

AREA SENSITIVITY IN GRASSLAND PASSERINES: EFFECTS OF PATCH SIZE, PATCH SHAPE, AND VEGETATION STRUCTURE ON BIRD ABUNDANCE AND OCCURRENCE IN SOUTHERN SASKATCHEWAN

STEPHEN K. DAVIS¹

Biology Department, University of Regina, Regina, Saskatchewan S4S 0A2, Canada; and
Saskatchewan Watershed Authority, 101-2022 Cornwall Street, Regina, Saskatchewan S4P 2K5, Canada

ABSTRACT.—Information on area sensitivity and effects of habitat fragmentation has come largely from forest and tallgrass-prairie habitats. Research from other ecosystems is required to determine whether the fragmentation paradigm derived from those studies is applicable to passerine communities elsewhere. I examined the effects of habitat fragmentation on abundance and occurrence of nine species of mixed-grass prairie passerines in southern Saskatchewan. I conducted 190 point-counts in 1996 and 1997 on 89 pastures ranging in size from 8 to 6,475 ha. Sprague's Pipit (*Anthus spragueii*), Baird's Sparrow (*Ammodramus bairdii*), Grasshopper Sparrow (*A. savannarum*), and Chestnut-collared Longspur (*Calcarius ornatus*) were found to be area-sensitive, in that they were more abundant or occurred more frequently, or both, in larger patches of mixed-grass prairie. However, the ratio of edge to interior habitat was a better predictor of area sensitivity than patch size in most cases. Horned Lark (*Eremophila alpestris*), Savannah Sparrow (*Passerculus sandwichensis*), Clay-colored Sparrow (*Spizella pallida*), Western Meadowlark (*Sturnella neglecta*), and Brown-headed Cowbird (*Molothrus ater*) were insensitive to patch size, though occurrence of Clay-colored Sparrow and Western Meadowlark tended to be greater in smaller pastures. Vegetation structure was also found to be an important predictor of grassland songbird abundance and occurrence, in that it explained additional variation not accounted for by patch size or the ratio of edge to interior habitat. Although protection of large contiguous tracts of habitat is essential to conservation of native species, small native-prairie patches with minimal edge habitat also play a vital role in conservation of grassland birds. Received 8 July 2003, accepted 24 June 2004.

RESUMEN.—La información acumulada sobre la sensibilidad al área y los efectos de la fragmentación del hábitat se ha basado principalmente en estudios desarrollados en ambientes de bosques y pradera de pastos altos. Se requiere investigación en otros ecosistemas para determinar si los paradigmas que han surgido a partir de aquellos estudios son aplicables a comunidades de aves paserinas en otros ecosistemas. En este estudio examiné los efectos de la fragmentación de hábitat sobre la abundancia y la presencia de nueve especies de aves paserinas de praderas de hierbas mixtas en el sur de Saskatchewan. Realicé 190 puntos de conteo en 1996 y 1997 en 89 praderas que variaron en tamaño desde 8 a 6,475 ha. Las especies *Anthus spragueii*, *Ammodramus bairdii*, *A. savannarum* y *Calcarius ornatus* fueron sensibles al tamaño de los fragmentos, de modo que fueron más abundantes y se presentaron con mayor frecuencia en parches de praderas mixtas de mayor tamaño. Sin embargo, en la mayoría de los casos, el cociente entre el hábitat de borde y el hábitat de interior predijo de mejor manera la sensibilidad al área, que el tamaño de los parches. Las especies *Eremophila alpestris*, *Passerculus sandwichensis*, *Spizella pallida*, *Sturnella neglecta* y *Molothrus ater* no fueron sensibles al tamaño de los fragmentos, aunque la ocurrencia de *S. pallida* y *S. neglecta* tendió a ser mayor en los pastizales de menor tamaño. La estructura de la vegetación también predijo la abundancia y la presencia de las aves paserinas de pastizal, explicando variación adicional no explicada por el tamaño de los fragmentos ni por el cociente entre hábitat de borde y de interior. A pesar de que fragmentos de gran extensión de hábitat son esenciales para la conservación de especies nativas, fragmentos de pastizales nativos pequeños que presenten un mínimo de hábitat de borde también pueden tener un papel importante para la conservación de aves de pastizal.

¹Present address: Canadian Wildlife Service, 300-2365 Albert Street, Regina, Saskatchewan S4P 4K1, Canada.
E-mail: stephen.davis@ec.gc.ca

THE GREAT PLAINS comprised nearly 162 million ha of native prairie before Europeans arrived in North America. Subsequent settlement and agricultural policies resulted in losses of 30–99.9% of native prairie on the continent (Samson and Knopf 1994). In Saskatchewan, only 20% of the original native prairie remains, mostly in the southwestern portion of the province (Hammermeister et al. 2001). In some areas of the province, where soils and landscapes are particularly suited for crop production, <0.1% of the original prairie vegetation remains (Riemer et al. 1997). Throughout the Great Plains, extant native prairie continues to be threatened by cultivation, invasion of exotic plant species and woody vegetation, improper grazing management, and urban development (Samson and Knopf 1994, Riemer et al. 1997). The loss and degradation of native prairie is believed to have caused grassland birds to undergo widespread declines (Peterjohn and Sauer 1999).

