THE EFFECTS OF WET MEADOW FRAGMENTATION ON GRASSLAND BIRDS

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Grassland birds are experiencing the steepest population declines of any group of birds in the continental United States. Habitat fragmentation has been implicated as a major cause of these declines, but little research has been done to substantiate this hypothesis. In particular, there have been only a few studies of the effects of habitat patch size on grassland birds, and these have ignored the potentially important effects of patch shape and edge type. I examined these effects on grassland birds in wet meadows along the central Platte River in Nebraska.

In the first study I measured variation in the abundance of grasshopper sparrows and bobolinks with respect to distance from edges. Line transects were set up perpendicular to three types of potential edges: 1)wooded riparian strips, 2) cornfields, and 3) two-track gravel roads. Grasshopper sparrows and bobolinks were significantly less abundant near wooded edges and grasshopper sparrows were significantly less abundant near cornfield edges.

In the second study I tested the relative effects of vegetation structure, patch size, perimeter-area ratio, and patch edge type on grassland bird species richness and individual species presence. In each of 45 patches, the area, perimeter-area ratio, edge type, and vegetation structure was measured. The relative importance of each variable to species richness and presence was tested using logistic regression. Perimeter-area ratio was found to be the most important predictor of both individual species presence and overall species richness, although area was also important to most species. Vegetation structure was important to some species. Incidence functions were created for grassland species with both area and perimeter-area ratio as independent variables. These results indicate that if grassland bird conservation efforts are to be successful, patches must be large (> 50 ha), and more importantly, have a shape which provides abundant core areas relatively free from the impacts of edges.

Introduction

The introduction of modern agriculture to the midwestern United States replaced much of the native tallgrass prairie with annual row crops. In many states, including Nebraska, the few remaining tallgrass fragments or "patches" are mostly small and isolated from each other. The effects of this fragmentation on communities such as grassland birds are largely unknown. While no grassland bird species has become extinct, almost all grassland nesters are experiencing dramatic population declines.

Vegetation structure has traditionally been viewed as the major factor controlling grassland bird species richness and the presence or absence of individual species. Recently, several studies have found that patch size may also have an important influence on grassland bird communities. However, many aspects of fragmentation, including patch shape and the types of patch edges, and their potential effects on grassland birds have not yet been studied.

Most research on the effects of fragmentation on birds has been conducted in forests. In general, the species richness of forest patches increases with patch size, and many species, especially long-distance migrants, are rare in small patches. In grasslands, several recent studies have found similar results; grassland bird species richness is positively correlated with patch size, and several species have been found to have mimimum patch size requirements.

In addition to a loss of large patches, fragmentation of grasslands has also expanded the number and extent of interfaces or "edges" between grasslands and other landscape structures such as woodlands, roads, and

cropfields. Wooded edges have been found to have negative impacts on grassland birds, particularly because of the increase in nest predation and parasitism which occurs in proximity to patch edges. In addition, the density of nests of several grassland birds has been found to be lower near wooded edges than away from them. However, there is no research on the relative effects of other types of patch edges, including cropfields and roads, on grassland birds.

The shape of a patch, along with its size, regulates the amount of a patch which is exposed to edges. The size of the core area of a patch, or the area free from edge effects, is dependent on both the size and shape of the patch. Compactly shaped patches have a larger core area than patches of the same size with elongated shapes or indented perimeters. Studies have found that core areas are important to many forest birds, but there is no research on their importance to grassland birds.

Very little research has been done on the many effects of the fragmentation of grasslands on native bird communities. While patch size has been found to be important, the relative effects of various types of patch edges and importance of patch shape have not been studied. The general objectives of my research were: 1) to determine the effects of different types of edges on grassland bird abundance and determine which edge types act as patch boundaries, 2) to determine the importance of patch shape to grassland birds, relative to that of patch size and vegetation structure, and 3) to calculate minimum patch size requirements for grassland birds in wet meadows along the central Platte river in Nebraska.

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Chapter 1
Changes in Grassland Bird Abundance Near Edges

INTRODUCTION

The decline of tallgrass prairie exceeds that of any other major ecosystem in North America (Samson and Knopf 1994). Less than 1% of the historic tallgrass prairie in the midwestern states of Illinois, Indiana, Iowa, Minnesota, Missouri, and Wisconsin remains (Samson and Knopf 1994). These extensive losses and the resulting fragmentation of the remaining grassland habitat has significantly contributed to the decline of many species of grassland breeding birds (Herkert 1991, 1995).

Fragmentation leads to both a reduction of total habitat area and the redistribution of the remaining habitat into smaller disjunct patches (Wilcove et al. 1986). The trend towards smaller patch sizes in grasslands may have serious consequences for grassland birds (Herkert 1991). Minimum patch size requirements have been found for some species of grassland birds, and grassland bird species richness is lower in small patches than in larger ones (Samson 1980, Herkert 1994, Vickery et al. 1994). However, while it is evident that large patches are important to the maintenance of grassland bird communities, the underlying reasons for the absence of certain species in small patches is not clear.

An associated effect of habitat fragmentation is an increase in the ratio of edge to interior habitat (Wilcove 1986). Many forest patches have been found to have high levels of nest predation and brood parasitism near their edges

(Gates and Gysel 1978, Wilcove 1985, Andren et al. 1985, Andren and Angelstam 1988, Burkey 1993, Marini et al. 1995). In grasslands, areas near wooded edges have been found to have higher predation rates than areas farther from them (Johnson and Temple 1986, 1990, Burger et al. 1994). Edges also have other properties which may affect birds, including higher disturbance levels (Ferris, 1979, Reijnen and Foppen 1994) and changes in microclimate (Forman and Baudry 1984, Kapos 1989).

It is likely that the avoidance of small patches by some species can be at least partially explained by the high edge-to-interior ratio of those patches. The size of the patch interior or core area (an area free from edge effects) of patches has been shown to be important to some species of forest birds (Temple 1986, Faaborg et al. 1993), and the absence of a patch interior in small patches is suspected to be a major factor contributing to the absence of some species (Whitcomb et al. 1981, Robbins et al. 1989).

Specific responses to edges by birds are often measured by changes in bird abundance near patch boundaries. Some forest bird species have been found to avoid occupying areas near forest margins (Whitcomb et al. 1981, Kroodsma 1984) and highways (Ferris 1979, Reijnen and Foppen 1994). In grasslands, some species of grassland birds had a higher probability of nest occurrence far (>45m) from wooded edges than near them (Johnson and Temple 1986). Additionally, in a study of grasshopper sparrows in Conservation Reserve Program (CRP) fields, Delisle (1995) found only 1 of 31 grasshopper sparrow territories within 50 m of field edges. However, there is no information on the relative effects of different edge types like woodlands, cropfields, and roads, on grassland bird abundance.

What is or is not an edge from a bird's perspective may not always be clear. Paton (1994) reviewed studies of the effects of edge on nest success and noted a need to formalize the criteria used to define patch edges. As an example, he found that in studies of forest patch edges, some authors considered narrow breaks in the forest to be patch edges, while others ignored corridors like roads and other breaks and assumed edges were the nearest farm field. Paton suggests that biological reasons need to be used to justify calling a particular habitat feature an edge to the organisms being studied.

One way in which biological justification can be used to define habitat patches for birds is to use data showing significant changes in the abundance, either of birds themselves or their nests, near different landscape structures. It stands to reason that if birds avoid a particular interface between habitats, that the interface acts as a patch boundary. This kind of change in abundance has been found, as noted earlier, in forest birds near roads and other forest patch edges (Ferris 1979, Whitcomb et al. 1981, Kroodsma 1984, Reijnen and Foppen 1994), and along wooded edges for grassland birds (Johnson and Temple 1986, and Burger et al. 1994). In addition, the reluctance of birds to travel across a particular interface could also be an important factor in defining it as a patch boundary.

The objective of this study is to determine the relative effects of three landscape structures (riparian woodlands, cornfields, and two-track gravel roads) on grassland bird abundance. This information can then be used as biological information in defining what types of landscape structures act as patch boundaries for grassland birds. It also will provide information about the potential importance of core areas of patches to grassland birds.

I concentrated on two common species of grassland birds in wet meadows along the central Platte River in Nebraska: grasshopper sparrows (*Ammodramus savannarum*) and bobolinks (*Dolichonyx oryzivorus*). These two species were chosen because of their relatively high densities in the study patches. Other common grassland birds in the area included western meadowlarks (*Sturnella neglecta*), upland sandpipers (*Bartramia longicauda*), dickcissels (*Spiza americana*), and red-winged blackbirds (*Agelaius phoeniceus*).

METHODS

Study Region

The study region was along the Platte River between Grand Island and Wood River, Nebraska. Wet meadows were common along existing and abandoned river channels and where the water table is near the surface. Few other grassland areas existed within the floodplain. The vegetation consisted mainly of native grasses such as big bluestem (*Andropogon gerardii*), prairie cordgrass (*Spartina pectinata*), and Indian grass (*Sorghastrum nutans*), introduced grasses including smooth brome (*Bromus tectorum*), Kentucky bluegrass (*Poa pratensis*), and redtop (*Agrostis stolonifera*), and many sedges and prairie forbs.

The landscape in which wet meadows were embedded consisted mostly of irrigated cropland with corn, soybeans, and alfalfa. Fields of alfalfa and occasionally winter wheat, along with roadsides, provided the only other habitat for grassland birds. Trees, such as cottonwood (*Populus deltoides*) and eastern redcedar (*Juniperus virginiana*), were commonly found along river and stream

channels, in windbreaks and shelterbelts, and in some places are encroaching into wet meadows.

Field Methods

Changes in the abundance of grasshopper sparrows and bobolinks were measured with respect to distance from three types of landscape structures: 1) woodlands, 2) cornfields, and 3) two-track gravel roads. Belt transects, perpendicular to each edge, were used to map bird locations. Transects extended 200 meters from wooded edges. Transects were shortened to 150 meters for the road and crop edge censuses after reviewing the results of the first wooded edge census. All transects were 100 meters wide. Birds were detected both by song and by direct visual observation. Only individuals found on the ground or perching within the transects were mapped with respect to their distance from the edge. Because birds often flushed during censusing, they sometimes were mapped in more than one location within the transect during the census period. In these cases, only the point at which the bird perched closest to the edge was included in the data analysis in order to provide conservative estimates of any negative responses of birds to the edges.

