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THE EFFECTS OF HABITAT FRAGMENTATION ON MIDWESTERN GRASSLAND BIRD COMMUNITIES¹

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Abstract. The influence of area and vegetation structure on breeding bird communities associated with 24 Illinois grassland fragments (0.5–600 ha) was studied between 1987 and 1989 to document the effects of habitat fragmentation in a severely fragmented midwestern landscape. Fragment area strongly influenced bird communities within grasslands and accounted for a high percentage of the variation in mean breeding bird species richness among fragments ($R^2 = 0.84$). Breeding bird species richness patterns within 4.5-ha subsections of these grasslands also significantly increased with fragment size. Eight of the 15 (53%) most common bird species had distributions among fragments that were significantly influenced by habitat area, whereas six species (40%) had distributions within fragments that were significantly influenced by vegetation structure only. The Dickcissel (*Spiza americana*) was the only species with a distribution within fragments that was not significantly associated with either habitat area or vegetation structure. Four groups of birds were identified by an analysis of habitat area and vegetation structure preferences of individual species: area-sensitive species (5 species), edge species (3), vegetation-restricted species (6), and the Dickcissel. Estimates of minimal area requirements for the five area-sensitive species ranged from 5 to 55 ha. Discriminant analyses of habitat suitability within fragments suggests that the absence of area-sensitive grassland bird species from some small fragments may result, in part, from limited habitat availability. All five area-sensitive species, however, also regularly avoided structurally suitable habitat on small grassland fragments. As a result of the considerable extent to which native and, more recently, agricultural grasslands have declined in the Midwest, habitat fragmentation is likely to have caused midwestern grassland bird declines, especially for area-sensitive species.

Key words: bird population declines; habitat fragmentation; habitat selection; midwestern grassland birds; species–area relationship.

INTRODUCTION

Agricultural and urban development have severely reduced and fragmented native habitats throughout the midwestern United States. The dynamics of populations inhabiting terrestrial habitat fragments have received considerable research attention, including studies of birds (e.g., Whitcomb et al. 1981, Robbins et al. 1989a, Robinson 1992), mammals (Gottfried 1979, Matthiae and Sterns 1981, Yahner 1992), invertebrates (Shreeve and Mason 1980, Murphy and Wilcox 1986, Webb 1989), and plants (Hoehne 1981, Levenson 1981, Weaver and Kellman 1981, Simberloff and Gotelli 1984, Soulé et al. 1992). Perhaps the most extensively studied system thus far is the breeding birds of eastern North American deciduous forests, where several researchers have shown that habitat fragmentation adversely affects many forest bird species (e.g., Galli et al. 1976, Robbins 1979, 1980, Whitcomb et al. 1981, Ambuel and Temple 1983, Howe 1984, Lynch and Whigham 1984, Freemark and Merriam 1986, Blake

and Karr 1987, Hagan and Johnston 1992). In particular, many characteristic forest bird species are absent from small habitat patches (Robbins et al. 1989a), and some long-term censuses of small woodlots have documented population declines (e.g., Lynch and Whitcomb 1978, Robbins 1979, Leck et al. 1981, 1988, Askins and Philbrick 1987, Johnston and Hagan 1992). Although there is general agreement on the effects of fragmentation on breeding birds within forest habitats, the mechanisms that account for these trends are not clear (Lynch 1987, Martin 1988).

The effect of habitat fragmentation on midwestern grassland bird communities has received comparatively little attention despite the fact that loss of grassland habitat has exceeded loss of forest habitat throughout much of the midwestern United States (e.g., Smith 1981, Iverson 1988, Sample 1989). In addition, many grassland bird species are currently experiencing significant population declines that exceed those exhibited by most forest species (Robbins et al. 1986, 1989b, Herkert 1991). Fifty percent of the 26 grassland bird species known to breed in Illinois (Graber and Graber 1963, Bohlen 1989) have populations that are significantly declining nationally and/or regionally, based on population estimates from the United States Fish and Wildlife Services' Breeding Bird Survey (BBS)

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TABLE 1. National and regional estimated population trends and relative abundance within fragments for 26 grassland bird species known to breed in Illinois.‡

Species	BBS population estimate (1966–1991)		Relative abundance within fragments		
	U.S. trend	Illinois trend	Transects		Average density where present (males/100 ha)
			No.	%	
Ring-necked Pheasant	-33*	-63	11	12	9.8
Greater Prairie-Chicken	-96	§	0
Northern Bobwhite	-46*	-57*	7	7	14.1
Killdeer	+16	+482**	3	3	8.9
Upland Sandpiper	+142**	0	14	15	10.9
Mourning Dove	-2	-14	4	4	9.1
Short-eared Owl	-2	§	0
Common Nighthawk	-2	-14	0
Horned Lark	-14	+10	4	4	18.0
Sedge Wren	+56	-7	12	13	39.0
Common Yellowthroat	-5	-18	38	42	24.1
Dickcissel	-35**	-62	44	49	27.0
Field Sparrow	-58**	-58**	27	30	27.7
Vesper Sparrow	-22	-2	3	3	12.0
Lark Sparrow	-59**	-95	0
Savannah Sparrow	-28*	-63*	23	25	25.4
Grasshopper Sparrow	-69**	-85†	42	47	31.1
Henslow's Sparrow	-68**	§	13	14	20.8
Song Sparrow	-7	-9	20	22	22.9
Swamp Sparrow	+64**	-18	9	10	24.0
Bobolink	-38**	-93**	23	25	81.8
Red-winged Blackbird	-24*	-16	84	93	50.7
Eastern Meadowlark	-43**	-61**	72	80	26.4
Western Meadowlark	-12	-86**	1	1	9.0
Brown-headed Cowbird	-16	+81†	6	8.9	
American Goldfinch	-28*	-24*	35	19.5	

† $P < .10$, * $P < .05$, ** $P < .01$.

‡ Population estimates are derived from the United States Fish and Wildlife Service's Breeding Bird Survey (BBS) for the period 1966–1991 (USFWS, unpublished data). Refer to Geissler and Sauer (1990) for details on how BBS trends are estimated and tested for statistical significance.