Aside from habitat loss, the reduction in average habitat-patch size that results from fragmentation may limit bird populations. Some remnants of habitat may be too small to accommodate species' territory requirements, and several studies have found that many forest (Robbins et al. 1989, Hobson and Bayne 2000) and grassland birds (reviewed by Johnson 2001) require parcels of habitat much larger than their territory size on which to settle and reproduce. Such species are referred to as "area-sensitive," because their densities decline as patch size gets smaller, and they are rare or absent in small habitat-patches.

Although potential mechanisms underlying area sensitivity have not been the focus of most fragmentation studies, reduced reproductive success in small patches, attributable in part to edge effects, is often advanced as a likely candidate. Grassland birds may avoid edge habitat because increased density and activity of nest predators and Brown-headed Cowbirds (*Molothrus ater*) cause reproductive success to be lower near edges (Gates and Gysel 1978, Johnson and Temple 1990, Winter et al. 2000). Alternatively, edge avoidance may be attributable to changes in vegetation structure near edges, such as increased density of woody vegetation and exotic species (Wilson and Belcher 1989, Davis and Duncan 1999, Ribic and Sample 2001). Such changes in vegetation may be incompatible with the species' habitat requirements

(e.g. inappropriate nesting or foraging habitat) or associated with changes in microclimate resulting in lower prey-densities (Burke and Nol 1998, Zanette et al. 2000). Subsequently, males establishing territories near edges may be unable to attract mates (Burke and Nol 1998).

Information on area sensitivity and effects of habitat fragmentation on grassland birds has come largely from studies conducted in tallgrass-prairie habitats, where edge habitat is often composed of woody vegetation (Johnson and Temple 1990, Winter and Faaborg 1999). However, edge habitat in mixed-grass prairie is composed mostly of nonwoody vegetation (predominantly near agricultural fields and along roads) that is structurally more similar to interior habitat. If patch-size effects are influenced by edge-related phenomena that are more pronounced near wooded edges than near agricultural edges (Pasitschniak-Arts and Messier 1995, Winter et al. 2000), fragmentation effects observed in tallgrass prairie might be fundamentally different from those found in mixed-grass prairie. Recently, however, Johnson and Igl (2001) examined area sensitivity of mixed-grass prairie birds in Conservation Reserve Program (CRP) fields that were typically surrounded by nonwoody vegetation. Those authors found that several species were area-sensitive, though in most species the affinity for larger grassland patches varied regionally. My study complements Johnson and Igl's (2001) research in CRP fields, because I quantify area sensitivity in native-prairie patches over a relatively large geographic area (180 km east and west and 137 km north and south) near Johnson and Igl's (2001) most northerly sites. Hence, comparisons of area sensitivity of grassland birds in CRP and mixed-grass prairie can be drawn for the same species to determine whether effects of habitat fragmentation on grassland-bird abundance and occurrence are consistent across time and space, thus giving "confidence in the findings and their generality" (Johnson 2002). Furthermore, I provide new information on area sensitivity for species of conservation concern that were uncommon or absent in Johnson and Igl's study (e.g. Baird's Sparrow [*Ammodramus bairdii*] and Sprague's Pipit [*Anthus spragueii*]).

METHODS

Study area and sites.—The study was concentrated in the southeastern portion of the Moist Mixed

Grassland ecoregion and along the boundary of the Mixed Grassland and Aspen Parkland ecoregions of southern Saskatchewan (49°48'N, 104°10'W; see Davis 2003 for detailed description). Native pastures were characterized by *Stipa* spp., June grass (*Koeleria cristata*), northern wheatgrass (*Elymus lanceolatus*), western wheatgrass (*Pascopyrum smithii*), blue grama grass (*Bouteloua gracilis*), *Carex* spp., club moss (*Selaginella densa*), pasture sage (*Artemisia frigida*), and other forbs. The most common shrubs were western snowberry (*Symphoricarpos occidentalis*), rose (*Rosa* spp.), and wolf willow (*Eleagnus commutata*).

I selected potential native-pasture sites from the Saskatchewan Wetland Conservation Corporation's (SWCC; now Saskatchewan Watershed Authority) native prairie inventory (Riemer et al. 1997) and from 1:20,000 aerial photographs of rural municipalities immediately adjacent to those included in the SWCC inventory. I considered sites for inclusion in the study only if they were native pastures in fair-to-good range condition (Abouguendia 1990) and under light-to-moderate grazing intensity. I rejected narrow riparian strips and native prairie sites that were heavily encroached by woody vegetation to reduce potential confounding effects of vegetation on pasture size and to maintain a consistent bird community among sites. Although I attempted to sample sites randomly from the overall pool of pastures identified from the SWCC database and from aerial photographs, many sites identified from aerial photos did not meet the criteria for inclusion (see above), or landowners did not grant access to their pastures. Pastures not surveyed in 1996 were surveyed in 1997, along with new sites located from aerial photos and those discovered while ground-truthing potential sites prior to the field season.

