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THE RELATIVE IMPORTANCE OF PATCH AREA AND PERIMETER–AREA RATIO TO GRASSLAND BREEDING BIRDS

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Abstract. Habitat fragmentation has been implicated as a major cause of population decline in grassland birds. We tested the hypothesis that a combination of area and shape determines the use of grassland patches by breeding birds. We compared both species richness and individual species presence in 45 wet meadow grasslands in the floodplain of the central Platte River, Nebraska. Bird data were collected through the use of belt transects and supplemented by walking and listening outside transects. Our data supported our primary hypothesis that perimeter–area ratio, which reflects both the area and shape of a patch, is the strongest predictor of both individual species presence and overall species richness. The probability of occurrence for all six common species (Grasshopper Sparrows, Bobolinks, Upland Sandpipers, Western Meadowlarks, Dickcissels, and Red-winged Blackbirds) was significantly inversely correlated with perimeter–area ratio. The probability of occurrence of Grasshopper Sparrows, Bobolinks, Upland Sandpipers, and Western Meadowlarks was also correlated with area. We conclude that species richness is maximized when patches are large (>50 ha) and shaped so that they provide abundant interior areas, free from the impacts of edges.

Key words: birds, grassland; habitat fragmentation; landscape ecology; Nebraska; patch area; patch shape; perimeter–area ratio; Platte River, Nebraska; population declines; species–area relationship; wet meadows.

INTRODUCTION

Landscape fragmentation has had a profound effect on the distribution and abundance of bird species in many parts of the world (Whitcomb et al. 1981, Howe 1984, Lynch and Whigham 1984, Opdam et al. 1985, Herkert 1994, Vickery et al. 1994, Hinsley et al. 1996). The strongest evidence of the impact of fragmentation has come from studies of woodland birds. Research in forested habitats suggests that forest-interior birds and neotropical migrants are especially sensitive to smaller habitat patches and the increasing patch isolation that accompanies fragmentation; in general, species richness and relative abundance of area-sensitive species significantly decrease as patch area decreases (Whitcomb et al. 1981, Ambuel and Temple 1983, Howe 1984, Lynch and Whigham 1984, Opdam et al. 1985, Robbins et al. 1989).

Although much less work has concentrated on birds in grasslands, studies suggest that grassland birds are experiencing extensive population declines because of the loss of large grassland patches (Samson 1980, Herkert 1994, Vickery et al. 1994). Recent analysis of data from the North American Breeding Bird Survey between 1966 and 1993 shows that grassland bird species are declining faster than any other group of breeding species in the midwestern United States (Herkert 1995). In particular, Grasshopper Sparrows (*Ammodramus savannarum*), Western Meadowlarks (*Sturnella neglecta*), and Bobolinks (*Dolichonyx oryzivorus*) are among the species that show the greatest declines (Herkert 1995). This loss of grassland birds is concomitant with the tremendous loss of tallgrass prairie, which currently exceeds that of any other major ecosystem type in North America (Samson and Knopf 1994).

Most studies of grassland bird habitat selection have focused only on the importance of vegetation structure (Wiens 1969, Rotenberry and Wiens 1980, Kantrud 1981, Cody 1985, Bowen and Kruse 1993). A few studies have investigated the spatial aspects of grassland fragmentation and found that patch area is an important variable affecting habitat occupancy (Samson 1980, Herkert 1994, Vickery et al. 1994).

Patch area may not adequately explain the effects of fragmentation on habitat occupancy by birds, however, because patches of equal area are not necessarily equal in their ability to support a given population. In fragmented landscapes, patches should be viewed in the context of the surrounding matrix because the matrix can determine the degree of patch isolation (see review in Andren [1994]) and the availability of supplementary resources (Dunning et al. 1992, Burke and Nol 1998). In addition, the matrix itself varies in its degree of hostility (Addicott et al. 1987, Franklin 1993).

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Patches of equal area may also vary significantly in the amount of their area exposed to edges. Negative impacts of edges on breeding birds have been documented in both forest and grassland habitats. In forest environments, nest predation and brood parasitism rates increase near edges (Gates and Gysel 1978, Wilcove 1985, Andren et al. 1985, Andren and Angelstam 1988, Burkey 1993, Marini et al. 1995). In grassland habitats, Johnson and Temple (1986, 1990) and Burger et al. (1994) found higher predation and parasitism rates on nests close to wooded edges relative to those away from edges. There is also evidence that some grassland bird species avoid nesting near patch edges (Johnson and Temple 1986, Delisle 1995, Helzer 1996).

Because patch shape, along with area, determines the amount of habitat exposed to edges, patch shape may have a significant effect on habitat occupancy by grassland breeding birds. We are not aware of any research on the effects of patch shape on grassland birds, but Temple (1986) found that the presence and abundance of woodland birds was better predicted by the ''core area'' (defined as areas >100 m from an edge) than by the total area of forest fragments. Patches that had elongated shapes, indented perimeters, or inclusions of open habitat within the fragment had fewer species and individuals than forest stands with compact shapes and unbroken perimeters.