The distance from each bird to the edge was estimated using a combination of two techniques. First, irrigation flags were placed at 25 meter intervals from the edge along the center line of each transect and were used as reference points with which to estimate distances. Second, the observer or an assistant kept track of paces from one end of the transect while censusing to further aid in distance estimation.

Transects were walked between May 25 and June 21, 1996. Half of the transects were walked from the patch edge towards the interior and the other half were walked from the interior toward the edge. Wooded edge transects were walked once between May 25 and June 5, and again between June 19 and 21. The second pass through each transect was walked in the direction opposite to the first. The road transects were censused June 11 and 12, and crop transects were censused between June 13 and 17. The crop and road transects were only censused once because the birds were beginning to fledge young before a second census could be conducted.

All transects were located at least 100 meters away from any edge type other than the one being specifically tested. To avoid double counting individual birds, transects were located at least 100 meters (edge to edge) from each other and transects which were relatively near each other were censused consecutively so that any movement between them would be observed. Transects were located in multiple patches which varied in management regime (hayed or grazed) but in which both target species were present.

Twenty-five transects extending from woodland edges were located in 6 separate large (>40 ha) meadow patches. Transects perpendicular to wooded edges were located along stretches of tall dense riparian woodlands which extended for at least 150 meters without a gap or visual break in the edge. Accordingly, the center line of each transect, was located at least 75 meters from any gap in a wooded edge.

The woodland edges were measured in several ways to provide data on the type of woodland used in this study. Both the height and visual obscurity of the woodland edges were measured at the point at which the edge was

intersected by each transect. The visual obscurity of the woodland was subjectively determined as the height of the tree line below which no sunlight could be seen through the trees by an observer standing in the transect, 100 meters from the edge. In addition, the width of the woodlands was measured by using aerial photos. The woodlands mainly consisted of a canopy layer of cottonwood, an understory of red mulberry, eastern redcedar, green ash, and American elm, and a shrub layer of dogwood.

Twenty-four transects were run away from cornfield borders. These transects were set in 9 patches over 20 ha in size. During the breeding season, the height of the corn ranged from several centimeters to close to a meter.

The third type of edge tested consisted of "two-track" roads (lightly traveled roads with two tire tracks with vegetation growing between them). Twenty-five 150 meter transects extended from roads which bisected two large patches (449 ha and 350 ha). The stretches of road along which transects were run had at least 300 meters of grassland on both sides of the road.

After completion of the road transect censuses, a second technique was used along the two-track roads to determine whether or not they affected the movement of birds. Because the two-track roads bisected large wet meadows, I hypothesized that this habitat interruption might effectively separate the meadows into distinct patches. To test this, an observer walked parallel to a road and flushed all birds within 25 meters of the road. The observer walked toward a bird, staying the same distance from the road as the bird, until it flushed. The 25 meter width of the zone was chosen arbitrarily to provide a means of dealing with birds which flew parallel to the road. If the bird flew out of the 25 meter zone, either away from the road or across it, the result was

recorded and the observer continued to the next bird. However, if the bird flew ahead or behind the observer, the process was repeated until the bird left the 25 meter zone. It was assumed that if no road was present, the chance of a bird flying one way or another out of the interval was equal. Departures from this 50:50 ratio would suggest that the road was impacting the movement of the birds. These data were collected on June 24 and 25, 1996.

Statistical Methods

Wilcoxon Rank Sum Tests and Analyses of Variance (ANOVA) were used to compare the number of birds in transect segments near edges to those farther away. Analyses were run using SAS NPAR1WAY and ANOVA procedures (SAS Institute 1982). Distributions of the abundance of each species at distance intervals were graphed and examined for obvious patterns. I then chose distance intervals to test against each other based on natural breaks in the patterns of abundance. Means of species abundance near the edge were tested against those away from the edge for significant differences.

RESULTS

Edge Structure Measurements

All edge structure measurements were made at the point at which transects intersected the edge and averaged over all transects (Table 1). The number of birds in each transect was too low to allow correlations between the relative abundance of birds in each transect and structure measurements.

Table 1. Measurements of roads and wooded edges.

Roads	N	Mean	Standard Error
Total Width	25	2.5 m	0.08
Track Width	25	0.7 m	0.05
Riparian Woodland			
Height	25	14.1 m	0.58
Height of Visual Obscurity	25	11.7 m	0.50
Width	25	109.3 m	7.43

Bird Abundance Results

Most of the transects contained adequate numbers of birds to allow for statistical analyses of changes in abundance at different distance intervals from edges (Table 2). However, only 6 bobolinks were found in the 24 cornfield edge transects, so no statistical analyses could be conducted on changes in bobolink abundance near cornfield edges.

Table 2. Total numbers of individual birds seen in each set of transect data. There were 25 woodland edge and road edge transects and 24 cornfield edge transects. Woodland transects were 200 m in length and cornfield and road transects were 150 m.

	Grasshopper Sparrows	Bobolinks
Woodland Edge Transects (1st Census)	46	33
Woodland Edge Transects (2nd Census)	32	26
Road Edge Transects	34	23
Cornfield Edge Transects	31	6

In the data from the first census of the wooded edge transects, there was a sharp rise in the number of grasshopper sparrows and bobolinks after the first 75 meters (Figure 1). Wilcoxon Rank Sum tests were used to compare the mean abundance of both species between and first and second 75 meters of the 25 transects. Both species differed in abundance between the two distance intervals (P<0.005, Table 3). In the second transect runs, there was a sharp rise in the abundance of both species after the first 100 meters (Figure 1). Comparing mean abundance in the first and second hundred meters for both species revealed higher numbers of birds in the distance intervals further from the wooded edge (P<0.001, Table 3).

Figure 1. Changes in abundance with distance from wooded edges.

Table 3. Results of Wilcoxon Rank Sum Tests on mean abundance of grasshopper sparrows and bobolinks between two distance intervals from wooded edges. The transects (N=25) were censused twice and each census was analyzed separately. In analyzing the data from the first census, the mean number of birds found in the first 75 meters of the transects was tested against the mean in the second 75 meters. For the analysis of the second run, the first 100 meters was tested against the second 100 meters.

Grasshopper Sparrow

Census	Distance Interval	N	Mean # of Birds Per Transect	Standard Error	Mean of Wilcoxon Scores	Z	P-value
1st	1st 75 m	25	0.16	0.07	16.0	-4.95	0.0001
	2nd 75 m	25	0.92	0.22	35.0		
2nd	1st 100 m	25	0.33	0.07	17.5	-4.38	0.0001
	2nd 200 m	25	0.99	0.20	33.5		

Bobolink

Census	Distance Interval	N	Mean # of Birds Per Transect	Standard Error	Mean of Wilcoxon Scores	Z	P-value
1st	1st 75 m	25	0.04	0.04	17.3	-4.62	0.0001
	2nd 75 m	25	0.76	0.21	33.7		
2nd	1st 100 m	25	0.12	0.09	19.5	-3.54	0.0005
	2nd 100 m	25	0.92	0.20	31.5		

The abundance of grasshopper sparrows rose sharply after the first 50 meters from the cornfield edges (Figure 2). Mean abundance was significantly higher between 50 and 150 meters from the edge in the 24 transects than in the first 50 meters from the edge (P=.02, Table 4).

Grasshopper Sparrow

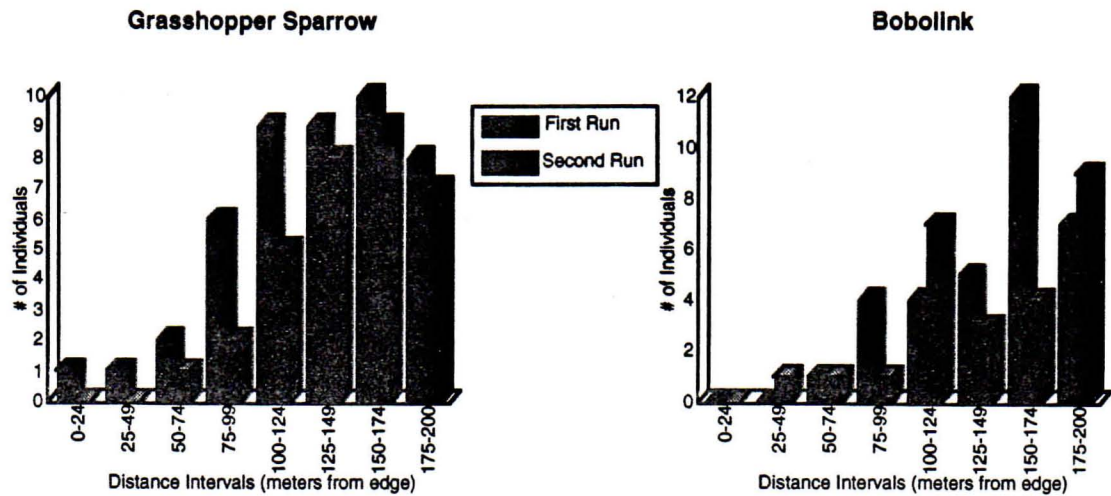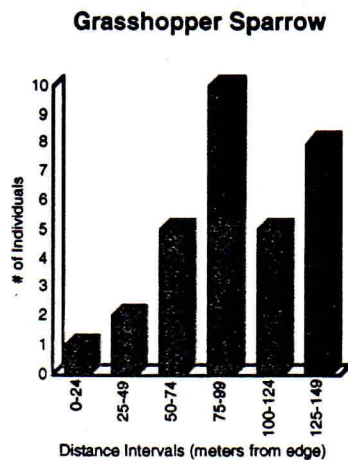**Figure 2.** Variation in grasshopper sparrow abundance with distance from cornfield edge.

Table 4. Results of Wilcoxon Rank Sum Tests on mean abundance of grasshopper sparrows between two distance intervals from cornfield edges. The data are from 24 transects.   The mean from first 50 meters of each transect (N=24) was tested against the mean from the remaining two 50 meter intervals (N=48).

