Effects of Prairie Fragmentation on the Nest Success of Breeding Birds in the Midcontinental United States

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Abstract: *Grassland fragmentation and habitat loss are hypothesized to be contributing to widespread grassland bird declines in North America due to the adverse effects of fragmentation on breeding bird abundance and reproductive success. To assess the effects of fragmentation on the reproductive success of grassland birds, we measured rates of nest predation and brood parasitism for four species of birds (Grasshopper Sparrow [*Ammodramus savannaru*], Henslow's Sparrow[*Ammodramus henslowii*], Eastern Meadowlark [*Sturnella magna*], and Dickcissel [*Spiza Americana*]) in 39 prairie fragments ranging from 24 to >40,000 ha in size in five states in the mid-continental United States. Throughout the region, nest-predation rates were significantly influenced by habitat fragmentation. Nest predation was highest in small (<100 ha) and lowest in large (>1000 ha) prairie fragments. Rates of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), however, were not consistently related to fragment size and instead were more strongly related to regional cowbird abundance, being significantly higher in regions with high cowbird abundance. Differences in nest-predation rates between large fragments (54–68% of all nests lost to predators) and small fragments (78–84% lost to predators) suggest that fragmentation of prairie habitats may be contributing to regional declines of grassland birds. Maintaining grassland bird populations, therefore, may require protection and restoration of large prairie areas.*

Efectos de la Fragmentación de Praderas sobre el Éxito de Nidos de Aves en el Centro de los Estados Unidos

Resumen: *Se presenta la hipótesis de que la fragmentación de pastizales y la pérdida de hábitat están contribuyendo a extensas declinaciones de aves de pastizal en Norte América debido a los efectos adversos de la fragmentación sobre la abundancia de aves reproductivas y el éxito reproductivo. Para evaluar los efectos de la fragmentación sobre el éxito reproductivo de aves de pastizal, medimos las tasas de depredación de nidos y parasitismo de crías para cuatro especies de aves (*Ammodramus savannarum, Ammodramus henslowii, Sturnella magna *y* Spiza americana*) en 39 fragmentos entre 24 y >40,0000 ha de extensión en cinco estados en el centro de los Estados Unidos. En toda la región, las tasas de depredación de nidos fueron significativamente afectadas por la fragmentación del hábitat. La depredación de nidos fue mayor en fragmentos de pradera pequeños (<100 ha) y menor en fragmentos grandes (>1000 ha). Sin embargo, las tasas de parasitismo por*

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Molothrus ater *no se relacionaban de manera constante con el tamaño del fragmento y en cambio se relacionaban más estrechamente con la abundancia regional de* M. ater*, siendo las tasas significativamente más altas en regiones de abundancia alta. Las diferencias entre las tasas de depredación entre fragmentos grandes (54-68% de nidos depredados) y pequeños (78-84% de nidos depredados) sugieren que la fragmentación de praderas puede estar contribuyendo a las declinaciones regionales de aves de pastizal. Por lo tanto, el mantenimiento de poblaciones de aves de pastizal puede requerir la protección y restauración de extensas áreas de pradera.*

Introduction

Populations of many North American species of grassland birds have declined over the last three decades. In fact, recent declines of grassland bird populations have been more precipitous and broader in extent than declines in any other behavioral or ecological group of North American birds (Knopf 1994; Herkert 1995; Peterjohn & Sauer 1999). The best-supported explanation of recent declines of grassland birds is the loss of grassland habitat on breeding grounds (Goriup 1988; Herkert et al. 1996; Vickery et al. 1999).

Prairies were once the largest vegetative province in North America, and loss of prairie has exceeded that of most other major ecosystems on the continent (Samson & Knopf 1994; Noss et al. 1995). For example, only 4% of an estimated 68 million ha of North American tallgrass prairie remains today (Steinauer & Collins 1996). One major consequence of this extensive habitat loss has been a significant increase in the degree of fragmentation of remaining grassland habitats. Grassland fragmentation reduces both the occurrence and density of breeding birds in small fragments (Herkert 1994; Vickery et al. 1994; Winter & Faaborg 1999). Density and nest success are often unrelated in grassland birds (e.g., Zimmerman 1971; Vickery et al. 1992; Winter & Faaborg 1999), however, so birds occurring at higher densities in larger fragments may not necessarily be reproducing more successfully at these sites.