Temple's findings on the effects of patch shape and core area in forest patches may not be directly applicable to grassland patches because the two breeding habitat types differ in terms of predator species, breeding bird behavior, and structural contrast between the habitat and surrounding edges. There is also some question of whether Temple's method of estimating core area can be extrapolated to different habitats and landscapes. The distance that edge effects extend into a patch vary widely (Faaborg et al. 1993) and edge effects vary between geographic regions (Freemark 1986). This variability points to the need for a relative measure such as perimeter–area ratio that accounts for the amount of patch area exposed to edges without requiring a subjective estimation of the distance that edge effects extend into a patch. Patches with elongated shapes or indented perimeters have higher perimeter–area ratios than patches of the same area with compact shapes and unbroken perimeters. In addition, small patches generally have higher perimeter–area ratios than large patches.

The objective of our study was to evaluate the relative importance of patch area and perimeter–area ratio to both grassland bird species richness and the likelihood of occurrence of individual grassland species. We hypothesized that in landscapes where habitat fragmentation has led to a variety of patch shapes and areas, patches with high perimeter–area ratios (containing little or no core area) are avoided by certain grassland bird species and thus have low species richness.

Methods

Study area

The study area was located in the floodplain of the central Platte River between Grand Island and Wood River, Nebraska. The floodplain is a relatively flat area composed of a mosaic of grassland, cropland, riparian forest, and stream channels. A dynamic hydrological interaction exists among the grasslands, main channels, side channels, and backwaters. Wet meadows (combinations of wet-mesic prairie, sedge meadow, and marsh communities) comprise the majority of grassland bird habitat in the region (Currier 1982). These remnant grasslands are topographically heterogeneous with ridge/swale structure. Vegetation in these meadows consists mainly of native grasses such as big bluestem (*Andropogon gerardii*), prairie cordgrass (*Spartina pectinata*), and Indian grass (*Sorghastrum nutans*), introduced grasses such as smooth brome (*Bromus tectorum*), Kentucky bluegrass (*Poa pratensis*), and redtop (*Agrostis stolonifera*), and many prairie forbs. Roughly half of the meadows used in this study were grazed while the other half were hayed. Four of the meadows also contained burned or idled areas. The majority of the land cover in the study region is irrigated cropland with corn, soybeans, and alfalfa as the major crop types. Alfalfa and winter wheat fields provide the only habitat for grassland birds besides wet meadows and grassed roadsides. Trees, including cottonwood (*Populus deltoides*), willows (*Salix* sp.), green ash (*Fraxinus pennsylvanica*), and eastern redcedar (*Juniperus virginiana*), are common along river and stream channels and in windbreaks and shelterbelts.

Bird censuses

Forty-one patches were censused for birds in 1995 and 45 patches in 1996. In 1996, all but three of the same patches were used, and seven new patches were added. Patch areas ranged from 0.12 ha to 347 ha in 1995, with a mean area of 31.9 ha and a median of 8.5 ha. The 1996 patch areas ranged from 0.12 ha to 449 ha, with a mean of 41.7 ha and a median of 9.3 ha.

Each patch was censused twice between 17 May and 5 July each year. Censuses took place in the morning between 0530 and 0900 on days without rain or strong winds. Two methods of counting birds were employed. First, belt transects of 100-m widths were used to provide estimates of relative abundance (Mikol 1980). Transect lengths varied with the patch area. In addition, each patch was searched by walking and listening in all areas other than those specifically covered by transects in order to supplement species lists (after Herkert 1994). Birds that flew over a patch without landing were not counted in the species list for that patch. All species seen within a patch were recorded, but only those species that nest exclusively in grassland or wet meadow habitat were used in assembling species richness lists. Thus, shrub and tree nesting species such as

Eastern Kingbirds (*Tyrannus tyrannus*) and Common Yellowthroats (*Geothlypis trichas*), and species such as Mourning Doves (*Zenaida macroura*), which nest in many habitats, were not counted because they are not exclusively grassland breeders. Species such as Red-winged Blackbirds (*Agelaius phoeniceus*) and Soras (*Porzana carolina*) were included because the wetland habitats they nest in are a common component of the wet meadows in this area. Ring-necked Pheasants (*Phasianus colchicus*) were also included in species richness data because they are considered to be a naturalized species in Nebraska and nest in open grasslands. Pheasants are also considered to be grassland breeders by the North American Breeding Bird Survey (Herkert 1995), and have been included as members of grassland bird communities by many other authors (e.g., Herkert 1991*a*, *b*, 1994, Zimmerman 1992, and Warner 1994).

Landscape measurements

National Aerial Photography Program (NAPP) black and white aerial photographs from 1993 (1:40 000) were used to measure patch area and perimeter length. A digital planimeter was used to make the measurements. Perimeter–area ratios were calculated for each patch by dividing the perimeter (in meters) by the area (in square meters).

Statistical methods

Logistic regression, using the SAS LOGISTIC procedure (SAS Institute 1982), was used to test for correlations between the landscape variables and species richness and probability of occurrence for each species. Logistic regression was used instead of linear regression because of the low number of species found in many patches. Area and perimeter–area ratio were used individually and in combination with each other in logistic models to determine their relative importance in predicting grassland bird species richness and presence.

Minimum patch area and perimeter–area ratio requirements for each of the common grassland breeding birds were estimated with incidence functions calculated using logistic regression. The SAS LOGISTIC procedure (SAS Institute 1982) was used for the calculations. Each of the two independent variables (patch area and perimeter–area ratio) was correlated with the occurrence of each species in a logistic regression model. An incidence value of 50% in the logistic models (the point at which the model predicts a 50% probability of the species occurring in a given patch) was used to define the minimum requirement of either patch area or perimeter–area ratio for a species (after Robbins et al. 1989). For comparison, this value is the same as that used by other researchers who have estimated minimum area requirements for grassland birds (Herkert 1994, Vickery et al. 1994).