§ Too rare for meaningful trend analysis.

data (Table 1). Grassland species such as the Grasshopper Sparrow (*Ammodramus savannarum*) and Henslow's Sparrow (*Ammodramus henslowii*) have declined by nearly 70% in the U.S. over the last 25 yr (Table 1). In Illinois, four grassland bird species, the Bobolink (*Dolichonyx oryzivorus*), Western Meadowlark (*Sturnella neglecta*), Grasshopper Sparrow, and Lark Sparrow (*Chondestes grammacus*) have declined by >85% since 1966 (Table 1).

The distinction between grasslands and row-crop agriculture may not be as sharp as the distinction between forest fragments and the surrounding landscape. Consequently grassland birds might respond to habitat fragmentation differently than do forest bird species. However, Samson (1980a) showed that several grassland bird species were influenced by fragment area in a study of 14 prairie fragments in Missouri. In addition, in a study of eight grassland fragments in Minnesota, Johnson and Temple (1986, 1990) showed that Grasshopper Sparrows and Western Meadowlarks were more likely to nest in large grassland fragments and that nest predation rates for grassland bird species were lower in large grasslands than they were in small fragments. Others have shown that area influences individual spe-

cies in other "grassland" habitats. In the northeastern United States, Bobolinks, Upland Sandpipers, Henslow's Sparrows, and Grasshopper Sparrows inhabiting hayfields, old fields, and pastures all appear to be area-sensitive (Peterson 1983, Bollinger 1988, Bollinger et al. 1990, Bollinger and Gavin 1992, Smith 1992).

The purposes of this paper are to (1) document the effects of habitat fragmentation on grassland birds in an extremely fragmented midwestern landscape and (2) assess the likelihood that habitat fragmentation may be causing declines in midwestern grassland bird populations. In Illinois <1000 ha of high-quality prairie habitat remains of the state's former 8.7×10^6 ha (Iverson 1988). Additionally, the amount of secondary grassland habitat (i.e., hayfields, pastures) has also recently declined. Between 1960 and 1989 the land area of hay in Illinois declined by more than half (850 000 to 400 000 ha) and Illinois pasture area has also declined by >75% since 1906 (Herkert 1991). The extent of this native (>99%) and more recent secondary (≈ 53 –75%) grassland habitat loss, and present intensity of row-crop agriculture (>90% of the surface area in many regions; O'Neill et al. 1988) probably ranks grassland habitat in Illinois among the most highly fragmented

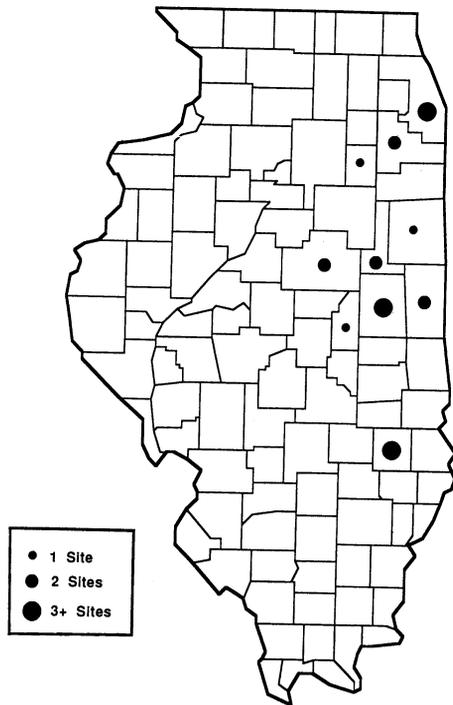


FIG. 1. Location of grassland study areas.

and endangered ecological systems in the eastern United States.

METHODS

Study areas

The breeding birds of 24 grassland areas in north-eastern and north-central Illinois (Fig. 1) were studied between 1987 and 1989 ($n = 8$ areas, 1987; $n = 24$ areas, 1988–1989). Study areas ranged from 0.5 to 650 ha and included native prairie, restored prairie, and cool-season grass fields. Study areas were selected to provide a representative sample of the grassland areas in the study region. No xeric grasslands, hill prairies, or agricultural areas (e.g., hayfields, pastures) were included. All study areas were publicly owned and were undisturbed (i.e., no mowing or burning) during the breeding season (1 May–30 June). Study areas were categorized into three classes for analyses: native prairie (12 sites, range 0.5–650 ha); restored prairie (4 sites, range 4–20 ha); and nonprairie grasslands (8 sites, range 6–238 ha). Dominant grass species from the native and restored prairie study areas included big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), panic grass (*Panicum* spp.), cord grass (*Spartina pectinata*), prairie dropseed (*Sporobolus heterolepis*), and upland sedges (*Carex* spp.). Dominant grass species from the nonprairie areas included Kentucky bluegrass (*Poa pratensis*), meadow fescue (*Festuca pratensis*), smooth brome grass (*Bromus inermis*), timothy (*Phleum pratense*), orchard grass (*Dactylis glomerata*),

and red-top (*Agrostis alba*). Plant species nomenclature follows Mohlenbrock (1986).

Bird community composition

Only birds that potentially breed in grassland habitat in Illinois (Graber and Graber 1963, Bohlen 1989) were included in the analyses. Bird censusing was conducted using strip transects (Emlen 1977, Conner and Dickson 1980). Strip transects were 300 m in length and all singing male birds within 75 m on either side of the transect were counted. Detection distances for all grassland bird species included in this study exceed 75 m (J. R. Herkert, unpublished data); therefore all species within transects should have been detectable. Each bird transect was censused 3–4 times between 15 May and 30 June, between 0600 and 1000 local time. Bird censuses were timed to correspond to the height of the nesting season for the target species (median first and last Illinois egg dates for the 19 grassland bird species encountered in the study are 9 May and 10 July respectively; Bohlen 1989). Sections of study areas not covered by strip transects were systematically searched to supplement the species list for each site, with the amount of additional census effort proportional to fragment area so that coverage per unit area was approximately equal for all sites. Records from all visits to a site were combined to yield a total species list. The Bobolink has a distribution that is restricted primarily to northern Illinois (Bohlen 1989; J. R. Herkert, personal observation). Therefore, analyses involving the Bobolink were restricted to sites north of 40° N latitude.

Vegetation sampling

Vegetation structure was sampled each year at 40 randomly located sites within each bird census transect by passing a 0.6-cm diameter metal rod vertically through the vegetation and counting the number of contacts by different vegetation types (live grasses, live forbs, and dead plant material) in successive 25-cm intervals of height (cf. Rotenberry and Wiens 1980). Eight vegetation variables were collected from each bird census transect: mean litter depth (LD), mean grass height (GHT), mean vegetation height (VGHT), mean number of live grass contacts (HTSGR), mean number of live forb contacts (HTSFB), mean number of total (live grass, live forb, dead plant material) contacts (TOTHT), percent live contacts (PCTLV), and woody stem density (SHRUB). Measurements of vegetation structure were collected each year between 10 and 25 May, with sampling beginning in the southernmost sites and progressing northward.