Distance Interval	N	Mean # of Birds Per Transect	SE	Mean of Wilcoxon Scores	Z	P-value
1st 50 meters	24	0.13	0.07	30.06	-2.3	0.02
2nd 100 meters	48	0.58	0.13	39.7		

Because there were no obvious breaks in bird abundance as distance from the road edge increased (Figure 3), an ANOVA was used to test the means from the first, second, and third 50 meter intervals from the edge. No significant differences were found for either grasshopper sparrows or bobolinks ($P<0.05$, see Table 5).

Grasshopper Sparrow   **Bobolink**
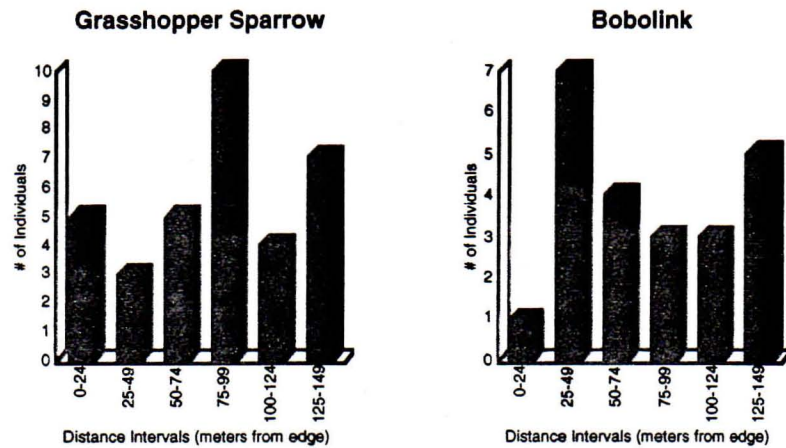
Figure 3. Changes in abundance with distance from road edges

Table 5. Results of ANOVAs comparing the mean abundance of grasshopper sparrows and bobolinks in three 50 meter intervals from road edges. (25 transects)

Grasshopper Sparrow

Source	DF	SS	MS	F Value	Pr > F
Model	2	1.0277778	0.5138889	0.96	0.3878
Error	69	36.9166667	0.5350242		
Corrected Total	71	37.9444444			

Bobolink

Source	DF	SS	MS	F Value	Pr > F
Model	2	0.0277778	0.0138889	0.03	0.9682
Error	69	29.6250000	0.4293478		
Corrected Total	71	29.6527778			

As neither species tested showed avoidance of the roads in terms of changes in abundance, I proceeded with the flushing method to test for influences of the road on bird movement. The numbers of birds that flew across the road and of those that flew away from it were recorded and tested with χ^2 analyses for statistical variation from the expected results. There no variations (χ^2 = P>0.05) from the expected distributions (Table 6). Therefore, the two-track roads did not appear to act as barriers to movement or limit patch area for grasshopper sparrows or bobolinks.

Table 6. Results from road flush data.

	# of Responses (Flushes)	
Species	Across Road	Away from Road
Grasshopper sparrow	20	18
Bobolink	14	19

DISCUSSION

Densities near Edges

The abundance of grasshopper sparrows increased significantly 75-100 meters from wooded edges and about 50 meters from cornfields. The abundance of bobolinks also increased significantly 75-100 meters from wooded edges. Although bobolinks were present in all study patches adjacent to cornfields, they did not have sufficiently high numbers to test for changes in abundance. The wet meadows that were adjacent to cornfields were primarily pastures, in which bobolinks occurred in lower abundance (Helzer unpublished data), while the meadows adjacent to the wooded edges were mostly hayed meadows. Therefore, the low abundance in the cornfield edge transects was not necessarily a response to cornfields.

By comparison, Johnson and Temple (1986) found that grasshopper sparrow nests were less likely to occur within 45 meters of wooded edges than at greater distances, but found that distance to wooded edges was not a significant predictor of the probability of bobolink nest occurrence. However, they found that both species achieved their highest rates of nest success in areas over 45 meters from forest edges Johnson and Temple (1986, 1990).

There was no evidence of an effect of the two-track roads on either grasshopper sparrow or bobolink abundance. This could be because the roads were of such limited width that the birds could hold territories on both sides. The roads presented no obstruction of sight or movement which might hinder territorial behavior, and the interruption of the habitat was relatively slight. On

the other hand, the cornfields and riparian woodlands were large enough that territories would not span them.

The low abundance of grasshopper sparrows and bobolinks near wooded edges may be a response to high predation and brood parasitism rates such as those found by both Johnson and Temple (1986, 1990) and Burger et al. (1994). However, there is no evidence to suggest the same explanation for avoidance of cornfield edges or two-track roads. Although higher predation rates have been found along forest/cropfield edges than in forest interiors (Wilcove 1985, Angelstam 1986, Andren and Angelstam 1988, Marini et al. 1995), there has been little research on predation rates near grassland/cropfield edges. In fact, Bryan and Best (1994) found that predation rates in linear grassed waterways in agricultural fields were similar to those found in non-linear grasslands in other studies. There are no data on predation rates along two-track or other low-traffic roads which bisect large open areas.

Another explanation which could explain the low abundance of birds near edges is that my data measured temporal, rather than spatial distributions of birds. Because there are no territories of grasshopper sparrows in cornfields, for example, a grasshopper sparrow male may defend a territory which extends to the edge of the cornfield but spends a small proportion of his time singing from the cornfield edge. Therefore, because I looked only at the location of birds at a moment in time, and not at territory or nest location, I may have found fewer birds near edges simply because they were spending a disproportionately short time there. However, other research in the same study region (Chapter 2)

found that the probability of occurrence of several species of grassland birds, including grasshopper sparrows and bobolinks, was significantly lower in patches with high perimeter-area ratios, and that edge type was not a significant factor.

Edges as Barriers

The avoidance of wooded edges by both grasshopper sparrows and bobolinks and the avoidance of cropfield edges by grasshopper sparrows suggests that these adjacent habitats act as patch boundaries. However, two-track gravel roads that bisected large patches of grass did not have any effect on either the abundance or movement of grasshopper sparrows or bobolinks. Therefore, I conclude that they are not acting as boundaries. Wide gravel roads were very common throughout the study area and may be perceived differently by birds than two-track roads. However, while research has shown effects of heavily traveled roads on forest bird abundance (Ferris 1979, Reijnen and Foppen 1994), there is no research on the effects of these kinds of roads on grassland bird abundance.

Summary and Conclusions

Both grasshopper sparrows and bobolinks were significantly less abundant within the first 75-100 meters from wooded edges than in more interior areas. Likewise, grasshopper sparrows were significantly less abundant in the first 50 meters from cornfield edges than in more interior areas, while bobolinks could not be tested because of insufficient data. Thus, dense woodlands acted as patch boundaries for grasshopper sparrows and bobolinks

and large cornfields acted as boundaries for grasshopper sparrows. Neither species had any evident reaction to two-track gravel roads which bisected large meadows.

This study indicates that patches need to provide core areas in which grassland birds can avoid edges such as treelines and cropfields. There is still much research needed on the effects of edges on grassland birds. However, my data supports the hypothesis that grassland birds in fragmented habitats may depend more on core areas of patches, free from edge effects, than on total area alone.

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Chapter 2

The Effects of Wet Meadow Fragmentation
on Grassland Birds

INTRODUCTION

Landscape fragmentation has had a profound effect on the distribution and diversity of birds in many parts of the world (Whitcomb et al. 1981, Lynch and Whigham 1984, Howe 1984, Opdam et al. 1985, Herkert 1994, Vickery et al. 1994, Hinsley et al. 1996). Results from research in forested habitats suggest that forest-interior birds and neotropical migrants are especially vulnerable to the smaller habitat patches and increasing patch isolation which accompanies fragmentation (Whitcomb et al. 1981, Ambuel and Temple 1983, Howe 1984, Lynch and Whigham 1984, Opdam et al. 1985, Robbins et al. 1989). The species richness and relative abundance of area-sensitive species has been found to significantly decrease as patch size 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 has shown that grassland bird species are declining faster than any other group of midwestern breeding species (Herkert 1995). In particular, grasshopper sparrows (*Ammodramus savannarum*), western meadowlarks (*Sturnella neglecta*), and bobolinks (*Dolichonyx oryzivorus*), are among the species which have shown the greatest

regional 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).

Until recently, vegetation structure has been identified as the most important predictor of grassland bird species presence and spatial distribution (Wiens 1969, Rotenberry and Wiens 1980, Kantrud 1981, Cody 1985, Bowen and Kruse 1993). In fragmented habitats, patch size has now been recognized as another important factor (Samson 1980, Herkert 1994, Vickery et al. 1994). Both total species richness and the probability of occurrence for several species of grassland birds have been positively correlated with patch size, (Samson 1980, Herkert 1994, Vickery et al. 1994). However, there has been little research on the potential effects of patch shape and the types of patch edges on habitat selection by grassland birds. In fragmented grasslands, grassland patches are embedded in a matrix of other habitat types. It is critical that conservationsists understand how the landscape matrix surrounding an individual patch impacts birds within the patch in order to effectively manage fragmented habitats.

Research on the effects of patch edges on birds has mainly concentrated on predation and nest parasitism rates near edges. Researchers in forest environments have found that 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). Additionally, Wilcove (1985) found that the type of edge can have an influence on predation rates. He found that woodlots in suburban areas had higher rates of predation than woodlots in rural settings. Less research has been done on edge effects

and grassland bird nest predation. Johnson and Temple (1986, 1990) and Burger et al. (1994) found higher predation and parasitism rates on nests close to wooded edges than closer to the center of patches.

There may be other effects of edges on birds as well. Microclimate conditions, including temperature, light, and moisture, change near habitat edges (Forman and Baudry 1984, Kapos 1989, Malcolm 1994, Young and Mitchell 1995, Carmargo and Kapos 1995), and these changes affect the vegetation near those edges (Malcolm 1994, Young and Mitchell 1995). However, there has been no research on how these habitat alterations affect birds. Disturbances from humans or other sources may increase near edges as well. Several species of birds have been found to have lower densities near highways (Ferris 1979, Reijnen and Foppen 1994), for example.