The data from the two years of the study were analyzed separately for two reasons. First, not all of the patches used in 1995 were used in 1996 and several new patches were added to improve the distribution of patch size and perimeter–area ratio in the data set. Secondly, studies have shown that some grassland birds tend to return to the same patches from year to year (e.g., Smith 1963, Gavin and Bollinger 1988, Bollinger and Gavin 1989), so data sets from each year could not be considered as independent samples and combined. We tested for differences in patterns between years for each species and for species richness by including a dummy variable (year) in a logistic model with area (and with perimeter–area ratio) and the presence data for each species and testing for the significance of the dummy variable.

Passive sampling hypothesis test

Because perimeter–area ratio generally decreases as area increases, it is possible that an inverse correlation between species richness and perimeter–area ratio could be explained by the passive sampling hypothesis (Connor and McCoy 1979). This hypothesis essentially states that the increase in species richness with increasing patch area is due simply to the larger population of individuals found in large patches. To test the validity of this hypothesis in regards to our data, we used transect segments of equal area from each patch (after Herkert 1994) and correlated species richness within those segments with patch perimeter–area ratio using logistic regression. Four randomly selected 100-m transect segments (4 ha total area) were selected from each patch. Where small patches did not contain adequate transect lengths, patches with similar perimeter–area ratios were combined and their perimeter–area ratio values averaged. Species richness in patches was based only on the birds found within the standardized 4-ha plots from each patch (or patch group).

Perimeter–area ratio index

Increasing deviation from a perfectly circular shape results in increasing perimeter–area ratio values. Thus, an irregularly shaped patch has to be larger than a circular patch to have the same perimeter–area ratio value. To demonstrate the importance of measuring perimeter–area ratio instead of area when investigating patch effects on grassland birds, we created an index that shows the size of a perfectly circular patch that would meet our estimated perimeter–area ratio requirement for each species. Then, because square-shaped patches are more likely to occur in agricultural areas, we calculated values for perfect squares as well.

RESULTS

Species richness

We found thirteen species of wet meadow breeding birds during the two field seasons (Table 1). Although only the six most common were used for individual species occurrence models, all thirteen were included

TABLE 1. Wet meadow breeding birds observed during the two years of the study in the Platte River valley. There were 41 grassland patches in 1995 and 45 patches in 1996.

Species	Percentage of patches occupied	
	1995	1996
Most common species		
Western Meadowlark (*Sturnella neglecta*)	68	71
Grasshopper Sparrow (*Ammodramus savannarum*)	54	53
Dickcissel (*Spiza americana*)	49	60
Bobolink (*Dolichonyx oryzivorus*)	29	40
Red-winged Blackbird (*Agelaius phoeniceus*)	27	47
Upland Sandpiper (*Bartramia longicauda*)	22	22
Other grassland birds		
Sedge Wren (*Cistothaurus platensis*)	5	5
Ring-necked Pheasant (*Phasianus colchicus*)	3	6
Henslow's Sparrow (*Ammodramus henslowii*)	2	7
Lark Sparrow (*Chondestes grammacus*)	2	†
Eastern Meadowlark (*Sturnella magna*)	†	7
Sora (*Porzana carolina*)	†	4
Swamp Sparrow (*Melospiza georgiana*)	†	2

† Not observed.

in species richness analyses. The larger number of patches occupied by several species in 1996 was likely due to the subtraction of three small patches and the addition of seven relatively large patches to the study in that year, although there may have been changes in regional populations as well.

Results from the logistic regression models (Table 2 and Fig. 1) indicated that species richness was positively correlated with perimeter–area ratio ($P < 0.0001$) and area ($P < 0.001$). When area and perimeter–area ratio were both included in the model with species richness, perimeter–area ratio alone was found to be significant ($P < 0.0001$). There were no significant ($P > 0.05$) differences in the relationships between 1995 and 1996.

Individual species

The occurrence of Grasshopper Sparrows, Western Meadowlarks, and Upland Sandpipers (*Bartramia longicauda*) was positively correlated ($P < 0.05$) with patch area in both years, Dickcissels (*Spiza americana*) and Bobolinks only in one year each, and Red-winged Blackbirds had no relationship with patch area. However, all six species were inversely correlated ($P < 0.05$) with perimeter–area ratio in both years (Table 2).

When both area and perimeter–area ratio were included together in the species models, the only significant correlations that appeared were with perimeter–area ratio (Table 3). For many species models, the variance explained by each variable overlapped enough to prevent significance of either.

Incidence functions were created for each species that calculated the minimum patch area and perimeter–area ratio values needed to predict a 50% chance of that species occurring in a patch (Table 4 and Figs. 2 and 3). There were no differences ($P > 0.05$) between the incidence function results from the 1995 data and those from 1996.

TABLE 2. Results of logistic regression models in which species richness and occurrence of individual species in grassland patches were modeled against the single variables area and perimeter–area ratio in a study of grassland-breeding birds in the Platte River floodplain.