Data analysis

The relationship between area and bird species richness was examined using exponential (semi-log) regression models. Several authors have suggested that species–area relationships may result simply from the fact that large areas typically contain more individuals,

and ultimately more species, than small areas (Connor and McCoy 1979, Coleman et al. 1982, Boecklen 1986). To test this possibility, bird species richness per unit area within small and large fragments was analyzed by comparing counts from standardized 4.5-ha transects within small and large fragments. If birds on small fragments are merely subsamples of birds found within large fragments, then bird species richness per unit area would be expected to be the same for all fragments regardless of size. Because species richness data from multiple transects within specific fragments and counts from the same transects between years may not be independent, the mean number of species per transect per fragment was used as the dependent variable in the regression model.

Stepwise regression (Neter et al. 1985) was used to assess the relative importance of area and habitat structure on breeding bird distribution patterns within fragments. The dependent variable in the regression models was the proportion of times each species was encountered in each transect (i.e., the probability of encountering each species within a specific transect). Prior to regression analyses proportions were transformed using the logistic transformation (Neter et al. 1985:362). Independent variables included in the regression analyses were the eight vegetation variables, area (\log_{10} -transformed), year, and a within-transect heterogeneity index (HETIND), which was calculated using a modification of Boecklen's (1986) habitat heterogeneity index. HETIND measures the average Euclidean distance for all sample points within a transect in a three-dimensional scaled space created by plotting sample points with respect to litter depth, vegetation height, and vegetation density. Transects in which litter depth, vegetation height, and vegetation density were uniform at all sample points would exhibit a tight cluster in the three-dimensional scaled space and result in a low heterogeneity index. Census transects with high variability in these measurements would form a loose cluster and receive a high heterogeneity index.

For species in which fragment area was found to be a significant predictor of transect occupancy, the relationship between grassland area and the probability of occurrence within fragments was modeled using logistic regression so that estimates of species minimal area requirements could be obtained (cf. Robbins et al. 1989a). For these analyses grasslands were divided into 12 size categories (2 fragments \times 2 yr [1988–1989] = 4 "sites" per category), and the proportion of occupied sites was determined. Proportions were then transformed using the logistic transformation (Neter et al. 1985:362) and regressed on fragment area. Robbins et al.'s (1989a) criteria for estimating minimum areas (area at which a species probability of occurrence equals 50% of its maximum) was then used to estimate minimum area requirements for the area-sensitive grassland bird species.

Because the occurrence within transects for all area-

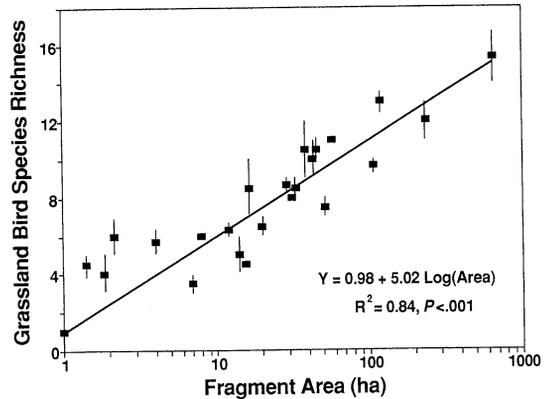


FIG. 2. Number of grassland breeding bird species plotted as a function of grassland fragment size. Symbols represent number of species encountered per site (mean \pm 1 SE) in 1987–1989 censuses.

sensitive species was also significantly influenced by vegetation structure (see *Results*), discriminant analysis was used to estimate the degree to which vegetation structure may have limited species distributions within fragments. First, discriminant function analyses were used to characterize the type of habitat used by area-sensitive species on large fragments. In order to minimize the influence of area on these habitat suitability assessments, initial discriminant functions were developed using only bird species presence or absence and vegetation data from census transects located in grasslands >100 ha. Census transects where the discriminant functions predicted a species to be present were classified as having suitable habitat for the species being analyzed. Transects where the discriminant function predicted a species to be absent were classified as unsuitable. Second, the initial discriminant functions (developed from the large grassland data) were used to evaluate habitat suitability for area-sensitive species on small grasslands (<100 ha) by predicting each species' presence or absence within these transects on the basis of habitat structure data only and not fragment area. These discriminant analyses in effect answered the question: if census transects on small grassland fragments were instead part of a large fragment, would you expect to encounter area-sensitive bird species within them based on the structure of their vegetation?

RESULTS

Area and bird species richness

Nineteen species of grassland birds were encountered during the study (Table 1) ranging from the nearly ubiquitous Red-winged Blackbird (which occurred on 93% of all transects) to the rare and local Western Meadowlark (which was recorded on only one transect).

The total number of breeding bird species encountered within fragments increased significantly with grassland area (Fig. 2). The relationship between grass-

TABLE 2. Regression results for tests of the effects of area, grassland type, and year on the number of breeding grassland bird species encountered within 24 grassland fragments in Illinois (total species richness).

Source of variation	ss	df	F	R ²
Full model	552.5	9	23.7***	0.83
Grassland area	50.6	1	19.5***	
Grassland type	5.9	2	1.2	
Year	3.5	2	0.7	
Grassland area × type interaction	5.2	2	1.7	
Grassland area × year interaction	5.2	2	1.0	
Error	116.4	45		

*** P < .001.

land area and grassland bird species richness was similar for all three grassland classes (native prairie, restored prairie, nonprairie) and was consistent among years (Table 2). The full regression model (Table 2) including grassland area and type, year, and interactions (area × year, grassland type × year) accounted for a high percentage of the variation in species richness among fragments (R² = 0.83). The simple regression of mean (1987–1989) species richness on fragment area alone also accounted for a high percentage of the variation in species richness among fragments (R² = 0.84). The comparison of species richness patterns within 4.5-ha census transects showed that species richness also significantly increased with fragment area within equivalent-sized subsections of these grasslands (Fig. 3). Although there was considerable variability among fragments, transects located within large grasslands had significantly (P < .05) more species recorded within them than transects located in small grassland fragments (Fig. 3).