Because the shape of a patch, along with its size, influences the amount of the patch which is exposed to edges, patch shape may be an important factor influencing grassland bird presence and species richness. Temple (1986) found that the presence and abundance of birds in forest fragments were better predicted by the core area rather than the total area of patches. He found that patches which had elongated shapes, indented perimeters, or inclusions of open habitat within the fragment had fewer species and individuals than solid forest stands with compact shapes and unbroken perimeters. However, there has been no research on the importance of patch shape or core area to grassland birds.

In his forest study, Temple (1986) defined core areas as those areas more than 100 meters from an edge. Estimates of the distance that edge effects extend into a patch can vary widely, however (Faaborg et al. 1993), and edge

effects can vary between different regional landscapes (Freemark et al. 1986). The perimeter-area ratio of a patch can account for the relative size of core areas, but does not require a subjective estimation of the distance that edge effects extend into a patch. Patches with elongated shapes or indented perimeters would have higher perimeter-area ratios than patches of the same size with compact shapes and unbroken perimeters. In addition, small patches would have higher perimeter-area ratios than large patches.

In summary, the importance of patch size to grassland bird communities has been recognized by several authors (Samson 1980, Herkert 1994, Vickery et al. 1994), but there has been no research on the effects of patch shape or the relative effects of different types of edges on grassland birds. The objectives of this study are to: 1) determine the relative impacts of patch area, perimeter-area ratio, and edge type on grassland breeding bird presence and compare the importance of those patch measures to that of vegetation structure; and 2) calculate minimum size requirements of grassland birds in Platte River wet meadows.

METHODS

Study Area

My study region was located along the Platte River between Grand Island and Wood River, Nebraska. Wet meadows, which were located along existing and former river channels and other places where the water table was near the surface, comprised the majority of grassland bird habitat in the region. The vegetation in these meadows consisted mainly of native grasses such as big bluestem (*Andropogon gerardii*), prairie cordgrass (*Spartina pectinata*), and

Indian grass (*Sorghastrum nutans*), introduced grasses like 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. A few of the meadows also contained burned or idled areas.

The majority of the land cover in the study region was irrigated cropland with corn, soybeans, and alfalfa as the major crop types. Alfalfa fields and a few winter wheat fields provided 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*), were common along river and stream channels and in windbreaks and shelterbelts. Gravel roads outlined most square-mile sections and several highways passed through the area.

Bird Censuses

Forty-one patches were censused for birds in 1995 and 45 were censused in 1996. Patch sizes in 1995 ranged from 0.12 ha to 347 ha with a mean size of 31.9 ha and a median of 8.5 ha. In 1996, all but three of the same patches were used, and seven new patches were added (total=45). The 1996 patch sizes ranged from 0.12 ha to 449 ha, with a mean of 41.69 ha and a median of 9.25 ha.

Each patch was censused twice between May 17 and July 5 each year. Censuses were between 5:30 a.m. and 9:00 a.m. on mornings when wind speeds were less than 32 kilometers per hour and there was no rain. 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 size, and where large patches were divided into discrete management units (such as pastures and haymeadows), each management unit was sampled with separate transects. Additionally, each patch was searched by walking and listening in all areas other than those specifically covered by line transects in order to supplement species lists.

Birds that flew over the patch without landing were not counted in the species list for the patch. All species seen within the patch were recorded, but only those species which nest exclusively in grassland or wet meadow habitat were used in 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 and key component of the wet meadows in this area. Ring-necked pheasants (*Phasianus colchicus*) were also included in species richness data because they are considered naturalized species and nest in open grasslands. Pheasants are also considered 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, including Zimmerman (1992), Herkert (1991a,b, 1994), and Warner (1994).

Vegetation Assessment

Vegetation structure was assessed within the same transects used for bird censuses. Measurements were taken every 20 meters along each transect at random distances perpendicular to the transect line. Vegetation was measured both early and late in the season. The height and density of vegetation, as well as the percent of live vegetation, was recorded by passing a thin metal rod vertically through the vegetation and counting the number of "hits" by live and dead grasses, forbs, and woody vegetation at decimeter intervals (after Rotenberry and Wiens 1980). Robel pole readings were made to estimate horizontal visual obscurity (after Robel et al. 1970). Litter depth was measured by the use of a ruler passed vertically through the litter layer to the ground.

Landscape Measurements

National Aerial Photography Program (NAPP) black and white aerial photographs from 1993 (1:40,000) were used to measure patch size, perimeter length, and the length of each edge type (roads, woodland, and cropland). A digital planimeter was used to make the actual measurements.

Perimeter-area ratios were calculated by dividing the perimeter (in meters) by the patch area (in square meters) . The length of each of three main edge types (woodland, roads, and cropland) was also measured for each patch. The percent of the total perimeter made up by each edge type was then calculated for each patch.

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. Area, perimeter-area ratio, and the percent edge type were used individually and in combination with each other in logistic models to determine their relative importance for predicting species richness and presence.

The importance of vegetation structure relative to the landscape variables was also tested using logistic regression. Because vegetation was sampled twice each year, each sampling run was analyzed separately. Therefore, there were a total of four vegetation models (twice a year for two years) for each species and for species richness.

The larger patches in the study area were often split into multiple management units. Some meadows were partially hayed and partially grazed, while others had separate pastures which received different grazing pressure. To avoid averaging over these discrete management units, the vegetation structure from each management unit was included in the logistic models as a separate unit, whether or not it made up an entire patch by itself. In the logistic regression equations, then, each management unit was assigned the size and perimeter-area ratio of the patch it was in. This was done assuming that the size and shape of the encompassing patch were recognized by the birds *a priori* and the characteristics of the management units were not. This assumption is discussed in detail later. Five vegetation variables were entered into each model, along with area and perimeter-area ratio. These variables (and their abbreviations) included: litter depth (Litter), Robel pole measurement

(Robel), mean vegetation height (Height), mean number of vegetation hits (Hits), and the percent of live vegetation (Live).

Minimum patch size requirements for each of the common grassland breeding birds were estimated with incidence functions calculated through logistic regression. The SAS LOGISTIC procedure (SAS Institute 1982) was used for the calculations. An incidence value of 50% in the logistic models (the point at which the model predicts a 50% probability of the species occurring) was used to define the minimum patch size for a species (after Robbins et al. 1989). This value is the same used by other researchers who have determined minimum size requirements for grassland birds (Herkert 1994, Vickery et al. 1994), and allows a comparison of my results to theirs. Because the data from 1995 and 1996 contained many of the same patches, and many birds return to the same patches from year to year (e.g. Smith 1963, Gavin and Bollinger 1988, Bollinger and Gavin 1989), data from each year could not be considered as independent samples and combined. Data from each year were therefore analyzed separately. I 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 the presence data for each species and testing for the significance of the dummy variable.

To test the hypothesis that species richness is higher in larger patches only because more individuals are present (Connor and McCoy 1979), I used transect segments of equal total area from each patch (after Herkert 1994) and tested species/area relationships within those sub-samples using logistic regression. Four randomly selected 100 m transect segments (4 ha total area) from each patch were used. In some cases, where small patches did not

contain 4 ha of transects, patches of similar size were combined, and their sizes averaged to create a patch group which was included in the model. If small patches are simply sub-samples of larger patches, there should be no difference in species richness between the 4 ha sub-samples of my patch data. If a species-area relationship exists within the data from the equally sized segments, however, then the passive sampling hypothesis does not adequately explain the increase in species richness in large patches.

RESULTS

Species Richness/Landscape Variables Results

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

Table 1. The percentage of patches occupied by wet meadow breeding birds observed during the two years of the study. There were 41 patches in 1995 and 45 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	0
Eastern Meadowlark (*Sturnellana magna*)	0	7
Sora (*Porzana carolina*)	0	4
Swamp Sparrow (*Melospiza georgiana*)	0	2

Results from the logistic regression models (Table 2) showed that species richness was positively correlated with both area ($P < 0.0005$) and perimeter-area ratio ($P < 0.0001$). Species richness increased with area and decreased with perimeter-area ratio (Figure 1). When area and perimeter-area ratio were both included in the model with species richness, only perimeter-area ratio was statistically significant (Table 3). When the three edge type variables were added to area and perimeter-area ratio as independent variables, perimeter-area ratio was again the only significant predictor of species richness (Table 3). There were no significant differences in the relationships between 1995 and 1996.

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Table 2. Results of logistic regression models in which species richness was modeled against the single variables area and perimeter-area ratio.

Species Richness	1995 Pr > Chi-Square	1996 Pr > Chi-Square
Area	0.0005	0.0005
Perimeter-Area Ratio	0.0001	0.0001
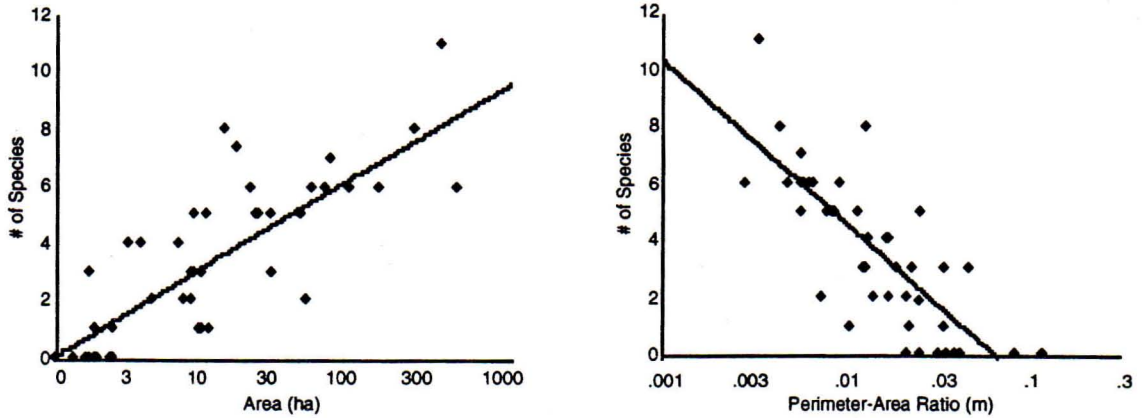
Figure 1. Scatterplots of species richness versus both area and perimeter-area ratio (on logarithmic scales) from 1996 data.