Species	Area						Perimeter–area ratio					
	1995			1996			1995			1996		
	Parameter estimate	Wald	P	Parameter estimate	Wald	P	Parameter estimate	Wald	P	Parameter estimate	Wald	P
Species richness	−0.044	12.54	0.0004*	−0.022	12.53	0.0004*	329.6	27.41	0.0001*	232.9	29.57	0.0001*
Grasshopper Sparrow	−0.475	6.28	0.0122*	−0.172	7.38	0.0066*	568.8	6.73	0.0094*	197.3	11.67	0.0006*
Western Meadowlark	−0.661	8.09	0.0045*	−0.305	6.35	0.0188*	381.5	6.05	0.0139*	190.9	11.16	0.0008*
Bobolink	−0.043	4.63	0.0315*	−0.025	3.42	0.0645	140.7	6.26	0.0123*	99.6	7.26	0.0071*
Upland Sandpiper	−0.053	5.55	0.0185*	−0.048	6.44	0.0112*	260.1	6.11	0.0134*	347.4	6.48	0.0109*
Dickcissel	−0.023	2.25	0.1338	−0.060	4.47	0.0345*	98.9	6.80	0.0091*	127.2	11.03	0.0009*
Red-winged Blackbird	−0.013	2.89	0.0894	−0.009	1.98	0.1589	95.3	4.23	0.0397*	79.4	6.59	0.0102*

Notes: Negative parameter estimate values indicate a positive relationship between the variables and vice versa. For information about the Wald coefficient, see SAS User's Guide (1982).

* Significant ($P < 0.05$).

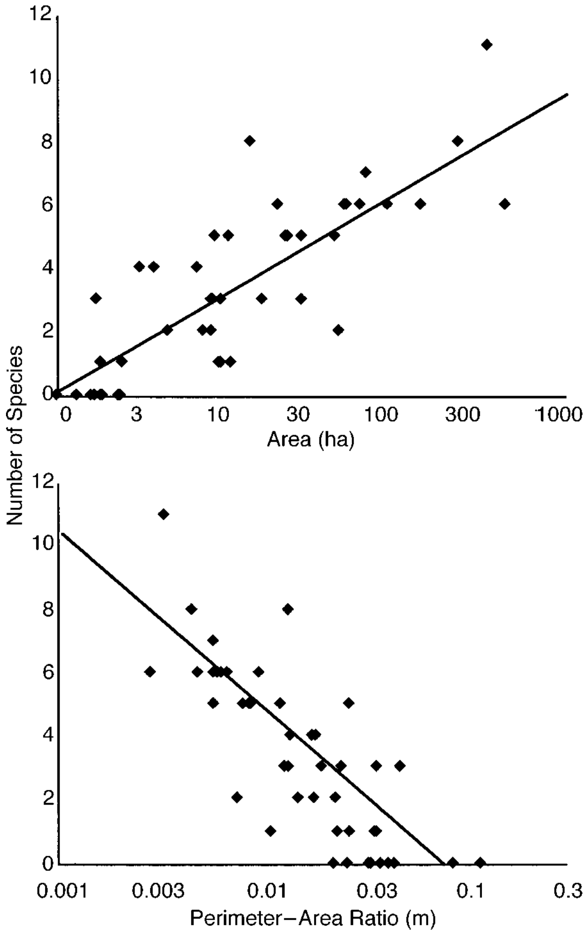

FIG. 1. Scatterplots of species richness vs. area and perimeter–area ratio (on logarithmic scales) from 1996 grassland-bird data from the Platte River wet meadows. There was no significant difference ($P < 0.05$) in correlations between 1995 and 1996 data.

Passive sampling hypothesis

As predicted, there was a high correlation between patch area and perimeter–area ratio ($R^2 = 0.94$). If birds in small patches are essentially small samples of the same statistical population of birds found in larger patches, there should have been no difference in species richness between the 4-ha subsamples of our data. However, species richness in the subsamples had a significant inverse correlation with perimeter–area ratio ($P < 0.005$) in both 1995 and 1996 (Fig. 4), indicating that passive sampling does not adequately explain the correlation between perimeter–area ratio and species richness.

Perimeter–area ratio index

Because of the irregular shapes of the patches in our study, the actual patch areas needed to provide for the perimeter–area ratio requirements of each species were much larger than those of the hypothetical circular and square-shaped patches in our index (Table 5). For most species, our index showed that the patches in our study area had to be about three times the size of circular patches to meet the same perimeter–area ratio requirement.

DISCUSSION

Relative importance of patch area and perimeter–area ratio

Both patch area and perimeter–area ratio were significant predictors of species richness and the probability of occurrence for wet meadow breeding birds. However, perimeter–area ratio had a consistently stronger correlation with both species richness and probability of occurrence than did patch area. We believe these results are important because of their implications for conservation efforts.

By comparison, a study of woodlot fragments in Wisconsin, Temple (1986) found that the core area of patches was a better predictor of bird presence and abun-

TABLE 3. Results of logistic regression models in which occurrence of each bird species in grassland patches was regressed against area and perimeter–area ratio of those patches at the same time, in a study of grassland-breeding birds in the Platte River floodplain.