Area and habitat relationships

The stepwise regression analyses showed that area significantly influenced individual bird species presence or absence within fragments for 8 of the 15 most

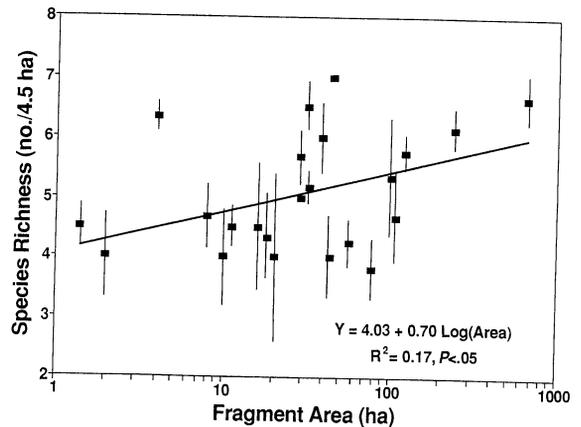


FIG. 3. Number of breeding grassland bird species encountered per 4.5-ha transect plotted as a function of grassland fragment size. Symbols represent the mean number of species encountered (1987–1989) per site (mean ± 1 SE).

common species (Table 3). Area positively influenced the probability of encountering Grasshopper Sparrows, Henslow's Sparrows, Bobolinks, Savannah Sparrows, and Eastern Meadowlarks. Area negatively influenced the probability of encountering Song Sparrows, Red-winged Blackbirds, and American Goldfinches. The probability of encountering Field Sparrows, Swamp Sparrows (*Melospiza georgiana*), Ring-necked Pheasants (*Phasianus colchicus*), Upland Sandpipers (*Bartramia longicauda*), Sedge Wrens (*Cistothorus platenis*), and Common Yellowthroats (*Geothlypis trichas*) was significantly influenced by vegetative features only (Table 3).

Although aspects of vegetation structure significantly influenced all but two of the bird species examined, the Dickcissel (*Spiza americana*) and Red-winged Blackbird, individual species' responses to vegetation attributes varied. For example, Henslow's Sparrows and Common Yellowthroats preferred grasslands with a high percentage of standing dead plant material,

TABLE 3. Variables identified as significant predictors of species occurrence within 24 grassland fragments within Illinois. Variables are listed in decreasing order of significance based on partial F tests. Square brackets indicate a negative relationship. Vegetation codes are defined in *Methods: Vegetation sampling*.

Species	Significant predictors of occurrence
Ring-necked Pheasant	VGHT***, [TOTHT]***, [HTSFB]*
Upland Sandpiper	PCTLV*
Sedge Wren	TOTHT***, [VGHT]***, HETIND**
Common Yellowthroat	GHT***, SHRUB*, [PCTLV]*, [HTSGR]*
Dickcissel	YEAR***
Field Sparrow	[GHT]***, VGHT**
Savannah Sparrow	LD**, AREA**, [HETIND]**, PCTLV*
Grasshopper Sparrow	[GHT]***, HTSGR**, AREA**
Henslow's Sparrow	AREA***, [PCTLV]*
Song Sparrow	[AREA]**, [LD]*, SHRUB*
Swamp Sparrow	TOTHT***, [HTSGR]***, HETIND***, GHT***, PCTLV***, [VGHT]***, [HTSFB]*
Bobolink	AREA***, HTSFB***, VGHT**, [HETIND]**, GHT*
Red-winged Blackbird	[AREA]**
Eastern Meadowlark	AREA**, PCTLV*, [GHT]*
American Goldfinch	[LD]**, HETIND**, [AREA]*, SHRUB*

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

whereas other species such as Eastern Meadowlarks, Upland Sandpipers, Savannah Sparrows, and Swamp Sparrows preferred areas dominated by live vegetation (Table 3). All but one of the nine vegetation variables examined had both positive and negative individual species' responses associated with them (Table 3). These

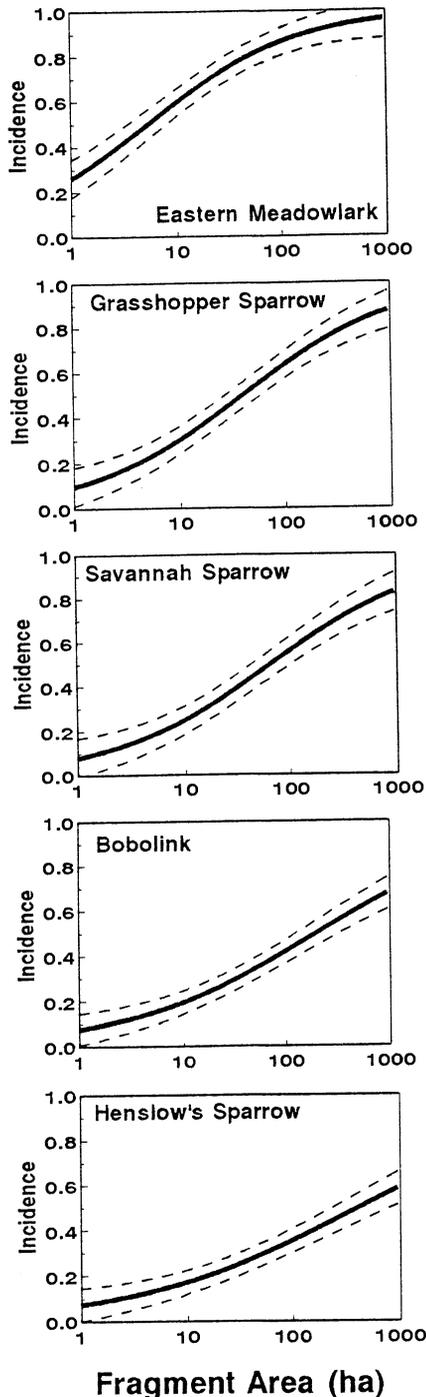


FIG. 4. Probability of encountering area-sensitive grassland bird species (incidence) in grassland fragments of various sizes. Dashed lines indicate 95% confidence intervals for the predicted probabilities.

TABLE 4. Discriminant analyses of habitat suitability for five area-sensitive bird species based on vegetation structure within 85 census transects located within large (> 100 ha, $N = 33$) and small (< 100 ha, $N = 52$) grassland fragments in Illinois.