Table 3. Results of two multinomial logistic regression models. In the first model, species richness was regressed against both area and perimeter-area ratio. In the second, the three edge types (% woodland, % cropfield, and % road) were added to area and perimeter-area ratio as independent variables.

Dependent Variable	Significant predictors of occurrence	
	Model 1 - vs. Area and PA	Model 2 - vs. Area, PA, and Edge Types
Species Richness		
1995	[PA]****	[PA]****
1996	[PA]****	[PA]****

****=P < 0.0001

Individual Species/Landscape Variables Results

The probability of occurrence for grasshopper sparrows, bobolinks, upland sandpipers, and western meadowlarks were positively correlated ($P < 0.05$) with patch area when area was the lone dependent variable in the logistic model. Of the other two common species, dickcissels showed a positive relationship ($P < 0.05$) in 1996, and the model for red-winged blackbirds showed no relationship ($P > 0.05$) in either year. The probability of occurrence for all six species was inversely correlated ($P < 0.05$) with perimeter-area ratio in both years of the study (Table 6). There were no differences ($P > 0.05$) in the models for any species between the 1995 and 1996 data.

When both area and perimeter-area ratio were included in the six species models, correlations with perimeter-area ratio were consistently more significant than with area (Table 4). No variable describing edge type showed any significance with any species in the models. Instead, the edge type variables shared a high proportion of the variance explained by area and perimeter-area ratio.

Table 4. Variables identified as significant predictors of species occurrence in two multinomial logistic regression models. The first model considered each species as a single dependent variable with patch area and perimeter-area ratio as the independent variables. The second model also included the three variables describing edge type, % crop, % tree, and % road in addition to area and perimeter-area ratio.

Species	Significant predictors of occurrence	
	Model 1 - vs. Area and PAR	Model 2 - vs. Area, PAR, and Edge
<u>Types</u>		
Grasshopper Sparrow		
1995	[Perimeter-area Ratio]*	None
1996	None	None
Western Meadowlark		
1995	None	No Convergence
1996	[Perimeter-Area Ratio]*	None
Bobolink		
1995	None	None
1996	None	None
Dickcissel		
1995	[Perimeter-Area Ratio]*	None
1996	[Perimeter-Area Ratio]**	None
Upland Sandpiper		
1995	None	None
1996	None	None
Red-winged Blackbird		
1995	None	None
1996	[Perimeter-Area Ratio]*	None

Asterisks (*) denote level of significance.   *=P < 0.05, **=P < 0.01,

Vegetation Analyses Results

The multinomial logistic regression models comparing the relative importance of the vegetation and landscape variables included the five vegetation variables (Litter, Robel , Height, Hits, and Live) along with area and perimeter-area ratio as independent variables. Because none of the edge variables was correlated ($P > 0.05$) with either species richness or individual species probability of occurrence, they were not included in these models.

Again, I calculated two models in each year of the study because vegetation data were collected twice each year and each sampling run was tested individually. Perimeter-area ratio was correlated ($P < 0.05$) with the probability of occurrence of almost all species, and usually showed the highest level of significance of any variable (Table 5). For species richness, the correlation with perimeter-area ratio was highly significant in all models, and was the most significant of any variable.

Table 5. Significant predictors of species occurrence and of species richness in management units using multinomial logistic regression models. Variables are listed in decreasing order of significance. Negative relationships are indicated by brackets. Each species was tested in four models because vegetation was sampled twice each season and analyzed separately. Codes are defined in Methods: Vegetation Assessment.

Species	Significant predictors of occurrence
Grasshopper Sparrow	
1995 (1)	[Perimeter-Area Ratio]**
1995 (2)	[Perimeter-Area Ratio]*, [Litter]*, Hits*, [Live]*
1996 (1)	[Perimeter-Area Ratio]**
1996 (2)	[Perimeter-Area Ratio]*
Western Meadowlark	
1995 (1)	[Perimeter-Area Ratio}*, [Area]*
1995 (2)	(No Convergence)
1996 (1)	[Perimeter-Area Ratio]**, [Height]**, Hits**, [Area]**, Robel*
1996 (2)	[Perimeter-Area Ratio]**
Bobolink	
1995 (1)	[Perimeter-Area Ratio]**, [Hits]*, Robel*, Litter*
1995 (2)	[Perimeter-Area Ratio]*
1996 (1)	[Perimeter-Area Ratio]*, [Robel]*, [Height]*
1996 (2)	[Perimeter-Area Ratio]*
Dickcissel	
1995 (1)	[Perimeter-Area Ratio]*
1995 (2)	None
1996 (1)	[Perimeter-Area Ratio]**
1996 (2)	[Perimeter-Area Ratio]**
Upland Sandpiper	
1995 (1)	None
1995 (2)	None
1996 (1)	None
1996 (2)	None
Red-winged Blackbird	
1995 (1)	None
1995 (2)	None
1996 (1)	[Perimeter-Area Ratio]*
1996 (2)	[Perimeter-Area Ratio]*, [Litter]*
Species Richness	
1995 (1)	[Perimeter-Area Ratio]****, Robel**
1995 (2)	[Perimeter-Area Ratio]****, Hits*
1996 (1)	[Perimeter-Area Ratio]****
1996 (2)	[Perimeter-Area Ratio]****

*P < .05, **P < .01, ***P < .001, ****P < .0001

Incidence Functions

Because perimeter-area ratio was a more important predictor of species presence than patch size (Table 6), separate incidence functions were created for each species with perimeter-area ratio (Figure 3) and area (Figure 2) as independent variables. Figure 4 combines the curves for the four species most sensitive to area and perimeter-area ratio.

Table 6. Results of logistic regression models in which each species was modeled against the single variables Area and Perimeter-Area Ratio.

| Species	1995		1996	
	50% Incidence	Pr > Chi-Square	50% Incidence	Pr > Chi-Square
Grasshopper Sparrow				
Area	8 ha	0.05	12 ha	0.01
Perimeter-Area Ratio	0.018	0.001	0.018	0.001
Western Meadowlark				
Area	5 ha	0.005	5 ha	0.05
Perimeter-Area Ratio	0.024	0.05	0.027	0.001
Bobolink				
Area	46 ha	0.05	_____	NS
Perimeter-Area Ratio	0.009	0.05	0.013	0.01
Upland Sandpiper				
Area	50 ha	0.05	61 ha	0.05
Perimeter-Area Ratio	0.008	0.05	0.007	0.01
Dickcissel				
Area	_____	NS	9 ha	0.05
Perimeter-Area Ratio	0.018	0.01	0.023	0.001
Red-winged Blackbird				
Area	_____	NS	_____	NS
Perimeter-Area Ratio	0.006	0.05	0.017	0.01

NS=Not significant
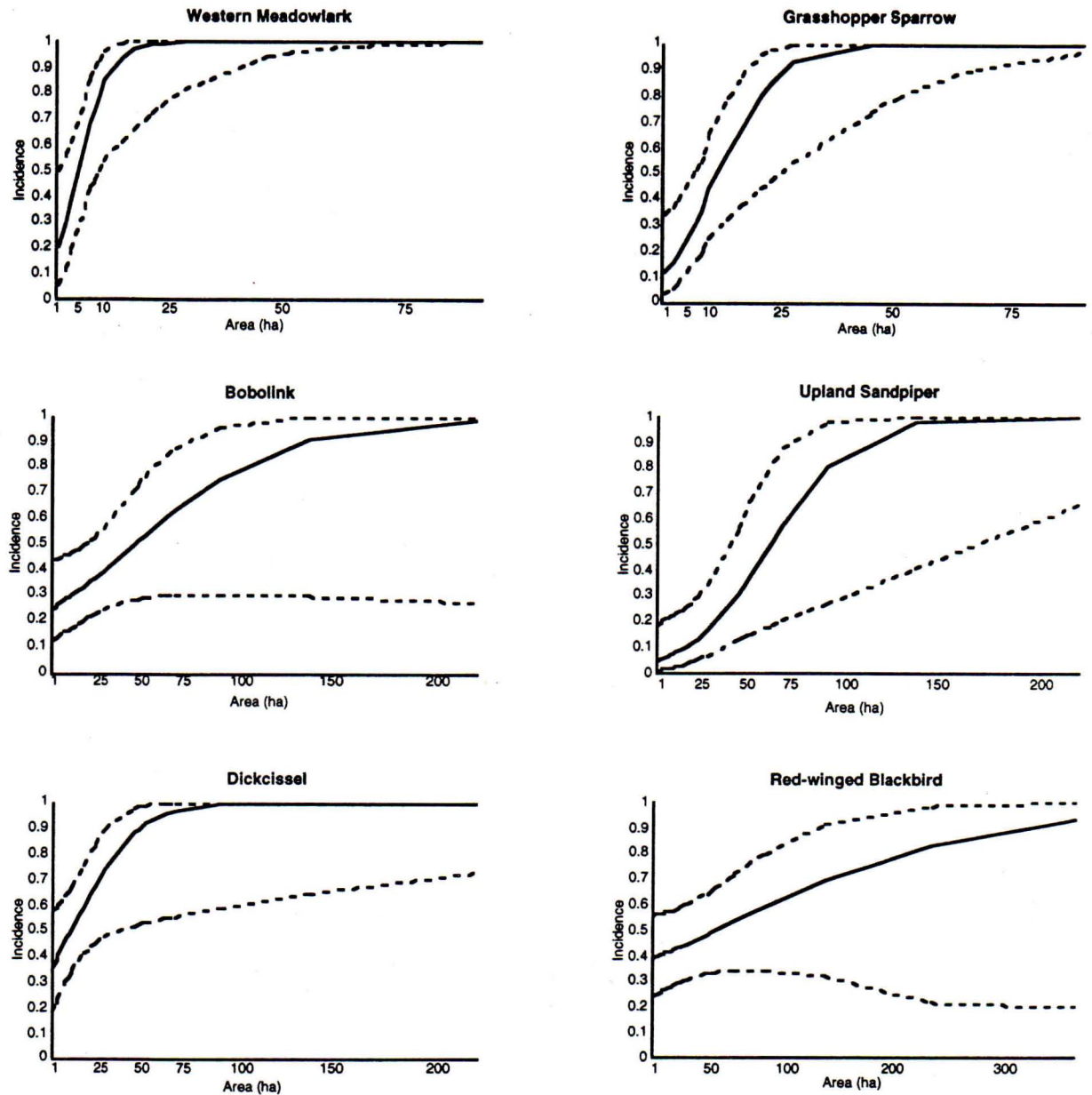
Figure 2. Incidence curves for common grassland species using 1996 data. Solid lines represent probability of occurrence at a particular patch size. Dotted lines represent 95% confidence intervals. Patterns were not significantly different in 1995, but see Table 5 for minimum size requirement estimates for both years.