Previous studies of the effects of habitat fragmentation on the reproductive success of grassland birds (e.g., Johnson & Temple 1990; Winter & Faaborg 1999) have focused on small geographic areas (single states and six or fewer counties) and have typically relied on relatively small samples of nests (generally <60 nests/species). Thus, it is unknown how accurately these previous studies reflect predation rates across a broader array of landscapes or whether these results can be applied broadly across the species' range.

Another potential problem associated with fragmented landscapes is increased rates of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*). Brown-headed Cowbirds lay their eggs in the nests of other species, which then raise cowbirds at the expense of their own young (Hill 1976; Elliot 1978; Zimmerman 1983; Davis & Sealy 2000). Fragmentation significantly increases rates of brood parasitism in forested areas of North America (e.g., Robinson et al. 1995), but the effects of fragmentation on brood parasitism rates in fragmented grasslands have not been studied extensively (but see Johnson & Temple 1990; Davis & Sealy 2000). We tested the hypothesis that nest-predation and brood-parasitism rates of four species of grassland songbirds are related to the area of prairie fragments within the midcontinental United States.

Methods

Grassland birds in the midcontinental United States occur in a variety of grassland types, including prairies, hayland, pasture, Conservation Reserve Program fields, and wildlife areas (Herkert et al. 1996). However, because (1) we were interested in examining a wide range of patch sizes, (2) we wanted to control for possible variation due to differences in grassland types, and (3) most grassland types in the midcontinental United States occur predominantly in small patches, we limited our analysis to native prairies in the region.

We measured rates of nest predation and brood parasitism in 39 prairie fragments ranging from 24 to >40,000 ha in size in five states: Illinois, Kansas, Missouri, North Dakota, and Oklahoma. The study involved the cooperative efforts of six teams of researchers, who collectively found and monitored nearly 3000 nests of four species of grassland birds, the Grasshopper Sparrow (*Ammodramus savannarum*, 573 nests), Henslow's Sparrow *(Ammodramus henslowii*, 82 nests), Eastern Meadowlark (*Sturnella magna*, 719 nests), and Dickcissel (*Spiza americana*, 1605 nests) within 16 counties between 1991 and 1998. Prairies were studied in Carroll, Grundy, Jo Daviess, Lee, and Whiteside counties in Illinois; Coffey, Geary, Greenwood, Lyon, and Riley counties in Kansas; Barton, Dade, and Vernon counties in Missouri; Stutsman County in North Dakota; and Osage and Washington counties in Oklahoma. Ranges of fragment sizes by state were as follows: Illinois, 24–2430 ha; Kansas, 10–6200 ha; Missouri, 31–1084 ha; North Dakota, 98–737 ha; and Oklahoma 591–40,500 ha. Within each study area, we monitored bird nests every 2–5 days in order to calculate daily rates of nest predation and brood parasitism. We used the Mayfield (1975) method of estimating daily nest-predation rates, which divides the total number of nest depredations by the total number of days in which nests were active and monitored (exposure days). Overall, we accumulated 33,992 exposure days for the four study species combined. We estimated rates of brood parasitism by dividing the total number of nests that contained at least one Brown-headed Cowbird egg or nestling by the total number of active nests for each species.

We used fragment size as the basis of our analyses. We defined fragment size as the total area of prairie that was contiguous with the study fragment. Four-lane and two-lane roads with manipulated or disturbed (e.g., mowed) roadsides were considered barriers and were used to define the edge of study fragments. Internal or two-lane roads without a disturbed roadside were not considered barriers and did not delineate the edge of a fragment. Wooded strips at least 50 m wide and that extended across at least 75% of any particular study fragment were also considered barriers, and such areas were considered two separate fragments. Wooded strips that were <50 m wide or extended across <75% of the study area were not considered barriers or edges and therefore did not delineate the edge of the fragment.