Species	Frag- ment size	Transects with suitable habitat*		Suitable transects occupied†	
		% of tran- sects	No. sects	%	No.
Savannah Sparrow	large	39	13	85	11
	small	35	18	22	4
Grasshopper Sparrow	large	66	22	82	18
	small	79	41	36	15
Henslow's Sparrow	large	33	11	73	8
	small	25	13	0	0
Bobolink‡	large	48	17	88	15
	small	74	28	7	2
Eastern Meadowlark	large	88	29	100	29
	small	100	52	77	40

* Transects where the discriminant function predicted the species to be present. See *Methods* for a discussion of how suitability was assessed.

† Sites where the species was predicted to be present and was also recorded on the transect on more than one visit.

‡ Only fragments north of 40° N latitude.

data indicate that, overall, grassland bird habitat affinities are diverse, with species often responding to habitat features in opposite ways.

The Dickcissel was the only species that exhibited no significant relationship with either area or any of the vegetation variables in the regression analyses. The Dickcissel was also the only species that was significantly influenced by year effects ($P < .001$, Table 3), with average densities within fragments varying by as much as 75% between years.

Area requirements

Grassland area had a significant positive influence on the probability of occurrence within fragments for five bird species (Fig. 4), with some species occurring on most medium to large fragments (e.g., Eastern Meadowlark), but others occurring only infrequently even on large fragments (e.g., Bobolink and Henslow's Sparrow). The estimated individual area requirements (area at which a species probability of occurrence equals 50% of its maximum; Fig. 4) for the five area-sensitive grassland bird species were variable and ranged from 5 to 55 ha (Eastern Meadowlark, 5 ha; Grasshopper Sparrow, 30 ha; Savannah Sparrow, 40 ha; Bobolink, 50 ha; Henslow's Sparrow, 55 ha).

Discriminant analyses of the vegetation data from bird census transects showed that vegetation structure may play some role in limiting area-sensitive bird species distributions within small fragments. For example, only 25% of all transects within small fragments had vegetation structure that was judged to be suitable for the Henslow's Sparrow (Table 4). Likewise for the Sa-

vannah Sparrow, only 35% of all transects within small fragments had habitat that was identified as suitable for this species. Area requirements, however, also appeared to limit species distributions within small fragments. Although only 25% of all transects within small grasslands had habitat that was identified as suitable for the Henslow's Sparrow, none of these transects was occupied by this species (Table 4). Moreover, for the Bobolink, 74% of all transects within small fragments had habitat identified as suitable for this species, yet it occupied just 7% of these transects (Table 4). Similar patterns of avoidance were exhibited by the other area-sensitive species (Table 4), suggesting that many of the unoccupied census transects within small fragments had vegetation attributes that were structurally appropriate for these species, yet were still unoccupied.

DISCUSSION

Species-area relationship

The results of this study, along with Samson's (1980a) earlier work on prairie fragments in Missouri, show that area strongly influences the structure of breeding bird communities within midwestern grassland fragments. Although the distinction between grassland fragments and agricultural crops is often not as sharp as the distinction between forest fragments and the surrounding landscape, grassland area accounted for a high proportion (84%) of the variation in mean species richness among grassland fragments in the present study (Fig. 2). This proportion was somewhat lower than in Samson's (1980a) study (98%) but was higher than most values typically reported for forest fragments (e.g., 48%, Ambuel and Temple 1983; 50%, Freemark and Merriam 1986; but see Blake and Karr 1987, 87-98%). The results from the regression analysis of species richness patterns within transects showed that the increase in species richness on large grassland fragments did not result from a simple "sampling" effect (i.e., Connor and McCoy 1979), but that the number of species per unit area also increased significantly with fragment area, especially in the largest grasslands (Fig. 3).

Area vs. habitat effects

Based on the habitat-area analyses (Table 3), four relatively distinct groupings of birds can be identified: area-sensitive species that were significantly more likely to occur in large grasslands (Grasshopper Sparrow, Henslow's Sparrow, Bobolink, Savannah Sparrow, and Eastern Meadowlark), edge species that were negatively associated with area (Song Sparrow, Red-winged Blackbird, and American Goldfinch), vegetation-restricted species that occurred in transects according to vegetation features only and not area (Field Sparrow, Swamp Sparrow, Ring-necked Pheasant, Upland Sandpiper, Sedge Wren, and Common Yellowthroat), and the Dickcissel, which varied greatly among years and for which neither area nor vegetation features were

significantly associated with its occurrence within transects (Table 3). These results clearly indicate that both area and vegetation structure significantly influence grassland bird species distribution patterns among fragments. Thirteen of the 15 (87%) most common bird species were significantly influenced by vegetation features within transects, and more than half (8) of these species were also significantly influenced by area effects.

What limits distributions of grassland bird species within small fragments? All of the area-sensitive species in this study regularly avoided small grassland fragments that greatly exceeded typical midwestern territory sizes. Wiens (1969) estimated that the average territory size for Eastern Meadowlarks in Wisconsin was 2.3 ha, yet this species only occasionally (<50%) occurred on fragments that were more than twice this territory size (5 ha; see Fig. 4). Average territory sizes for the Grasshopper, Savannah, and Henslow's Sparrows in the Midwest are all typically <1 ha (e.g., Wiens 1969), yet these species rarely (<30%) occurred on grasslands that were even 10 times this average territory size (10 ha) in Illinois (Fig. 4). The discriminant analyses of habitat suitability of transects located in small grassland fragments suggest that vegetation structure may limit the distribution of area-sensitive grassland birds in some, but not all, small grassland fragments. Area-sensitive species, such as the Henslow's Sparrow and Savannah Sparrow, may be partially limited by habitat availability within small fragments because only a relatively small percentage of these sites (25 and 35%, respectively) appeared to have suitable habitat. All five of the area-sensitive grassland bird species, however, also regularly avoided structurally suitable habitat on small grassland fragments (Table 4).

Area requirements

The area requirements for the five area-sensitive grassland bird species in this study were variable, ranging from 5 to 55 ha. These figures are in general agreement with the estimates provided in Samson (1980b) for 13 grassland bird species in Missouri (although the methods used to derive his estimates are unclear). Samson's estimates ranged from <10 ha for the Horned Lark (*Eremophila alpestris*), American Goldfinch, Grasshopper Sparrow, Savannah Sparrow, and Dickcissel to >100 ha for the Greater Prairie-Chicken (*Tympanuchus cupido*).

