grassland-nesting birds. The only reliable information on area sensitivity from census data is based on the presence and or absence of a species. If a species is consistently absent from small habitat fragments, such as Greater Prairie-Chickens in southwestern Missouri, we can be certain that the species is highly area sensitive, at least for that particular area. A species that is less common in small than large fragments, however, may be as sensitive to habitat fragmentation as a species that occurs in similar densities in habitat fragments of any size. This is the case when nesting success is reduced in small fragments, as shown in this study for the Dickcissel in southwestern Missouri. Although it is well known that habitat loss negatively affects Dickcissels because nesting success is low in alternative habitats such as agricultural fields and grassed

waterways (e.g., Patterson & Best 1996), our study shows that Dickcissels also are negatively affected by the size of fragments of high-quality habitat. Small prairie fragments thus might be population sinks for this species (sensu Pulliam 1988), as has been shown for birds breeding in small forest fragments (Donovan et al. 1995*a*, 1995*b*; Robinson et al. 1995). We did not estimate the demographic viability of populations because the survival rates that must be included in the calculations for these models are unknown, and any estimate likely would be unreliable.

We need more nesting data to better understand how habitat fragmentation affects grassland-nesting birds. Because area sensitivity may be caused by many different factors (vegetation characteristics, patch size, proximity to edge, predator community, landscape characteristics), we will not fully understand the reason for population declines in many grassland-nesting birds unless we take all of the above factors into account, including other factors that might influence these birds during other portions of their annual cycle (i.e., winter or migration). Without understanding the interactions among grassland bird populations and patch size, vegetation characteristics, predator communities, and landscape configuration—and the variation of these interactions among years—it will be difficult to manage the remaining grassland habitat in a way that ensures the long-term survival of grassland-nesting birds.

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Appendix

Mean density (±SE) of grassland birds in fragments of native tallgrass prairie (in ha) in southwestern Missouri, 1995-1997.

Species	Fragment size												
	31.2	32.0	32.4	43.7	47.0	64.0	77.7	113.0	122.3	130.0	259.2	506.0	1084
Henslow's Sparrow *Ammodramus henslowii*	4.7 ± 1.34	2.5 ± 1.49	2.1 ± 0.82	7.6 ± 3.66	5.2 ± 1.67	4.0 ± 1.70	6.1 ± 2.12	0.2 ± 0.09	13.1 ± 1.86	10.1 ± 1.93	14.3 ± 2.24	8.3 ± 1.57	9.6 ± 3.39
Grasshopper Sparrow *Ammodramus savannarum*	4.4 ± 1.13	3.0 ± 1.73	0.6 ± 0.45	2.2 ± 1.21	3.9 ± 1.31	6.8 ± 1.03	6.1 ± 1.43	6.5 ± 0.49	2.8 ± 0.90	3.1 ± 0.95	1.2 ± 0.49	3.8 ± 0.92	2.4 ± 0.71
Dickcissel *Spiza americana*	8.6 ± 0.42	3.8 ± 1.25	7.9 ± 2.81	4.0 ± 2.21	0.8 ± 0.32	1.8 ± 0.32	1.4 ± 0.27	0.2 ± 0.07	4.1 ± 0.97	1.5 ± 0.33	3.3 ± 0.71	2.1 ± 0.70	11.7 ± 1.54
Eastern Meadowlark *Sturna magna*	2.8 ± 0.86	3.6 ± 0.82	3.3 ± 0.61	2.9 ± 1.41	2.8 ± 0.57	4.7 ± 0.57	2.9 ± 0.55	1.8 ± 0.59	3.6 ± 0.51	2.7 ± 0.37	2.9 ± 0.46	3.1 ± 0.40	2.0 ± 0.28
Eastern Kingbird *Tyrannus tyrannus*	0.2 ± 0.13	0.2 ± 0.14	0.04 ± 0.05	0	0.4 ± 0.27	0.2 ± 0.08	0.2 ± 0.10	0.05 ± 0.05	0.02 ± 0.02	0.07 ± 0.07	0.04 ± 0.04	0.1 ± 0.06	0.07 ± 0.04
American Goldfinch *Carduelis tristis*	0.2 ± 0.10	0.3 ± 0.27	0.05 ± 0.05	0	0.03 ± 0.03	0.04 ± 0.03	0	0	0	0.08 ± 0.05	0	0.2 ± 0.07	0
Brown-headed Cowbird *Molothrus ater*	0	0	0.06 ± 0.06	0	0	0.03 ± 0.03	0.07 ± 0.04	0	0	0.03 ± 0.03	0.07 ± 0.07	0.04 ± 0.03	0.1 ± 0.10
Red-winged Blackbird *Agelaius phoeniceus*	0	0.5 ± 0.27	1.6 ± 1.40	0	0	0	0	0.02 ± 0.02	0	0	0.2 ± 0.11	0.02 ± 0.02	0.1 ± 0.11
Common Yellowthroat *Geothlypis trichas*	0	0	0	0	0.07 ± 0.07	0	0	0	0	0	0.04 ± 0.03	0.2 ± 0.08	0.2 ± 0.16
Upland Sandpiper *Bartramia longicauda*	0	0	0	0	0	0	0.03 ± 0.03	0.04 ± 0.04	0.02 ± 0.02	0	0	0	0
Greater Prairie-Chicken *Tympanuchus cupido*	0	0	0	0	0	0	0	0	0	0.02 ± 0.05	0.4 ± 0.27	0	0.4 ± 0.23