We also evaluated the potential influence of fragment isolation on nest-predation rates. Fragments were not considered isolated if the study area was contiguous with other nonprairie grasslands (e.g., Conservation Reserve Program field). In such cases, fragment size was just the size of the prairie. Fields adjacent to other grasslands (either prairie or other types of grasslands) but across one of our barriers (described above) were also not considered isolated. Adjacent areas had to be at least half as big as the study fragment for the fragment not to be designated as isolated. We evaluated the potential influence of fragment isolation on nest-predation rates by comparing nest-predation rates for isolated and nonisolated fragments separately within each size class and for each species separately. Each individual comparison of nest-predation rates was performed with the program CONTRAST (Sauer & Hines 1989). Species-level significance was then assessed by with a combined probability test (Sokal & Rohlf 1995) of the three separate size-class comparisons for each species. None of the species-level comparisons was significant (Dickcissel, $p > 0.10$; Eastern Meadowlark, $p > 0.86$; Grasshopper Sparrow, $p > 0.81$; Henslow's Sparrow, $p > 0.37$). Because our initial comparisons of nest-predation rates in isolated versus nonisolated fragments revealed that isolation did not significantly influence predation rates within fragments for any of the four species, fragment isolation was not included in the final analyses.

Because a majority of the fragments studied had fewer than five nests per species per year, and because estimates of nest-predation rates based on such small samples of nests typically have large variances associated with them (J. H., unpublished data), we pooled nest data from all years of study to come up with a single estimate of nest-predation and brood-parasitism rates for each species within each prairie fragment. This initial pooling still resulted in over 50% of all fragments studied having fewer than five nests per species per prairie fragment, so we further pooled data from individual fragments into three size classes for analyses. Size classes were nests in prairie fragments that were <100, 100–1000, and >1000 ha in size. We compared daily nest-predation rates among size classes for each species separately with the analytical program CONTRAST (Sauer & Hines 1989). Brood-parasitism rates were compared among size classes with chi-square contingency tests. We tested the hypothesis that nest-predation rates are related to fragment area for all species by combining the probabilities from the species-specific analyses (Sokal & Rohlf 1995).

Because our initial analyses showed that nest-parasitism rates were only weakly associated with fragment size (see results) and previous studies have shown that nest-parasitism rates can be influenced by regional cowbird abundance (e.g., Hoover & Brittingham 1993; Basili 1997; Smith & Myers-Smith 1998), we also examined the relationship between regional cowbird abundance and regional frequency of brood parasitism. We used states (U.S.) and provinces (Canada) as our regions in this analysis. We used data from the Breeding Bird Survey (BBS; Sauer et al. 1999) to estimate regional cowbird abundance. We obtained state-level data on nest parasitism by combining our data by states. To strengthen our analysis, we supplemented our data with nest-parasitism rates reported in the literature for additional states not included in our study. Additional sources of data on brood parasitism included George (1952), Hergenrader (1962), Wray et al. (1982), Peck and James (1987), Terrill (1961), Frawley (1989), Johnson and Temple (1990), Steigman (1990), Basili (1997), and Davis and Sealy (2000). We then compared regional rates of brood parasitism with regional cowbird abundance (mean number of cowbirds detected per BBS route per region) with Person's correlation (Sokal & Rohlf 1995), weighted by the square root of the number of nests involved in the parasitism rate estimate. Due to the small number of states for which we had or could find nesting data for Henslow's Sparrows, we were unable to include this species in the regional parasitism analysis.

Results

For all four species, daily nest-predation rates declined with increasing fragment area (Fig. 1). Differences in predation rates among size classes were highly signifi-