	Area						Perimeter–area ratio					
	1995			1996			1995			1996		
Species	Parameter estimate	Wald	P	Parameter estimate	Wald	P	Parameter estimate	Wald	P	Parameter estimate	Wald	P
Species richness	−0.012	2.554	0.1101	−0.007	2.64	0.1045	282.5	19.84	0.0001*	208.6	22.35	0.0001*
Grasshopper Sparrow	−0.011	0.004	0.9469	−0.098	0.83	0.9469	552.4	4.05	0.0442*	125.2	2.72	0.0990
Western Meadowlark	−0.111	0.157	0.6915	−0.016	005	0.8275	342.9	3.15	0.0758	177.8	5.71	0.0168*
Bobolink	−0.022	1.228	0.2679	−0.009	0.85	0.3567	69.3	1.21	0.2719	71.6	3.06	0.0803
Upland Sandpiper	−0.026	1.832	0.2767	−0.017	0.88	0.3476	120.5	1.24	0.2664	194.8	1.76	0.1852
Dickcissel	−0.005	0.236	0.6273	−0.006	0.17	0.6775	84.2	3.80	0.0514*	115.2	0.11	0.7450
Red-winged Blackbird	−0.006	0.650	0.4198	−0.002	0.11	0.7450	70.2	1.89	0.1698	73.7	4.51	0.0337*

Notes: Negative parameter estimate values indicate a positive relationship between the variables and vice versa. For information about the Wald coefficient, see SAS User's Guide (1982).

* Significant ($P < 0.05$).

TABLE 4. Patch areas and perimeter–area ratio values at which each species reached 50% probability of occurrence in grassland patches in a study of Platte River wet meadows, based on incidence functions.

Species	Area (ha) 1995	Area (ha) 1996	Perimeter–area ratio 1995	Perimeter–area ratio 1996
Grasshopper Sparrow	8	12	0.018	0.018
Western Meadowlark	5	5	0.024	0.027
Bobolink	46	NS	0.009	0.013
Upland Sandpiper	50	61	0.008	0.007
Dickcissel	NS	9	0.018	0.023
Red-winged Blackbird	NS	NS	0.006	0.017

Note: NS = no significant relationship.

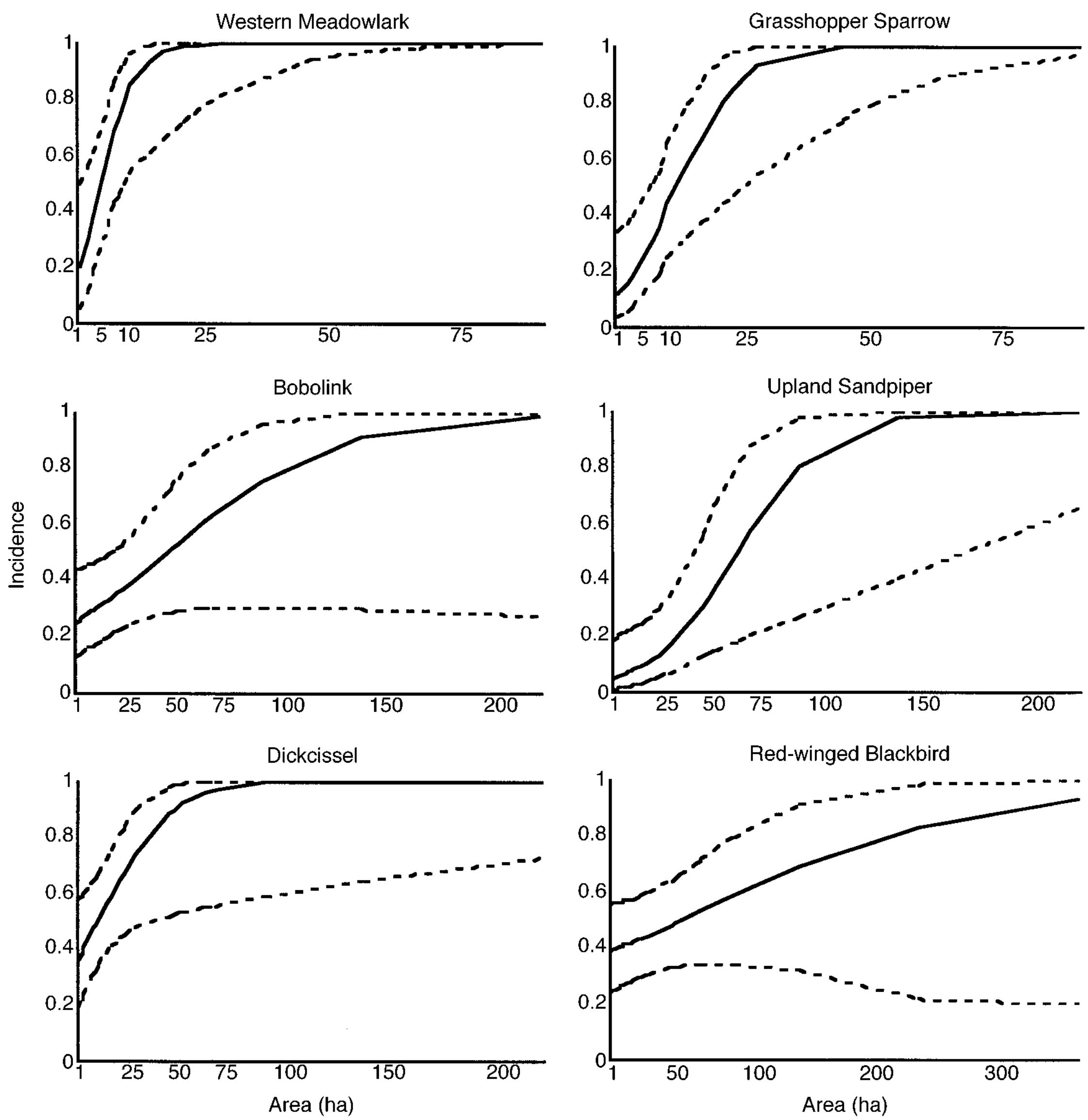

FIG. 2. Incidence curves for common grassland bird species in the Platte River wet meadows using 1996 data. Solid lines represent probability of occurrence at a particular patch area. Dashed lines represent 95% confidence intervals. Patterns were not significantly different ($P < 0.05$) in 1995, but see Table 4 for minimum area requirement estimates for both years.