Figure 3. Incidence curves for common grassland birds. Solid lines represent probability of occurrence at a particular perimeter-area ratio value. Dotted lines represent 95% confidence intervals. Patterns were not significantly different in 1995, but see Table 5 for minimum size requirement estimates for both years.
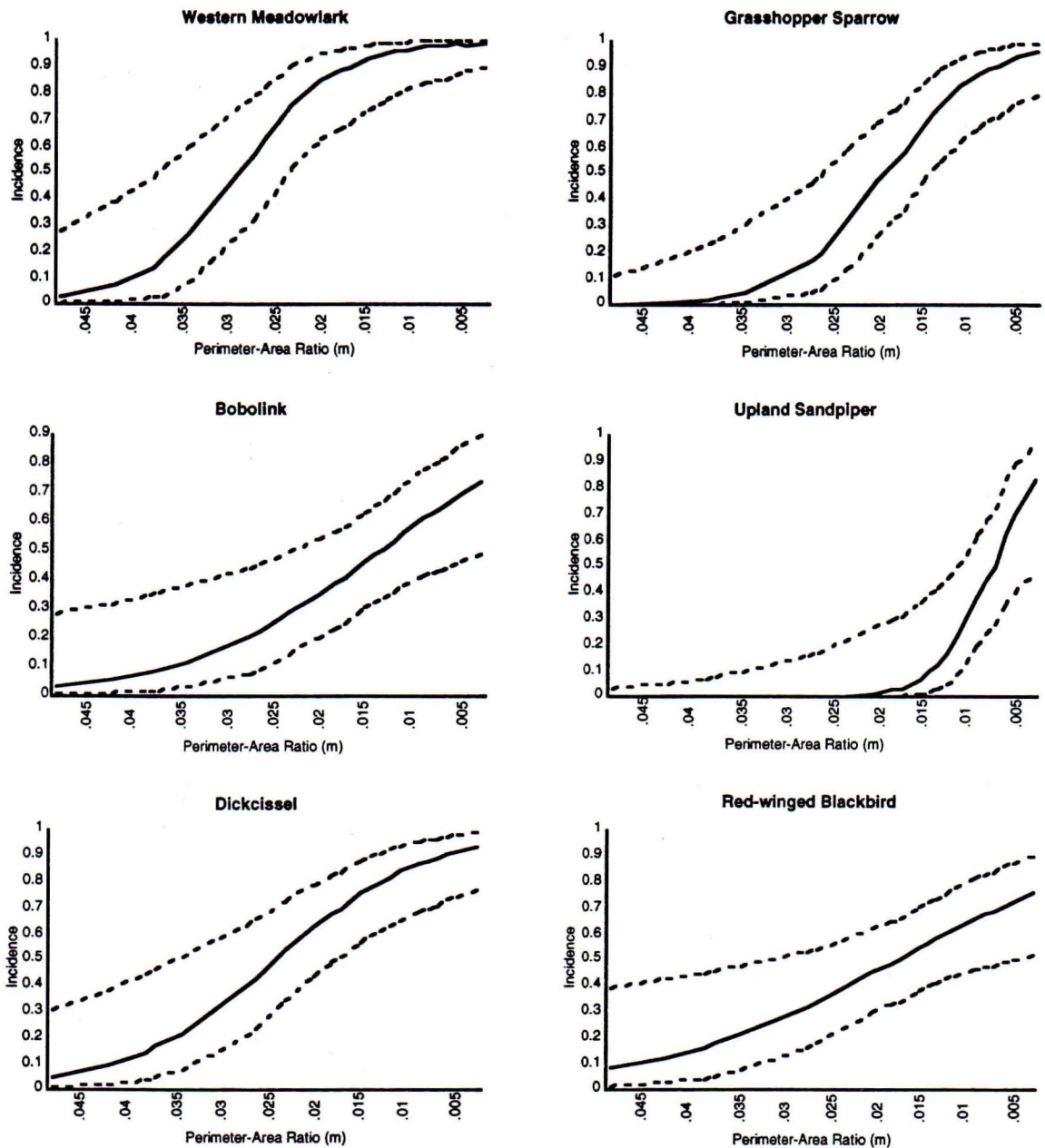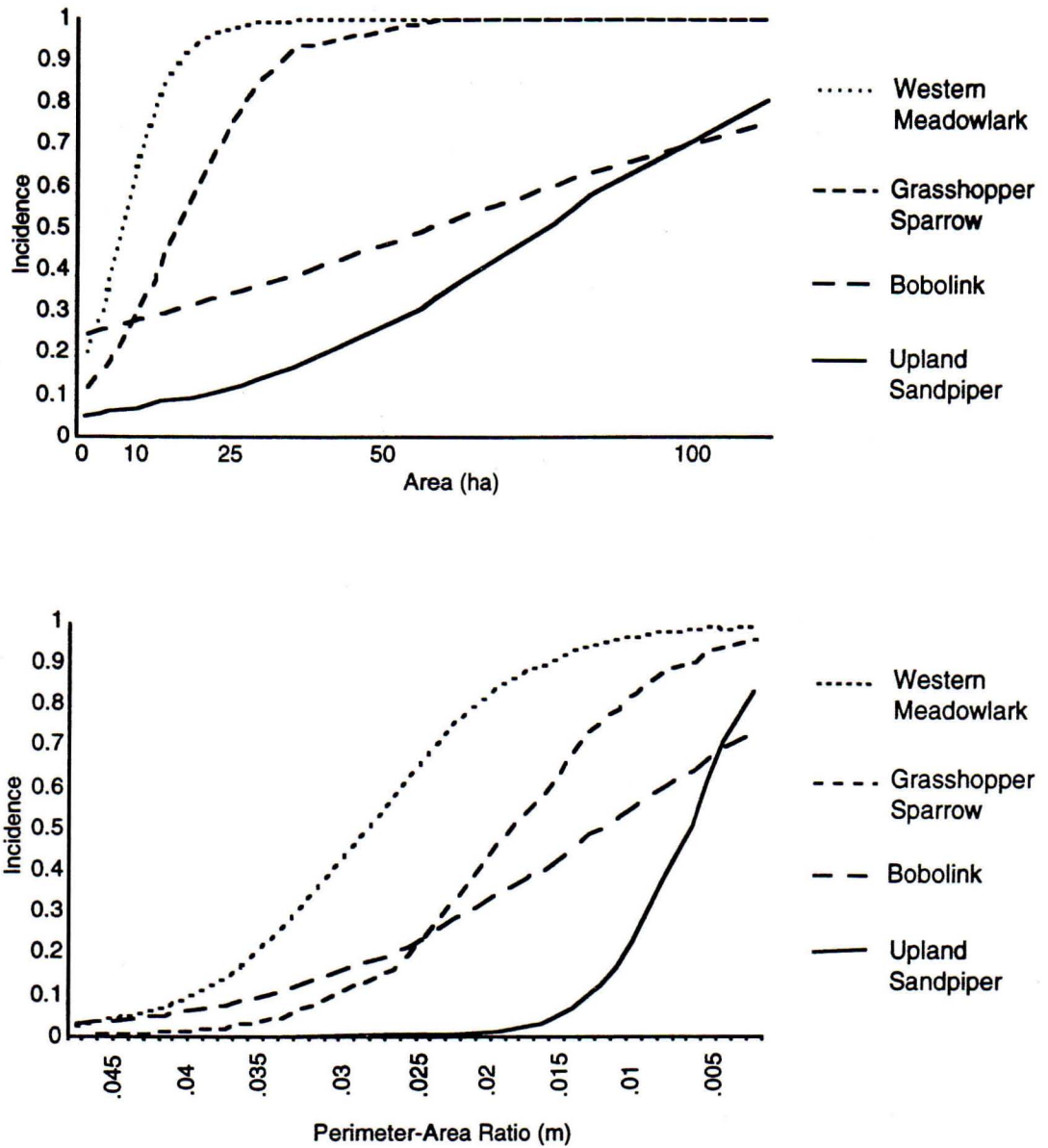
Figure 4. Graphs showing relative incidence function results from four common species with both Area and Perimeter-Area Ratio (1996 data).

Passive Sampling Hypothesis Results

Perimeter-area ratio had a stronger relationship with species richness than did area alone. However, there is a close relationship between perimeter-area ratio and area. In general, perimeter-area ratio decreases as area increases (Figure 5). Because of this relationship, the passive sampling hypothesis may explain the increases in species richness. Thus, I tested the correlation between species richness and perimeter-area ratio using equally sized sub-samples from each patch. Four randomly selected 100 meter 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 ratio values were combined and their perimeter-area ratio values averaged. Species richness in patches was based only on the birds in the standardized 4 ha plots from each patch (or patch group). Multinomial logistic regression models found that species richness still was negatively correlated with perimeter-area ratio ($P < 0.005$) in both 1995 and 1996 (Figure 6).
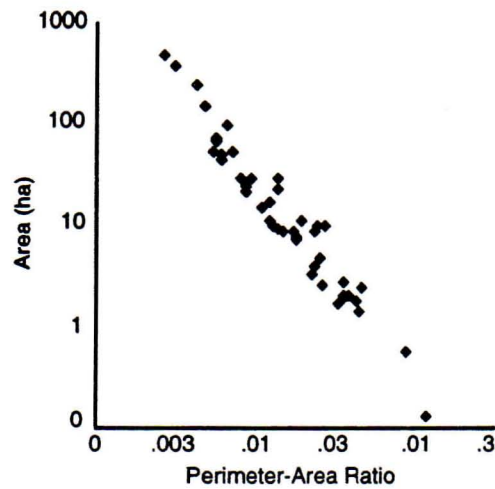
Figure 5. Relationship between area and perimeter-area ratio (Log Scale) in the patches used in 1996.