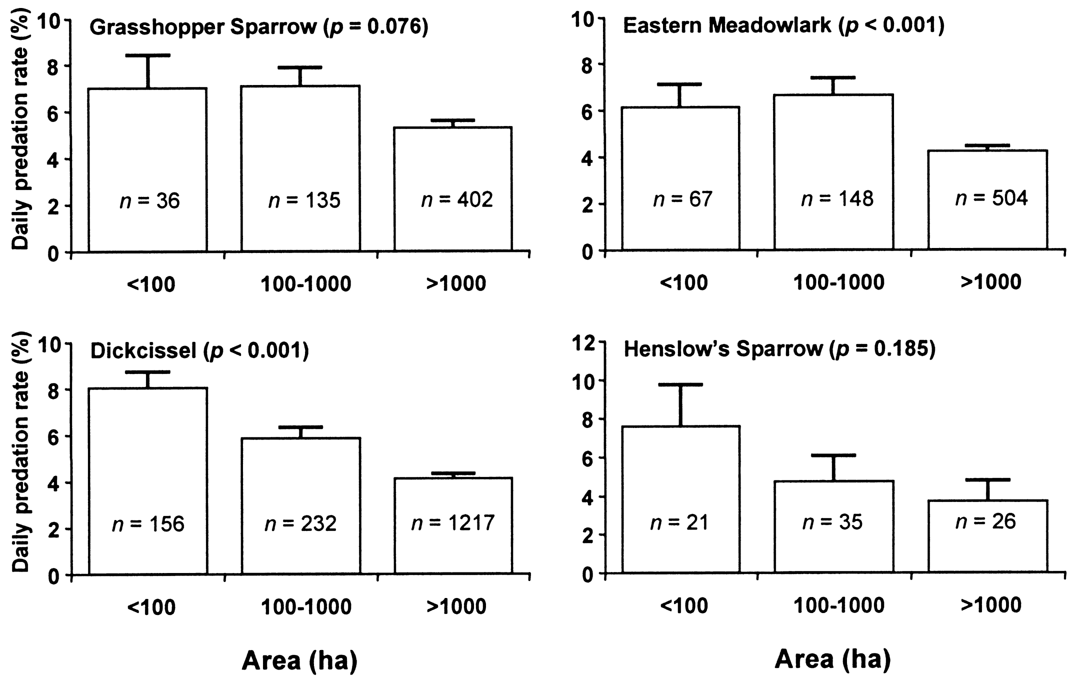

Figure 1. Daily predation rates for grassland birds in fragments of various sizes. Bars represent SE. The p *values from the comparison of nest-predation rates among size classes are also shown for each species. Sample sizes of nests are within bars.*

cant for Dickcissels and Eastern Meadowlarks (χ^2 = 33.88, df = 2, $p < 0.001$, and χ^2 = 15.07, df = 2, $p <$ 0.001, respectively) and marginally significant (χ^2 = 5.15, df = 2, p = 0.076) for Grasshopper Sparrows (Fig. 1). The combined probabilities test (Sokal & Rohlf 1995: 794) indicated that, overall, nest-predation rates were significantly negatively related to fragment area (χ^2 = 45.96, df = 8, $p < 0.001$). Species-level estimates of overall nest-predation rates ranged from 78–84% of all nests failing as a result of predation on small (<100 ha) prairies to 54–68% total predation losses on large (>1000 ha) prairies. Nest-predation rates declined consistently with increasing prairie size for Dickcissels and Henslow's Sparrows (Fig. 1). Reduced predation rates for Grasshopper Sparrows and Eastern Meadowlarks, however, were most evident in prairies larger than 1000 ha (Fig. 1). The pattern of reduced nest-predation rates in large prairies was also consistent across all study regions, with daily rates of nest predation being lowest in prairies larger than 1000 ha in all states and for all species (Table 1).

The relationship between brood-parasitism rates and fragment area in our data was more variable. Overall brood-parasitism rates for Eastern Meadowlarks increased significantly with decreasing prairie size (χ^2 = 9.70, df = 2, p = 0.008). With 19.4% of meadowlark nests being parasitized on small fragments (<100 ha), 12.8% parasitized on mid-sized fragments (100–1,000 ha), and 8.1% on large fragments. Overall brood-parasitism rates for Dickcissels, Grasshopper Sparrows, and Henslow's Sparrows, however, were not significantly related to fragment size ($p >$ 0.10 for all three species). Furthermore, in contrast to the daily nest-predation rates, the relationship between brood-parasitism rates and fragment size was not consistent among states, even for the Eastern Meadowlark (Table 1). Brood-parasitism rates for Eastern Meadowlarks were highest on small prairies in Illinois, but also highest on large prairies in Kansas and Missouri (Table 1). Parasitism rates of the Grasshopper Sparrow were also variable and were highest on large prairies in Kansas and Illinois (Table 1). Dickcissel parasitism rates tended to be highest in mid-sized fragments in most areas (Table 1).