Simple presence/absence data, however, provide only rough approximations of bird species' actual minimal area requirements. Long-term demographic data are needed to establish precise estimates of the area required to maintain truly viable populations (Hayden et al. 1985). These data, however, are currently not available for midwestern grassland bird populations. Johnson and Temple (1986, 1990) have provided some short-term (1983-1984) demographic data for five

grassland bird species occurring on grassland fragments in Minnesota. Using estimates of standard avian mortality patterns, Johnson and Temple concluded that none of the grassland bird species they studied were maintaining stable population numbers because of high rates of nest predation and nest parasitism. This negative net productivity even included grassland bird populations inhabiting fragments 130–486 ha in size, suggesting that the actual area required to maintain stable midwestern grassland bird populations may be considerably greater than the estimates derived from the presence/absence data in this study.

*Midwestern grassland bird declines—
is fragmentation the problem?*

All four of the bird groups (area-sensitive, edge, and vegetation-restricted species, plus the Dickcissel) contain species that are exhibiting national and/or regional population declines (Table 1). All five of the area-sensitive species have populations that are significantly declining in the United States. The BBS data also show that four of these species (Bobolink, Grasshopper Sparrow, Savannah Sparrow, and Eastern Meadowlark) are also significantly declining in Illinois (Table 1). The fifth area-sensitive species, the Henslow's Sparrow, is too rare in Illinois for accurate BBS population trend estimation. However, Richard and Jean Graber estimated that between 1958 and 1979, Henslow's Sparrow populations in Illinois declined by >90% (Illinois Natural History Survey 1983). Of the three edge species, the American Goldfinch is significantly declining both nationally and regionally, and the Red-winged Blackbird is significantly declining nationally (Table 1). Two of the vegetation-restricted species, Field Sparrow and Ring-necked Pheasant, are also significantly declining both nationally and regionally (Table 1). Furthermore, the only species for which neither area nor vegetation structure was significantly associated with occurrence within fragments, the Dickcissel, is also experiencing a significant national population decline and a large but variable population decline in Illinois (Table 1).

Area-sensitive species would be expected to be the birds most strongly influenced by habitat fragmentation. As habitat fragmentation intensifies, area-sensitive species would be negatively affected by reductions in average patch size as well as the overall loss of grassland habitat. In fact, all five of the area-sensitive species identified in this study are among the grassland bird species showing the greatest declines in the Midwest and elsewhere (Table 1). Distributions of area-sensitive species are undoubtedly strongly influenced by the scarcity of large grassland areas in Illinois and other regions of the Midwest. In Illinois <20% of the state's 245 native prairie remnants are >10 ha and only nine are >40 ha (Illinois Department of Conservation, unpublished data), indicating that a large majority of native prairie remnants in Illinois are too small for area-

sensitive grassland bird species. Moreover, the amount of "secondary" grassland areas (such as hayfields and pastures) has also substantially declined in Illinois (Vance 1976, Herkert 1991) and elsewhere in the midwestern and eastern U.S. (e.g., Sample 1989, Bollinger and Gavin 1992). The loss of these secondary grassland habitats—the areas that initially buffered the loss of native grasslands for these birds (Graber and Graber 1963)—is significantly contributing to the highly fragmented nature of grassland habitat in the Midwest.

For declining edge and vegetation-restricted species, reductions in average patch size are unlikely to be driving regional declines. Rather, overall loss of breeding grassland habitat, area- or edge-related demographic processes, or winter habitat and resource losses may be contributing to population declines. Several studies have shown that rates of nest predation and nest parasitism are higher in the types of edges that dominate small grassland fragments (e.g., Gates and Gysel 1978, Johnson and Temple 1986, 1990). Johnson and Temple's (1990) data from grassland fragments in Minnesota suggest that this increase in nest predation and parasitism may be sufficient to produce local and possibly even regional declines in some grassland bird species. Johnson and Temple (1990) have also shown that these high rates of nest predation and nest parasitism also affect grassland birds nesting on large grassland fragments (130–486 ha), and therefore have the potential to contribute to area-sensitive grassland species declines as well. Moreover, disturbances in agriculturally associated grasslands (primarily hayfields) have intensified in recent years (Sample 1989, Warner and Etter 1989, Bollinger and Gavin 1992), and have been shown to significantly influence grassland bird species distributions (Sample 1989, Frawley and Best 1991) and nest success (Warner and Etter 1989, Bollinger et al. 1990, Bollinger and Gavin 1992). In the late 1950s, the combination of high densities and relatively large area resulted in hayfields being the major grassland habitat in many areas of the Midwest (Graber and Graber 1963). For example, Graber and Graber (1963) showed that Bobolink densities in mixed (grass and forb) and alfalfa hayfields were nearly 10 times as great as comparable densities in undisturbed grasslands. Moreover, in some regions these hayfield habitats were also nearly 10 times as abundant as undisturbed grasslands (Graber and Graber 1963). Clearly, recent shifts in agricultural practices that reduce bird densities (Sample 1989, Bollinger and Gavin 1992), or reduce adult, nest, nestling, or fledgling survival (Warner and Etter 1989, Bollinger et al. 1990) in these secondary grassland areas have the potential to significantly influence regional populations of Bobolinks and other grassland birds.

Winter habitat and winter resources have also been implicated in the declines of some grassland species (Fretwell 1986, Lymn 1991). Fretwell (1972, 1986) has suggested that Dickcissel numbers, at least historically

and possibly still, are winter-limited by the supply of seeds on the tropical winter areas. More recently, Lymn (1991) has shown that the amount of suitable winter grassland habitat in the southeast United States decreased substantially between 1950 and 1987 due to conversion to row-crop agriculture and pine plantations. Lymn has also suggested that the quality of many remaining grassland areas in the southeastern United States may be reduced due to the accidental introduction of the exotic red fire ant in the 1930s. This loss and degradation of winter grassland habitat may also be contributing to midwestern grassland bird declines. Seven of the 13 Illinois grassland bird species with nationally or regionally declining populations winter primarily or partially in the southeastern United States Gulf Coast region (American Ornithologists' Union 1983, Root 1988). The area-sensitivity of some midwestern grassland bird species could therefore reflect in part the preference of the few remaining individuals for the largest available tracts.