Figure 6. Scatterplots showing species richness results from tests of the passive sampling hypothesis. Standardized 4 ha plots were sampled from each patch and the species richness of the plots were then plotted against the log of the perimeter-area ratio. Logistic regression models showed the relationships from both years to be significant ($P > 0.005$).

Perimeter-Area Ratio Index

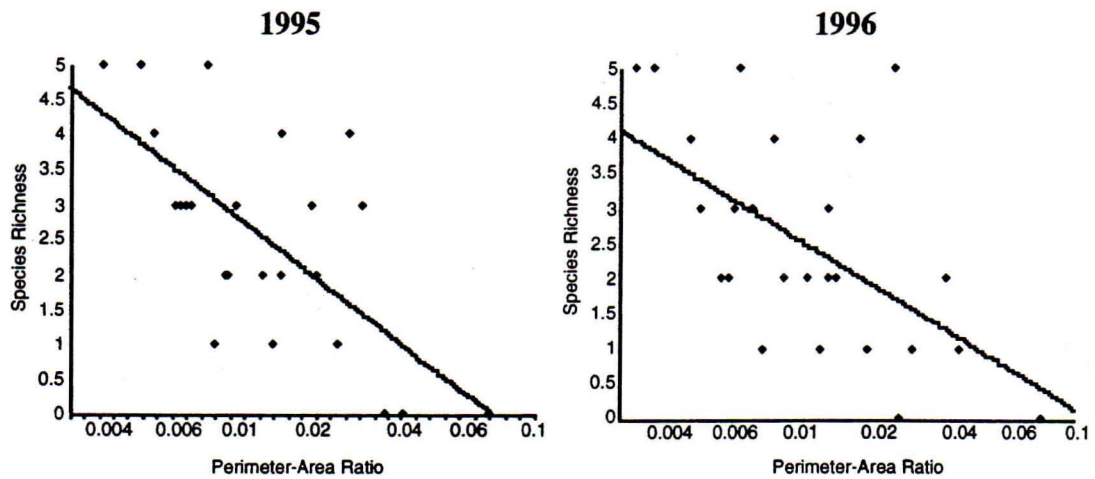Because perimeter-area ratios are difficult to visualize conceptually, I calculated the size of a perfectly circular patch which would be needed to meet the estimated perimeter-area ratio requirement of each species. Then, because square-shaped patches are more likely to occur in agricultural areas, I calculated values for perfect squares as well. The results of these calculations are shown in Table 7, along with the mean minimum patch sizes calculated from the actual patches. Increasing deviation from a perfectly circular shape will result in increasing perimeter-area ratio values. Therefore, even perfect squares have a higher perimeter-area ratio values than circles of the same area. The patches in my study area were often relatively elliptical in shape or had indented perimeters. This is borne out in the much higher sizes of the patches which were actually needed to obtain 50% incidence for each species. This index is meant only as an illustration of the importance of considering the shape of patches rather than size alone.

Table 7. Perimeter-area ratio index values. A comparison of the sizes of hypothetical circular and square shaped patches which would meet estimated perimeter-area ratio value requirements for five species is given, along with the actual patch sizes at which those species reached 50% incidence. The sizes and perimeter-area ratio values from actual patches are averages of the statistically significant results of the two years of the study.

Species	PA value (meters)	Patch Sizes (ha)		
		Circle	Square	Actual Patches
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
Bobolink	0.012	10.4	13.2	46
Upland Sandpiper	0.008	22.2	28.4	56

DISCUSSION

Relative Importance of Landscape Variables

Both patch area and perimeter-area ratio were significant predictors of species richness and the probability of occurrence for wet meadow breeding birds. The probability of occurrence of grasshopper sparrows, bobolinks, upland sandpipers and western meadowlarks was correlated ($P < 0.05$) with area. However, the probability of occurrence for all six common species was correlated ($P < 0.05$) with perimeter-area ratio. Furthermore, perimeter-area ratio had a consistently stronger correlation with both species richness and probability of occurrence than did area.

The types of edges surrounding the patches did not affect the probability of finding species in a patch or species richness. However, nearly 65% of the patches in the study had more than one type of edge, including almost all of the larger patches. This impaired my ability to analyze the relative importance of the three main types of edges, woodland, cropland, and roads. In a related study (Chapter 1) I found weak evidence that woodland edges had a stronger negative effect on the density of grasshopper sparrows than cropland edges, but much more research is needed to answer questions about the relative effects of edge types.

In a study of woodlot fragments in Wisconsin, Temple (1986) found that the core-area of patches was a better predictor of bird presence and abundance than total-area. In my study I found similar results using grassland species, but used perimeter-area ratio as a relative measure rather than core-area, which requires a subjective estimation of the area of each patch which is free from

edge effects. Because of the current ambiguity about how far edge effects extend into patches (Faaborg et al. 1993), and the potential for differences between types of edges and between geographic regions (Freemark et al. 1986), the use of a relative measure seems prudent.

Relative Importance of Vegetation and Landscape Variables

I found vegetation structure important in predicting the presence of some species. However, perimeter-area ratio was more strongly correlated with the probability of finding each of the six most common species in the meadows than the vegetation structure variables were. In addition, perimeter-area ratio was more strongly correlated with species richness models than vegetation structure, although visual obscurity and mean number of vegetation contacts also had positive correlations with species richness in the 1995 data.

While vegetation structure was less significant as an overall predictor of species richness and individual species presence in my patches than perimeter-area ratio, it was not unimportant to the spatial distribution of grassland birds. For example, grasshopper sparrows and western meadowlarks were found in almost every management unit within the large patches of my study, suggesting that the differences in vegetation structure between those management units fell within acceptable bounds for those species' habitat requirements. Bobolinks, dickcissels, red-winged blackbirds, and upland sandpipers, on the other hand, were more spotty in their distribution, suggesting a stronger tie to particular vegetation structure types or other within-patch environmental differences. The relatively wide confidence limits in the larger patch sizes and the shallow slopes of the incidence curves of

bobolinks, dickcissels, and red-winged blackbirds further suggests that these species were sensitive to within-site variation. Similarly, Hinsley et al. (1996), found that forest birds whose specific habitat requirements were only met in portions of larger woodland patches had incidence curves with shallower slopes than species with more even within-patch distributions.

The multiple management units contained within the large patches of my study prevented me from averaging vegetation characteristics over entire patches. Most of these patches were either split into several pastures with discrete grazing regimes or were split into hayed and grazed portions. Because of this, I used management unit means in the vegetation logistic regression models and analyzed the data with each management unit assigned the patch size and perimeter-area ratio of its encompassing patch. Although some species seemed to prefer some management units over others, I made the assumption that the non-grassland borders (woodland, cropland, roads, etc.), and not management unit borders, would be recognized as actual patch edges by the birds. The vast majority of management units well exceeded the average territory size for the six most common species as given by Wiens (1969), so the size of the management units should not have been a constraint. There is currently no research that has shown any adverse effects on grassland birds from borders between grassland management units which have contrasting vegetation structure.

Incidence Functions - Area

Although patch size was determined to be less important than perimeter-area ratio as a predictor of species presence, it is still an important variable.

Further, the minimum patch size requirements generated from our data allow comparisons with results from other studies.

Grasshopper sparrows reached 50% incidence in my study at 8 ha and 12 ha in 1995 and 1996, respectively. By comparison, Herkert (1994) calculated the minimum size needed by grasshopper sparrows in an Illinois study at 30 ha. In Maine, Vickery et al. (1994) found 50% incidence at 100 ha, although they hypothesized that the large estimated size requirement was due to increased selectivity by grasshopper sparrows because of low numbers of the species in their region. Similarly, Hinsley et al. (1996) found that when the regional abundance of an area-sensitive species was low, its incidence curve shifted to the right, toward larger patches.

Bobolinks had an estimated minimum patch size requirement of 46 ha in 1995. The correlation between the probability of finding bobolinks and patch size was not quite significant in 1996 ($P = 0.1$), but the estimated minimum patch size requirement was 43 ha, similar to that in 1995. Herkert (1994) found 50% incidence for this species at 50 ha. Vickery et al. (1994) found that while area was an important factor for predicting bobolink presence, bobolinks occurred in too few patches to allow the calculation of incidence functions. As mentioned earlier, vegetation structure seemed important to bobolinks. They occurred much more often in hay meadows than in pastures. The preference of bobolinks for haymeadows over pastures also was found by Kantrud (1981) in North Dakota. Others noted the general preference of bobolinks for relatively dense vegetation as well (Good and Dambach 1943, Wiens 1969, Skinner 1975, Johnson and Schwartz 1993). Bobolinks were absent from several of the larger patches in my study which were moderately grazed, which widened

confidence limits in the incidence functions. Therefore, although bobolinks had a strong affinity for large patches, their vegetation structure requirements probably reduced the significance of their correlation with patch size.

Upland sandpipers reached 50% incidence at 50 and 61 ha respectively in 1995 and 1996. Vickery et al. (1994) found 50% incidence in Maine at 200 ha. In Illinois, Herkert (1991a) did not observe upland sandpipers in patches of less than 30 ha. Upland sandpipers were difficult to study for several reasons. First, they were relatively scarce throughout the study area, occurring in only 22 percent of the patches censused. Secondly, they were often difficult to detect because the incubating bird would not easily flush until nearly stepped on. Third, they seemed to be very mobile during the day. Small groups of upland sandpipers were often seen flying over patches during censuses, and I sometimes would see them in a patch during vegetation sampling (normally during late morning or afternoon), but not in the same patch during early morning bird censuses. Upland sandpipers tend to prefer relatively short vegetation (Skinner 1975, Kantrud 1981), so their distribution, like that of bobolinks, dickcissels, and red-winged blackbirds, was likely restricted by vegetation structure differences between patches as well.

I found a minimum size requirement for western meadowlarks at 5 ha in both years of my study. No other study has calculated size requirements for western meadowlarks, though the minimum patch size requirement for eastern meadowlarks was 5 ha in Illinois (Herkert 1994). Johnson and Temple (1986) found that western meadowlarks had their highest probability of nest occurrence in areas of grassland patches near forest edges. The lack of

avoidance of edges may explain the relatively low area requirements and high perimeter-area ratio values for this species.