Our analysis of geographical patterns of rates of brood parasitism showed that these rates were associated more consistently with regional cowbird abundance than fragment size, with brood-parasitism rates being higher in areas with higher regional abundances of Brown-headed Cowbirds (Fig. 2). Rates of brood parasitism on Dickcissels and Grasshopper Sparrows were significantly (r = 0.906, n = 8, p = 0.002, and r = 0.671, n = 12, p = 0.02, respectively) higher in regions with high regional cowbird abundance, whereas rates of parasitism on Eastern Meadowlarks were marginally (r = 0.729, n = 6, p = 0.09) related to regional cowbird abundance. The combined probabilities test of these data revealed that, overall, rates of brood parasitism for these three species were significantly higher (χ^2 = 24.87, df = 6, $p < 0.001$) in areas with higher regional abundances of cowbirds.

Table 1. Comparison of daily nest-predation and brood-parasitism rates in small (<100 ha), medium (100–1000 ha), and large (>1000 ha) prairie fragments in five states in the midcontinental United States.*

		Prairie fragment size class (ha)		
Species	*State*	*<100 (%)*	*100–1000 (%)*	*>1000 (%)*
Daily nest-predation rate				
Dickcissel	IL	7.23 (3)	7.19 (71)	6.97 (25)
	KS	11.00 (48)	5.80 (20)	2.58 (229)
	MO	7.03 (105)	4.81 (64)	3.72 (45)
	OK	—	5.62 (77)	4.68 (918)
Eastern Meadowlark	IL	5.61 (15)	12.97 (22)	2.22 (13)
	KS	5.77 (33)	5.88 (23)	3.41 (36)
	MO	7.20 (19)	4.98 (25)	3.17 (2)
	OK	—	6.35 (78)	4.64 (453)
Grasshopper Sparrow	IL	7.63 (10)	7.15 (61)	6.08 (169)
	KS	7.02 (13)	10.09 (20)	4.16 (28)
	MO	7.35 (8)	8.26 (12)	3.45 (3)
	OK	—	5.51 (37)	5.03 (202)
	ND	6.02 (5)	10.13 (5)	—
Henslow's Sparrow	MO	7.59 (21)	4.77 (34)	2.47 (4)
	OK	—	—	3.89 (22)
Brood-parasitism rate				
Dickcissel	IL	0.00 (3)	29.58 (71)	20.00 (25)
	KS	45.83 (48)	50.00 (20)	78.17 (229)
	MO	10.48 (105)	12.50 (64)	0.00 (45)
	OK	—	35.06 (77)	16.34 (918)
Eastern Meadowlark	IL	6.67 (15)	4.55 (22)	0.00 (13)
	KS	33.33 (33)	30.43 (23)	52.78 (36)
	MO	5.26 (19)	8.00 (25)	50.00 (2)
	OK	—	11.54 (78)	4.64 (453)
Grasshopper Sparrow	IL	0.00 (10)	4.92 (61)	5.92 (169)
	KS	30.77 (13)	20.00 (20)	57.14 (28)
	MO	0.00 (8)	0.00 (12)	0.00 (3)
	OK	—	8.11 (37)	5.45 (202)
	ND	60.00 (5)	20.00 (5)	—
Henslow's Sparrow	MO	9.52 (21)	2.94 (34)	0.00 (4)
	OK	—	—	9.09 (22)

**Number of nests are shown in parentheses. Abbreviations: IL, Illinois; KS, Kansas; MO, Missouri; ND, North Dakota; OK, Oklahoma.*