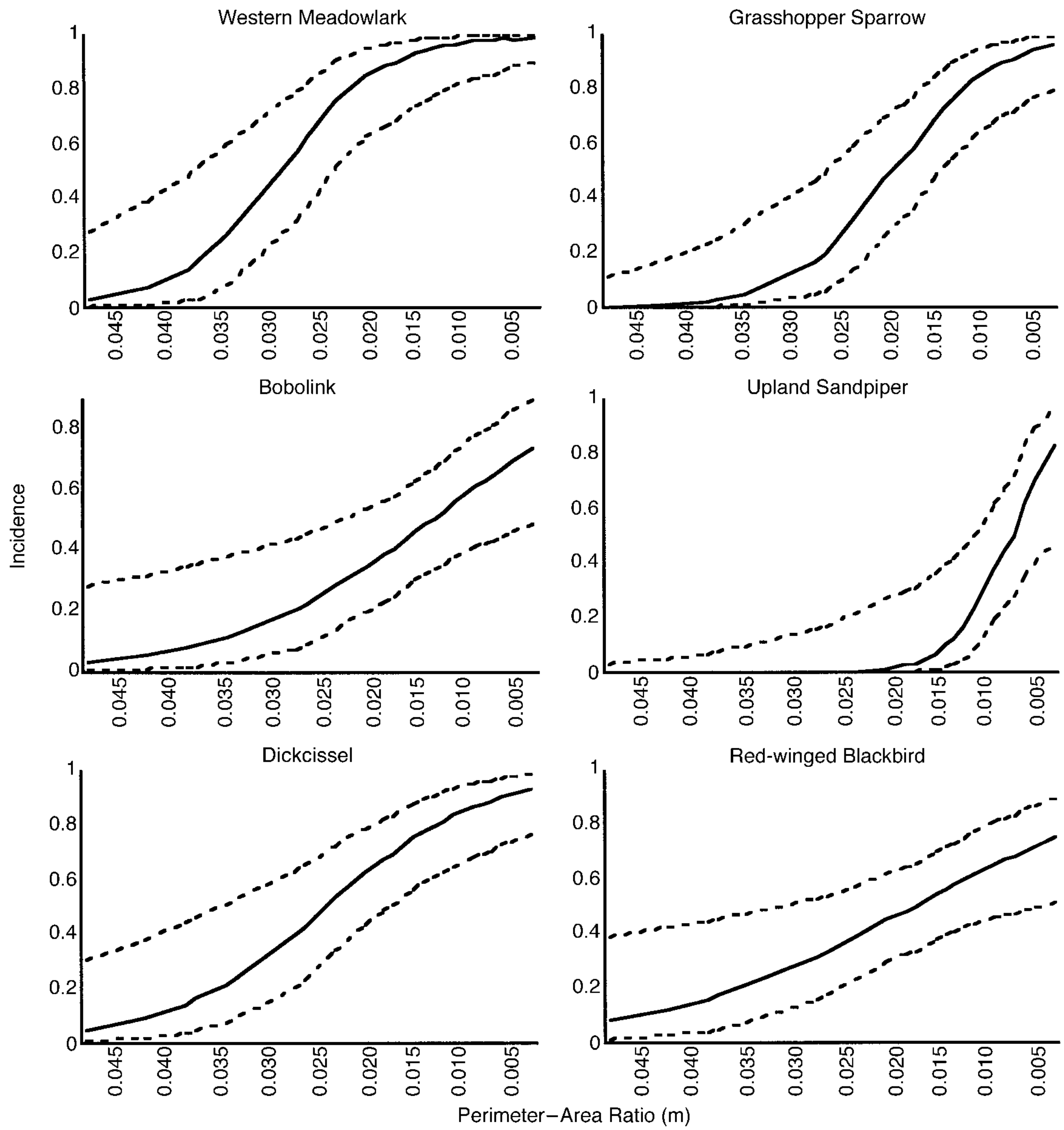

FIG. 3. Incidence curves for common grassland birds in the Platte River wet meadows. Solid lines represent probability of occurrence at a particular perimeter–area ratio value. Dashed lines represent 95% confidence intervals. Patterns were not significantly different ($P > 0.05$) in 1995, but see Table 4 for threshold estimates for both years.

dance than total area. We found similar results for grassland species, but we used perimeter–area ratio as a relative measure instead of core area, which requires a subjective estimation of the area of each patch that is free from edge effects. Because of the ambiguity about how far edge effects extend into patches (Faaborg et al. 1993) and the difference in edge effects between geographic regions (Freemark 1986), the use of a relative measure such as perimeter–area ratio seems appropriate.