Management implications

The results of the present study show that both area and vegetation structure significantly influence midwestern grassland bird populations. Therefore, conservation plans or policies that address only the issue of area are likely to meet with limited success. Efforts must be made to ensure that structurally suitable habitat is also available, especially for grassland birds with particularly restrictive habitat requirements (e.g., Henslow's Sparrow).

Although the mechanisms that are driving midwestern grassland bird declines remain somewhat poorly understood, management efforts directed toward the protection of large, contiguous grassland areas (on the breeding grounds and possibly on the wintering grounds as well) offer the most promising avenue for avoiding further population declines of these species. Small grasslands tend to be avoided by several regionally declining grassland bird species and consequently are of minimal conservation value to many grassland bird species. Management directed toward minimizing breeding season disturbances within grassland areas (e.g., hay-cutting), and eliminating and controlling habitat features that attract nest predators and nest parasites (e.g., woody encroachment, scattered trees; see Johnson and Temple 1986, 1990, Burger 1988) would also benefit midwestern grassland bird populations.

Finally, although none of the breeding birds of midwestern grasslands are currently in danger of global extinction, many species are experiencing significant population declines throughout much of the region. The magnitude of several of these declines suggests that although global extinction may not be an immediate threat to these species, local or even regional extinctions are likely, especially if the loss and fragmentation of midwestern grassland habitat continues.

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LITERATURE CITED

- Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* **64**:1057–1068.
- American Ornithologists' Union. 1983. Check-list of North American birds. Allen, Lawrence, Kansas, USA.
- Askins, R. A., and M. J. Philbrick. 1987. Effects of changes in regional forest abundance on the decline and recovery of a forest bird community. *Wilson Bulletin* **99**:7–21.
- Blake, J. G., and J. R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. *Ecology* **68**:1724–1734.
- Boecklen, W. L. 1986. Effects of habitat heterogeneity on species-area relationships of forest birds. *Journal of Biogeography* **13**:59–68.
- Bohlen, H. D. 1989. The birds of Illinois. Indiana University Press, Bloomington, Indiana, USA.
- Bollinger, E. K. 1988. Breeding dispersion and reproductive success of Bobolinks in an agricultural landscape. Dissertation. Cornell University, Ithaca, New York, USA.
- Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping on eastern populations of the bobolink. *Wildlife Society Bulletin* **18**:142–150.
- Bollinger, E. K., and T. A. Gavin. 1992. Eastern bobolink populations: ecology and conservation in an agricultural landscape. Pages. 497–506 in J. M. Hagan III and D. W. Johnston, editors. *Ecology and conservation of neotropical landbirds*. Smithsonian Institution, Washington, D.C., USA.
- Burger, L. D. 1988. Relations between forest and prairie fragmentation and depredation of artificial nests in Missouri. Thesis. University of Missouri, Columbia, Missouri, USA.
- Coleman, B. D., M. A. Mares, M. R. Willig, and Y. Hsieh. 1982. Randomness, area, and species-richness. *Ecology* **63**:1121–1133.
- Conner, R. N., and J. G. Dickson. 1980. Strip transect sampling and analysis for avian habitat studies. *Wildlife Society Bulletin* **8**:4–10.
- Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. *American Naturalist* **113**:791–833.
- Emlen, J. T. 1977. Estimating breeding season bird densities from transect counts. *Auk* **94**:455–468.
- Frawley, B. J., and L. B. Best. 1991. Effects of mowing on breeding bird abundance and species composition in alfalfa fields. *Wildlife Society Bulletin* **19**:135–142.
- Freemark, K. E., and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biological Conservation* **36**:115–141.
- Fretwell, S. D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton, New Jersey, USA.