I found a correlation (P < 0.05) between the probability of occurrence for dickcissels and area in 1996 only. The variance in the models from both years was high (as illustrated by the confidence limits of the incidence curves), and even in 1996, when they showed a significant correlation with area, dickcissels were predicted to have a 36 % probability of occurrence even in the smallest patches of the study. Thus, although their probability of occurring increased as patch size increased, they were still common in small patches. Herkert (1994) found no area relationship with dickcissels in his Illinois study.

Dickcissels prefer tall weedy vegetation (Zimmerman 1971). This kind of habitat was patchily distributed within the study area, in areas such as fence lines, roadsides, and unhayed field corners. The increase in the probability of finding dickcissels in large patches may have been a function of the greater chance of finding the type of vegetation structure they preferred in large patches, rather than a function of any area sensitivity, *per se*.

Red-winged blackbirds were not correlated (P > 0.05) with area in either year of my study, although, like dickcissels, they tended to be more commonly found in large patches than small. By contrast, Herkert (1994) found red-winged blackbirds significantly more common in small patches than in large ones. Red-winged blackbirds prefer vegetation structure similar to that preferred by dickcissels, and often occur in wetter areas than the other common species in my study (Good and Dambach 1943, Skinner 1975, Johnson and Schwartz 1993). Thus, like dickcissels, red-winged blackbirds were probably

found more commonly in large areas because of the increased habitat heterogeneity found there.

Incidence Functions - Perimeter-Area Ratio

All six common wet meadow breeders were significantly more likely to occur in patches with low perimeter-area ratios. It is interesting to note that even the two species not significantly related to area, dickcissels and red-winged blackbirds, were strongly correlated with perimeter-area ratio, although they occurred more frequently in patches of high perimeter-area ratio than the other four species. The two species that showed the strongest avoidance of patches with high perimeter-area ratios were grasshopper sparrows and upland sandpipers. Grasshopper sparrows also avoided both wooded and crop edges in other research (Chapter 1). No other researchers have published results of incidence functions using perimeter-area ratio or similar shape indices.

Species-Area Models

Models which 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. 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 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. This hypothesis states that larger patches have more species simply because they contain more individuals . In other words, birds in small patches are simply a sub-sample of those in large patches and large patches have more species because they have a larger sample of the same population. Herkert (1994) and Vickery et al. (1994) disproved the passive sampling hypothesis in their studies by finding more species in larger patches using sub-samples of their data which represented equal sampling effort from each patch. I found similar results using perimeter-area ratio data. Based on my 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 plays a large role in the higher species richness of grassland birds found in large patches in my study. Species such as upland sandpipers, red-winged blackbirds, dickcissels, and bobolinks, which require specific vegetation structure or other micro-environment features, were more likely to find them in large patches. Large patches in my study region were more likely to have multiple management units, which varied in vegetation structure, micro-topography, and distance to groundwater. Large patches also tended to have a wider range of habitats simply because they extended over a larger topographical area than small patches. Patches which provided both tall and short vegetation, as well as 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, soras, and sedge wrens. Also, if habitat near the edge of patches is seen 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 with the current amount of information. The processes of colonization and extinction are complicated by the seasonal migration of grassland breeders, most of which are long-distance migrants. Therefore, in one sense, there is extinction of all patches each year. However, since most birds return to the same general area year after year, migration may be more similar to hibernation than extinction.

Local extinctions may occur in grassland bird patches in two ways: through the failure of birds to return after migration, and because of disturbances such as mowing or grazing during the breeding season. There is evidence of strong nest-site fidelity in birds and evidence of a positive correlation between nest-site fidelity and breeding success (Gavin and Bollinger 1988, Bollinger and Gavin 1989). Because large patches are preferred habitat for 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), area-sensitive species may choose the largest available patches in which to nest. In times of low regional abundance, small patches should be less likely than large patches to attract breeding birds returning from wintering areas. This is supported by Hinsley et al. (1996), who found that incidence curves shifted to the right, away from

smaller patches, in years of low regional abundance. Therefore, it could be argued that small patches have a greater chance of periodic local extinction than larger patches. Additionally, because large patches can hold more breeding birds than small patches, there is a better chance that at least some birds which nest there in one season will survive migration to return the next year.

Disturbances which displace breeding birds are less likely to affect the total area of large patches than of small patches. Haying, burning, or intensive grazing which can cause the abandonment of nesting efforts during the breeding season. However, large patches, at least in my study area, are likely to be split into multiple management units, which receive different management treatments and would lessen the chance of total-patch extinctions. Also, even in single management units, large patches would have a better chance of retaining some areas free from the disturbance.

Colonization of patches may also be correlated with patch size. If large patches provide higher nest success rates than small ones, they should have a higher return rate of 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 mounting evidence suggests (Baker 1993), then both the size and the proximity of patches to the natal area of the bird might affect the chance the bird will find it during post-fledging exploration.

Most likely, the species-area relationship is explained by a combination of the passive sampling, habitat diversity, and fragmentation models. More information on nest-site fidelity, post-fledging exploration, and habitat selection

and preference in grassland birds is needed to further understand the relevance of each model. In addition, we know that larger patches which provide core areas hold more area-sensitive species than patches which do not provide core areas, but it is not yet clear whether there is a threshold core area size, above which there is no increase in species richness.

Importance of Other Landscape Characteristics

Other landscape characteristics besides area and perimeter-area ratio may also be 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 outside of their breeding patch. Some species of grassland birds have also been found to forage in cropfields (Wiens 1969). Therefore, the proximity of other patch types, such as cropfields, may be important. In addition, alfalfa fields were used by grassland birds in our study region as nesting habitats, but were cut periodically. The proximity of a grassland patch to these fields may increase the probability of colonization by species such as bobolinks and dickcissels which leave the fields after cutting.

Limitations of Presence/Absence Data

While I found significant effects of landscape characteristics on the probability of grassland bird presence in patches, it is also necessary to understand their effects on abundance and breeding success. Several authors have found that grassland birds suffer their lowest predation rates in large patches and away from wooded edges (Johnson and Temple 1986, 1990,

Burger et al. 1994), so it is likely that nest success would be higher in patches with lower perimeter-area ratios. In another study (Chapter 1), I found that some birds have lower densities near edges, so it is also likely that densities of birds would be lower in patches which have little or no area free from edge effects than in larger patches. However, it is important that these hypotheses be tested empirically.

Summary and Conclusions

The perimeter-area ratio of patches was the most significant factor influencing grassland bird species presence and species richness in this study. Although patch size is correlated with perimeter-area ratio, and is also important to grassland birds, it was a less significant factor in my results. In addition, the types of edges that surround a patch did not significantly affect grassland bird presence or species richness.

Vegetation structure variables had weaker correlations with the probability of occurrence for species and species richness than perimeter-area ratio. However, the vegetation structure of some patches may have limited the within-patch distribution of species such as upland sandpipers, bobolinks, dickcissels, and red-winged blackbirds, causing shallow incidence curve slopes. Additionally, the absence of these species from some large patches may have been due to the absence of preferred vegetation structure in those patches.

My species-area incidence function results were similar in most cases to those generated by other authors. Because of the relative importance of perimeter-area ratio to area, I also generated incidence functions based on

perimeter-area ratios. The use of perimeter-area ratio as a predictor of species richness and presence is new to studies of grassland birds. However, other authors have recognized the importance of interior or core areas of woodland patches which provide birds with areas free from edge effects (Whitcomb et al. 1981, Temple 1986, Faaborg et al. 1993,). Perimeter-area ratio may be a better variable than core area because it is a relative measure of the amount of a patch affected by the edge and does not require an arbitrary estimation of the distance that edge effects extend into a patch.

Traditional grassland bird research and management has focused on the importance of vegetation structure and similar variables in determining the spatial distribution of grassland birds. With the increasing fragmentation of grasslands, there has been a recognition of the importance of maintaining large patches of habitat in order to sustain diverse grassland communities. My research shows that maintaining patches with a large area is not sufficient. In order to insure a high species diversity of grassland birds, patches must also be shaped so that they provide core areas, free from the effects of edges.

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Conclusion and Management Recommendations

The fragmentation of grasslands by modern agriculture presents many challenges to both grassland birds and grassland conservationists. In addition to the loss of total grassland area, there has also been a decrease in habitat patch size and an increase in edge habitat throughout much of the breeding range of grassland birds. Because of limited funds and workforces, management agencies and conservation organizations are forced to select the highest priority areas for protection and managment. My research provides criteria to aid in that selection process.

Prior to this study, vegetation structure and patch size were recognized as important factors influencing grassland bird presence and abundance. Additionally, areas near wooded edges had been found to have higher rates of nest predation and parasitism on grassland bird nests. Several species of grassland birds were also found to have significantly lower nest densities near wooded edges than toward the center of patches. However, the effects of other common grassland patch edge types such as cropfields and roads had not been studied. In addition, there was no research on the importance of patch shape to grassland birds.

In this study, I found that grasshopper sparrows and bobolinks were significantly less abundant near wooded edges than toward the center of patches. I also found that grasshopper sparrows were significantly less abundant near cropfields than in patch interiors. Neither species showed any response to two-track gravel roads which passed through large meadows.

These data suggest not only that edges such as woodlands and cropfields define patch boundaries for some species of grassland birds, but that some birds may not use the areas near those edges, thereby decreasing the amount of useful habitat in a patch.

The perimeter-area ratio of a patch, which is dependent upon both patch size and shape, a more significant factor than size alone in determining grassland bird species richness in this study. Therefore, the size and vegetation structure of patches are not sufficient measures with which to gauge the value of habitat patches to grassland birds. Patches which are managed for grassland bird species richness must also be shaped so that they contain core areas, where birds can escape edge effects.

In highly fragmented grassland ecosystems, maintaining large contiguous tracts of prairie should be the highest priority of management agencies and conservation groups. This is especially important in states like Nebraska, where there is little prairie left. Large compactly-shaped patches have more habitat heterogeneity and more grassland species than small patches, and they provide core areas which are necessary for many grassland bird species. These native birds will suffer both local and regional extinctions without the maintenance of large compactly-shaped prairie patches, regardless of the total area of remaining grassland preserved.