Discussion

Predators on grassland bird nests vary and include mice, snakes, ground squirrels, weasels, badgers, foxes, coyotes, skunks, raccoons, deer, crows, and hawks. Some of these nest predators can be more common near edges in some landscapes (e.g., Dijak & Thompson 2000; Winter et al. 2000), but several nest predators such as mice and snakes are not known to be influenced by fragmentation at the scales we considered. Our results indicate that, despite the fact that nest-predator assemblages may have varied among study regions, the pattern of reduced nest-predation rates on large prairies was consistent throughout the study region. The fact that predation rates were most consistently lower on prairies larger than 1000 ha also suggests that edge effects (e.g., Johnson & Temple 1990; Patton 1994; Winter et al. 2000) likely had little influence on the pattern of higher nest success on large prairies. Because edge effects in grassland birds appear to be most pronounced in areas <50 m from an edge (Johnson & Temple 1990; Winter et al. 2000), these effects should have been most evident in prairies of <100 ha, the prairies with the highest ratios of edge to interior habitat. This was not the case for at least two of the four species we studied (Fig. 1).

The reason for higher nest success on larger prairie areas is not known. It is possible that landscape effects, such as the amount of grassland habitat in the surrounding landscape (i.e., McKee et al. 1998; Bakker 2000; Niemuth 2000), may have influenced the predation rates we observed and that our largest prairies were generally located in landscapes that had higher proportions of grass in the surrounding landscape matrix and thus were more favorable for successful nesting by grassland birds. This should have been especially true for prairies over 1000 ha, the size class in which nest-predation rates were most consistently the lowest (Table 1; Fig. 1). Presently, no regional grassland land-coverage data are available,

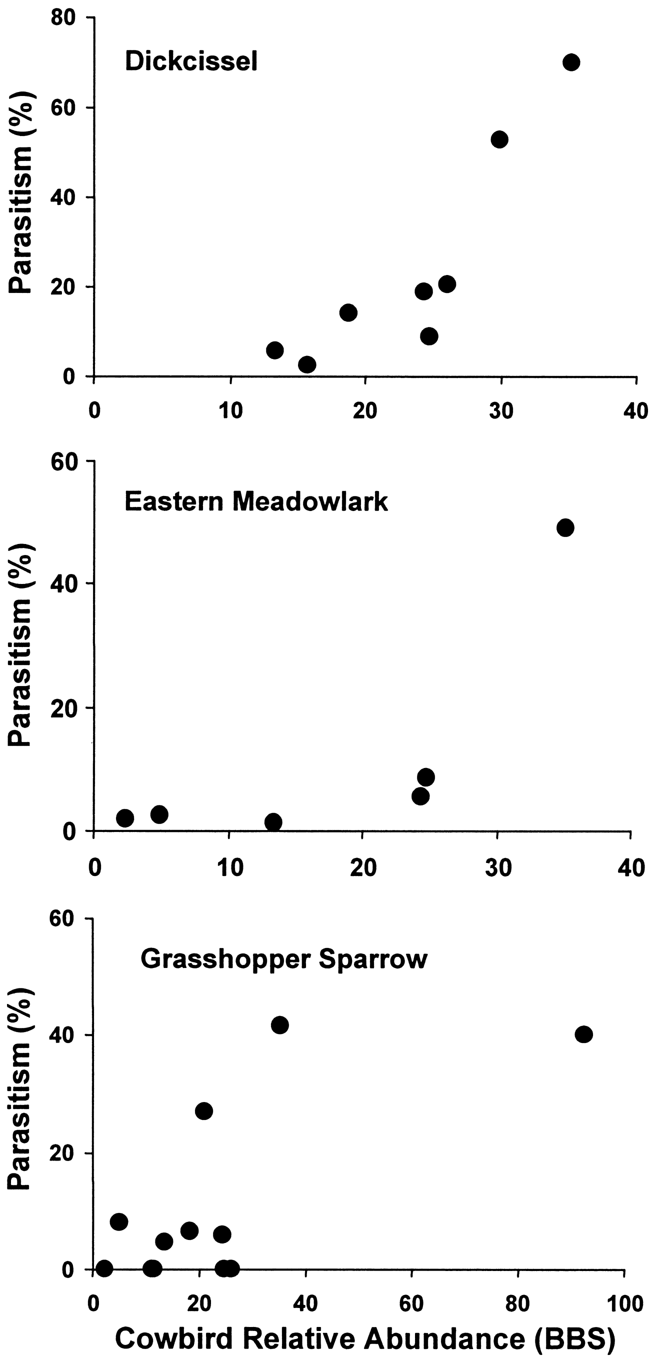

Figure 2. Frequency of brood parasitism of grassland bird nests in relation to the mean relative abundance of Brown-headed Cowbirds detected on Breeding Bird Survey routes within the same state. Cowbird relative abundance data were obtained from Sauer et al. (1999). Data on rate of brood parasitism are from this study, supplemented with additional data from the literature.

however, so we were unable to evaluate this aspect with our data.