Perimeter–area ratio was strongly correlated with area in our data set. This was expected because area is a component of the perimeter–area ratio expression. Moreover, when patch shape is a constant, there is an inverse linear relationship between the two variables (when plotted on a logarithmic scale). However, our data show that even slight deviations from that linear relationship, due to indented or elongated patch shapes, can be significant in terms of the use of patches by grassland breeding birds. Our index (Table 5) shows how much larger irregularly shaped patches need to be to have the same perimeter–area ratio as circular patches. Perimeter–area ratio is a more effective measure of habitat patch quality than is area because it reflects both size and shape.

It is important that the same units (meters per square

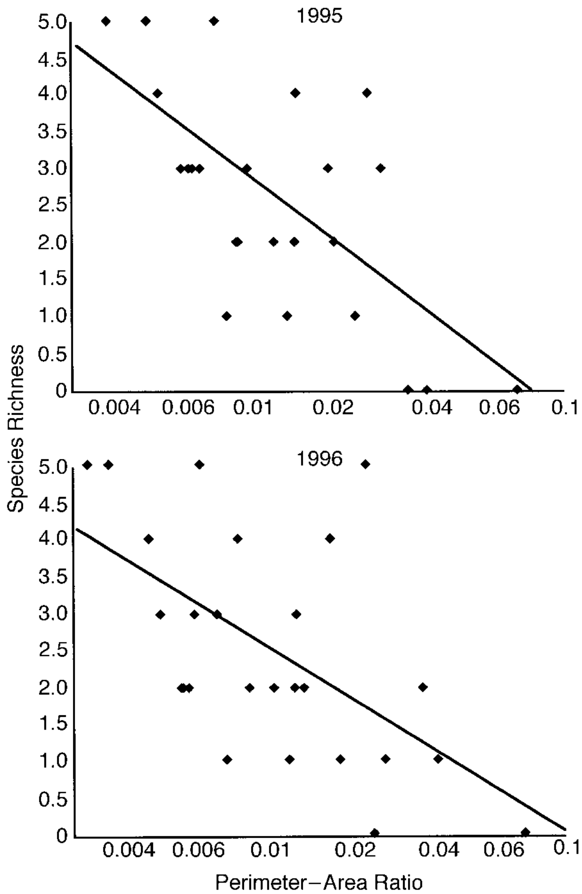

FIG. 4. Scatterplots showing bird species richness results from tests of the passive sampling hypothesis. Standardized 4-ha plots were sampled from each grassland patch in the Platte River floodplain, and the species richness value of each plot was then plotted against the log of the perimeter–area ratio of the plot. These values were correlated in both years ($P < 0.005$).

meter) be used when comparing perimeter–area ratios to those calculated in our study. Different units affect the ratio between the relationship between area and perimeter because area is measured in units *squared.* For example, a circular patch with a diameter of 8 m would have a perimeter–area ratio of 2, while the same patch measured in feet would have a perimeter–area ratio of 6.56.

Incidence functions vs. area

We are unaware of any other studies that have calculated perimeter–area requirements for grassland birds. Several authors have estimated minimum patch area requirements for grassland bird species, however, and our results can be compared with those authors' findings. Because other authors have not recorded the perimeter–area ratio values for their study patches it is not possible to analyze the potential impact of patch shape on minimum patch area calculations between studies.

Our 46-ha minimum area requirement estimate for Bobolinks was nearly identical to the 50 ha estimated by Herkert (1994) in Illinois, although our model was only significant in one of the two study years. In addition, the 5-ha patch size requirement we calculated for Western Meadowlarks was the same that Herkert calculated for Eastern Meadowlarks (*Sturnella magna*). Upland Sandpipers had the largest patch size requirement of the species we studied. They were also the most area sensitive species in studies by both Herkert (1994) and Vickery et al. (1994), although Vickery et al. calculated a minimum patch size requirement of 200 ha compared to 50 and 61 ha, respectively, in the two years of our study. Herkert found too few Upland Sandpipers to calculate minimum size requirements, but they were never recorded in patches of <30 ha (Herkert 1991*b*).

The only species we studied that was also studied by both Herkert and Vickery et al. was the Grasshopper Sparrow, and there were widely different estimations of patch size requirement among the three studies. Grasshopper Sparrows reached 50% incidence in our study at 8 ha and 12 ha in 1995 and 1996, respectively. By comparison, Herkert calculated the minimum area needed by Grasshopper Sparrows at 30 ha and Vickery et al. at 100 ha. Vickery et al. hypothesized that their large estimated area requirement was due to increased habitat selectivity of Grasshopper Sparrows because of low population numbers of the species in Maine. This suggestion is supported by Hinsley et al. (1996) who found that when the regional abundances of area-sensitive species were low, their incidence curve shifted to the right, toward larger patches. In our study region, Grasshopper Sparrows were common and found in a wide range of vegetation structure.

We found a significant correlation between the probability of occurrence for Dickcissels and area in 1996 only. Red-winged Blackbirds showed no significant correlation with area in either year of our study, al-

TABLE 5. Comparison of the sizes of hypothetical circular and square-shaped patches that would meet the perimeter–area ratio (PA) values at which six grassland bird species reached 50% incidence in actual study sites in the Platte River floodplain.