- . 1986. Distribution and abundance of the Dickcissel. *Current Ornithology* 4:211–242.
- Galli, A. E., C. F. Leck, and R. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. *Auk* 93:356–364.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledgling success in field–forest ecotones. *Ecology* 59:871–883.
- Geissler, P. H., and J. R. Sauer. 1990. Topics in route regression analysis. Pages 54–57 in J. R. Sauer and S. Droege, editors. Survey designs and statistical methods for the estimation of avian population trends. U.S. Fish and Wildlife Service, Biological Report 90(1).
- Gottfried, B. M. 1979. Small mammal populations in woodlot islands. *American Midland Naturalist* 102:105–112.
- Graber, R. R., and J. W. Graber. 1963. A comparative study of bird populations in Illinois, 1906–1909, and 1956–1958. *Illinois Natural History Bulletin* 28:383–519.
- Hagan, J. M., III, and D. W. Johnston, editors. 1992. *Ecology and conservation of neotropical landbirds*. Smithsonian Institution, Washington, D.C., USA.
- Hayden, T. J., J. Faaborg, and R. L. Clawson. 1985. Estimates of minimum area requirements for Missouri forest birds. *Transactions of the Missouri Academy of Science* 19:11–22.
- Herkert, J. R. 1991. Prairie birds of Illinois: population response to two centuries of habitat change. *Illinois Natural History Survey Bulletin* 34:393–399.
- Hoehne, L. M. 1981. The groundlayer vegetation of forest islands in an urban–suburban matrix. Pages 41–54 in R. L. Burgess and D. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Howe, R. W. 1984. Local dynamics of bird assemblages in small forest habitat islands in Australia and North America. *Ecology* 65:1585–1601.
- Illinois Natural History Survey. 1983. The declining grassland birds. *Illinois Natural History Survey Notes Number* 227.
- Iverson, L. R. 1988. Land-use changes in Illinois, USA: the influence of landscape attributes on current and historic land use. *Landscape Ecology* 2:45–61.
- Johnson, R. G., and S. A. Temple. 1986. Assessing habitat quality for birds nesting in fragmented tallgrass prairies. Pages 245–250 in J. A. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Johnson, R. G., and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *Journal of Wildlife Management* 54:106–111.
- Johnston, D. W., and J. M. Hagan III. 1992. An analysis of long-term breeding bird censuses from eastern deciduous forests. Pages 75–84 in J. M. Hagan III and D. W. Johnston, editors. *Ecology and conservation of neotropical landbirds*. Smithsonian Institution, Washington, D.C., USA.
- Leck, C. F., B. G. Murry, Jr., and J. Swinebroad. 1981. Changes in breeding bird population at Hutcheson Memorial forest since 1958. *Hutcheson Memorial Forest Bulletin* 6:8–14.
- Leck, C. F., B. G. Murry Jr., and J. Swinebroad. 1988. Long-term changes in the breeding bird populations of a New Jersey forest. *Biological Conservation* 46:145–157.
- Levenson, J. B. 1981. Woodlots as biogeographic islands in southeastern Wisconsin. Pages 13–40 in R. L. Burgess and D. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Lynn, N. 1991. Land use changes in the Gulf Coast region: a link to the decline of Midwestern loggerhead shrike populations. Thesis. University of Wisconsin-Madison, Madison, Wisconsin, USA.
- Lynch, J. F. 1987. Responses of breeding bird communities to forest fragmentation. Pages 123–140 in D. A. Saunders, G. W. Arnold, A. A. Burbidge, and A. J. M. Hopkins, editors. *Nature conservation: the role of remnants of native vegetation*. Surrey Beatty and Sons, Sydney, Australia.
- Lynch, J. F., and D. F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation* 28:287–324.
- Lynch, J. F., and R. F. Whitcomb. 1978. Effects of the insularization of the eastern deciduous forest on avifaunal diversity and turnover. Pages 461–489 in A. Marmelstein, editor. *Classification, inventory, and evaluation of fish and wildlife habitat*. U.S. Fish and Wildlife Service Publication **OBS-78716**.
- Martin, T. E. 1988. Habitat and area effects on forest bird assemblages: is nest predation an influence? *Ecology* 69:74–84.
- Matthiae, P. M., and F. Sterns. 1981. Mammals in forest islands in southeastern Wisconsin. Pages 55–66 in R. L. Burgess and D. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Mohlenbrock, R. H. 1986. *Guide to the vascular flora of Illinois*. Second edition. Southern Illinois University Press, Carbondale, Illinois, USA.
- Murphy, D. D., and B. A. Wilcox. 1986. Butterfly diversity in natural habitat fragments: a test of the validity of vertebrate-based management. Pages 287–292 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Neter, J., W. Wasserman, and M. H. Kutner. 1985. *Applied linear statistical models*. Richard D. Irwin, Homewood, Illinois, USA.
- O'Neill, R. V., J. R. Krummel, R. H. Gardner, G. Sugihara, B. Jackson, D. L. DeAngelis, B. T. Milne, M. G. Turner, B. Zygmunt, S. W. Christensen, V. H. Dale, and R. L. Graham. 1988. Indices of landscape pattern. *Landscape Ecology* 1:153–162.
- Peterson, A. 1983. Observations on habitat selection by Henslow's Sparrow in Broome County, New York. *Kingbird* 33:155–163.
- Robbins, C. S. 1979. Effects of forest fragmentation on bird populations. Pages 198–212 in R. M. Degraaf and N. Tilghman, editors. *Proceedings of the Workshop on Management of North-Central and Northeastern Forests for Non-game Birds*. United States Forest Service General Technical Report **NC-51**.
- . 1980. Effect of forest fragmentation on breeding bird populations in the Piedmont of the Mid-Atlantic Region. *Atlantic Naturalist* 33:131–136.
- Robbins, C. S., D. Bystrak, and P. H. Geigler. 1986. The breeding bird survey: its first fifteen years, 1965–1979. U.S. Fish and Wildlife Service Resource Publication 157.
- Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989a. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs Number* 103.
- Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989b. Population declines in North American birds that migrate to the Neotropics. *Proceedings of the National Academy of Sciences (USA)* 86:7658–7662.
- Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pages 408–418 in J. M. Hagan III and D. W. Johnston, editors. *Ecology and conservation of neotropical landbirds*. Smithsonian Institution Press, Washington, D.C., USA.
- Root, T. 1988. *Atlas of wintering North American birds:*

- an atlas of Christmas Bird Count data. University of Chicago Press, Chicago, Illinois, USA.
- Rotenberry, J. T., and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American Steppe vegetation: a multivariate analysis. *Ecology* **61**:1228–1250.
- Sample, D. W. 1989. Grassland birds in southern Wisconsin: habitat preference, population trends, and response to land use changes. Thesis. University of Wisconsin-Madison, Madison, Wisconsin, USA.
- Samson, F. B. 1980a. Island biogeography and the conservation of prairie birds. *Proceedings of the North American Prairie Conference* **7**:293–305.
- . 1980b. Island biogeography and the conservation of nongame birds. *Transactions of the 45th North American Wildlife Conference*: 245–251.
- Schwegman, J. 1983. Illinois prairie: then and now. *Illinois Audubon Bulletin* **205**:2–14.
- Shreeve, T. G., and C. F. Mason. 1980. The number of butterfly species in woodlands. *Oecologia* **45**:414–418.
- Simberloff, D. S., and N. J. Gotelli. 1984. Effects of insularization on plant species richness in the prairie-forest ecotone. *Biological Conservation*. **29**:27–46.
- Smith, C. R. 1992. Henslow's sparrow, *Ammodramus henslowii*. Pages 315–330 in K. J. Schneider and D. M. Pence, editors. *Migratory nongame birds of management concern in the Northeast*. U.S. Department of Interior, Fish and Wildlife Service, Newton Corner, Massachusetts, USA.
- Smith, D. P. 1981. Iowa prairie—an endangered ecosystem. *Proceedings of the Iowa Academy of Sciences* **88**:7–10.
- Soulé, M. E., A. C. Alberts, and D. T. Bolger. 1992. The effects of habitat fragmentation on chaparral plants and vertebrates. *Oikos* **63**:39–47.
- Vance, D. R. 1976. Changes in land use and wildlife populations in southeastern Illinois. *Wildlife Society Bulletin* **4**:11–15.
- Warner, R. E., and S. L. Etter. 1989. Hay cutting and the survival of pheasants: a long-term perspective. *Journal of Wildlife Management* **53**:455–461.
- Weaver, M., and M. Kellman. 1981. The effects of forest fragmentation on woodlot tree biotas in southern Ontario. *Journal of Biogeography* **8**:199–210.
- Webb, N.R. 1989. Studies on the invertebrate fauna of fragmented heathland in Dorset, U.K. and implications for conservation. *Biological Conservation* **47**:153–165.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewilz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forests. Pages 125–205 in R. L. Burgess and D. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Whittaker, R. H. 1975. *Communities and ecosystems*. Second edition. MacMillan, New York, New York, USA.
- Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithological Monographs* Number **8**.
- Yahner, R. H. 1992. Dynamics of a small mammal community on a fragmented forest. *American Midland Naturalist* **127**:381–391.