Overall, brood-parasitism rates for only one species, Eastern Meadowlark, increased significantly with decreasing prairie size. This pattern was, however, not consistent among states (Table 1). Brood-parasitism rates for Eastern Meadowlarks were lowest in large prairies in Illinois and Oklahoma but highest in large prairies in Kansas and Missouri (Table 1). Thus, even for Eastern Meadowlarks, patterns of brood parasitism rates varied among regions. The other three species (Dickcissel, Henslow's Sparrow, Grasshopper Sparrow) did not show a consistent, or overall significant, relationship between fragment size and nest-parasitism rates (Table 1). This is in contrast to the pattern reported in forested landscapes, where rates of brood parasitism on forest-nesting bird species are significantly and consistently higher in more fragmented landscapes (e.g., Robinson et al. 1995).

Rates of brood parasitism on grassland birds, however, were significantly related to regional cowbird abundance. This result is in agreement with Hoover and Brittingham's (1993) study of Wood Thrushes (*Hylocichla mustelina*) and Smith and Myers-Smith's (1998) study of Song Sparrows (*Melospiza melodia*), in which brood-parasitism rates are highest in areas of high regional cowbird abundance. Both Hoover and Brittingham (1993) and Smith and Myers-Smith (1998) also found that brood-parasitism rates are more strongly associated with regional cowbird abundance than general measures of landscape composition. Thus, studies of birds in three essentially nonoverlapping habitats, hardwood forests (Wood Thrush), prairies (Grasshopper Sparrow, Dickcissel, Eastern Meadowlark), and shrublands and forest-edge (Song Sparrow), have all shown regional cowbird abundance to be a stronger influence on brood-parasitism rates than fragmentation or landscape effects. Our data lend further support to Smith and Myers-Smith's (1998) suggestion that common variables drive regional patterns in the frequency of brood parasitism and that these factors appear to be largely independent of the host's habitat and the local landscape configuration of the host's habitat.

Because of small sample sizes within particular fragments, we pooled our data among years and by size classes for analysis. Thus, although greater nest success on large prairies was a consistent trend throughout the study, 1000 ha should not be viewed as the minimum size required for high nesting success. Our analyses based on size class did not allow us to determine the specific size range at which the nest success of grassland birds was consistently the highest. The pooling of data also precluded us from determining the extent to which nest-success rates within fragments may vary between years. Additional work is needed to determine whether 1000 ha is the most appropriate cutoff for areas with generally high and low nesting success (or if it is a continuous function) and to determine the extent to which the nest success of grassland birds varies among years. Until more-detailed data become available, however, our data support the general conservation approach that bigger is better with respect to grassland-bird nest success within prairie fragments and that prairies 1000 ha or greater in size tend to support the most productive populations of grassland birds.

Our results show that fragmentation significantly and consistently affected rates of nest predation within prairie fragments but did not consistently influence rates of brood parasitism. Thus, the fragmentation of grassland habitats, especially native prairie, could be contributing to regional declines of grassland birds as a result of increased nest-predation rates on small fragments. Additional data are needed, however, to determine whether this pattern holds for non-native grasslands as well. Non-native grasslands are generally more common than native grasslands in many portions of the midwestern and eastern United States (e.g., Askins 1993; Herkert et al. 1996) and thus are important bird habitat. Conservation of grassland birds may depend on the identification, protection, and—in some areas—restoration of large grassland tracts that will provide areas where the nest success of grassland birds is sufficient to maintain populations. Continued loss and fragmentation of grassland habitats may further diminish already significantly reduced populations of grassland birds.

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