Species	PA value	Patch area (ha)		Actual patch area (ha)
		Circle	Square	
Western Meadowlark	0.026	1.9	2.5	5
Dickcissel	0.021	3.0	3.8	9
Grasshopper Sparrow	0.018	3.9	5.0	10
Red-winged Blackbird	0.012	9.5	12.1	NS
Bobolink	0.012	10.4	13.2	46
Upland Sandpiper	0.008	22.2	28.4	56

Note: The areas and perimeter–area ratio values from actual patches are averages of the statistically significant results from the two years of the study.

though we found them more often in large patches than in small ones. Herkert (1994) found no relationship between Dickcissel occurrence and area and found Red-winged Blackbirds more commonly in small patches than in large ones. Both species tended to be more commonly found in large patches than in small patches in our study, but were also found with some regularity in small patches as well. The increased probability of finding these species in large patches may have been a function of the greater chance of finding the tall vegetation structure they preferred in large patches, rather than a function of any area sensitivity.

Application of species–area models to grassland birds

Models that attempt to explain the species–area relationship can be divided into three categories: the passive sampling model, habitat diversity models, and fragmentation models (Hart and Horwitz 1991). The passive sampling model explains the increase in the number of species in large areas as a simple mathematical result of the larger sample size of individuals found in large areas. In other words, in this model birds in small patches are simply a subsample of those in large patches and large patches have more species because they have a larger sample of the same population. Habitat diversity models suggest that larger areas tend to have more habitat diversity and thus meet the habitat requirements of more species. Fragmentation models assume that patch area affects both the relationship between the patch and other landscape features and temporal dynamics within the patch.

Hart and Horwitz (1991) suggested that the passive sampling model should be the null hypothesis in any study of species–area relationships. Herkert (1994) and Vickery et al. (1994) found no support for the passive sampling hypothesis in their studies because they found more species in larger patches using subsamples of their data, representing equal sampling effort from each patch. We found similar results using perimeter–area ratio data. Based on our results and those of Herkert and Vickery it appears that small patches with high perimeter–area ratios have fundamentally different communities of birds than large patches with low perimeter–area ratios.

Increased habitat diversity in larger patches probably explains at least some of the correlations found between species richness and patch area and perimeter–area ratio in our study. Species such as Upland Sandpipers, Red-winged Blackbirds, Dickcissels, and Bobolinks are known to cue in on specific vegetation structure and microenvironment features (Wiens 1969, Cody 1985), and were more likely to find these features in large patches. Large patches in our study area were almost always separated into multiple management units (e.g., partly grazed, partly hayed), tended to have areas that were not hayed or grazed (old farmsteads, rough terrain, etc.), and also had greater variation in moisture conditions (i.e., distance to groundwater) than smaller patches. Patches that provided both tall and short vegetation and both wet and dry sites were more likely to have the six most common grassland nesters in the area, in addition to meeting other less-common species' requirements such as those of Henslow's Sparrows (*Ammodramus henslowii*), Soras, and Sedge Wrens (*Cistothorus platensis*). Also, if habitat near the edge of patches is perceived differently by grassland birds than areas away from edges, large patches had the advantage of providing both.

The relevance of fragmentation models to grassland bird communities is difficult to judge because of the lack of research on the effects of the landscape outside of breeding patches on grassland birds. Local extinctions may occur in grassland bird patches in two ways: through the failure of birds to return after migration, and through nest failure and abandonment because of predation or brood parasitism or disturbances such as mowing or grazing. Large patches are apparently preferred habitat for many grassland birds (Samson 1980, Herkert 1994, Vickery et al. 1994) and provide higher rates of nesting success than small patches (Johnson and Temple 1986, 1990, Burger et al. 1994), so area-sensitive species may choose the largest available patches in which to nest. Thus, in times of low regional abundance, small patches should be less likely than large patches to attract breeding birds returning from wintering areas, a phenomenon that has been recorded by Hinsley et al. (1996). Therefore, small patches have a greater chance of periodic local extinction than larger patches. In addition, because large patches can support higher numbers of breeding birds than small patches there may be a greater rate of survival from one year to the next based on probability alone.

Colonization of patches may also be correlated with patch area. If large patches provide higher nest success rates than small ones they should have a higher return rate of the previous year's nesters and be the most attractive for juveniles and previously unsuccessful nesters. In addition, if juveniles search for the next year's breeding sites between fledging and migration as some evidence suggests (Baker 1993), then both the area and the proximity to the natal area of the bird might affect the chance a bird will find a patch during postfledging exploration.

Most likely, the species–area relationship in grassland birds is explained by a combination of the habitat diversity and fragmentation models. More information on nest-site fidelity, postfledging exploration, and habitat selection in grassland birds is needed to further understand the relevance of each model. More research is also needed to determine whether or not other landscape characteristics besides area and perimeter–area ratio are important to grassland birds. The proximity of other grassland patches, for example, may increase the probability of occurrence by some birds in a particular patch. This may be especially true for species such as Upland Sandpipers, which apparently forage well outside of their breeding territories. The types of adjacent landscape structures may be important as well, particularly if those structures have particularly positive features (such as feeding areas) or negative features (such as habitat or perch sites for predators or nest parasites).

Conclusion

The perimeter–area ratio of patches had more influence on the presence and richness of grassland bird species than did patch area in this study. Therefore, while the maintenance of large patches is important to the conservation of grassland birds, patch characteristics such as patch shape and core area should also be recognized and taken into account when planning for conservation.

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