Bird surveys.—Three trained observers quantified relative abundance of singing males, using 100-m fixed-radius point-counts (Hutto et al. 1986) of 5-min duration. Surveys commenced 15 min before sunrise and ended no later than 0900 hours CST. The same observers conducted surveys twice at each site between 23 May and 7 July in 1996 and 1997, on days with no precipitation and winds <20 km h⁻¹. Where possible, observers located point-counts near the center of smaller pastures (<65 ha), with the perimeter of each circle situated ≥50 m from fencelines and wetlands. On larger pastures, where more than one point-count was conducted, perimeters of neighboring circles were typically situated ≥400 m apart. Number of point counts was approximately proportional to the size of the pasture and ranged from 1 to 19 per pasture.

Vegetation sampling.—Observers located sampling points by pacing a random distance (1–100 m) from the center of the 100-m-radius circle in each of the four cardinal directions. Observers quantified vegetation at each sampling point by passing a 0.6-cm metal rod vertically through the vegetation and recorded the number of contacts by vegetative types (standing

dead vegetation and live grass, forbs, and shrubs) in successive 10-cm height intervals (Rotenberry and Wiens 1980). Observers measured litter depth by inserting a 30-cm rule into the litter (unconsolidated plant material not anchored to the ground) until contacting the ground below and measured vegetation height as the highest point where vegetation contacted the rod. Observers estimated shrub distance from center of the point-count to the nearest shrub in each quadrant. Measurements from the four sampling points were averaged for each point-count prior to use in analyses.

Patch-size delineation.—Observers ground-truthed each patch and made corrections on 1:20,000 aerial photos in the field. I later transferred all corrections onto classified Landsat thematic mapper imagery using ARCVIEW geographic information system (GIS) software, version 3.2 (ESRI, Redlands, California). I defined habitat patches as areas of contiguous native prairie and considered cropland, seeded pasture and hayland, wooded riparian areas, and roads with ditches as delineating native-prairie patches. Each observer estimated distance to habitat edge (defined as the point where land-use changed) from center of the circle, and I later checked those estimates, along with patch size (hectares) and perimeter (kilometers), using the GIS.

Data analysis.—I used SAS statistical software (SAS Institute 1999) for all analyses. I evaluated the relationship between relative abundance (maximum of the two counts) and occurrence of singing males in 100-m point counts to patch size and vegetation characteristics using Poisson (PROC GENMOD) and logistic (PROC LOGISTIC) regression techniques, respectively, for each common species (occurring in >15% of point-counts) recorded in the study. I used statistical methods developed by Johnson and Igl (2001) to determine whether species occurrence varied as a function of patch size; their methodology accounts for potential lack of independence among point-counts in pastures with multiple samples. As Johnson and Igl (2001) indicated, treating point-counts as independent sampling units would be considered pseudoreplication (Hurlbert 1984) if counts were more similar within fields than among fields; therefore, they calculated a weighting scheme that reduces the effective sample size within species according to the dependence of plots within pastures for a given species. The weighting scheme involved calculating correlation coefficients (r) for point-counts within patches, using generalized estimating equations (GEEs; PROC GENMOD) for each species. Values of r were used to calculate weights (w) for logistic regression analyses by means of the formula

$$w = 1 - r(n - 1) / n$$

where n is number of point-counts within a patch.

Thus, observations that are not correlated ($r = 0$) receive full weight; whereas perfectly correlated observations ($r = 1$) are weighted by $1/n$, which is equivalent to having only one observation for the patch (Johnson and Igl 2001). Because the present study was conducted over two breeding seasons, I determined whether the relationships between occurrence and patch size were consistent over the two years by conducting weighted logistic-regression analyses using occurrence as the response variable and patch size, year, and patch size $\times$ year interaction as predictor variables. No significant patch size $\times$ year interactions were detected for the occurrence of eight species ($P > 0.14$), so I pooled data for the two years. However, the relationship between patch size and Savannah Sparrow (*Passerculus sandwichensis*) occurrence appeared to be influenced by year ($\chi^2 = 3.33$, $df = 1$, $P = 0.069$); thus, in that case, I analyzed years separately. To quantify minimum size requirements for each species, I used weighted logistic-regression models to derive incidence curves with 95% confidence intervals by plotting predicted probability of a species occurrence over the range of pasture sizes examined in the study. I considered the minimum size requirement to be the patch size at which the species reached 50% of its predicted maximum occurrence (Robbins et al. 1989, Vickery et al. 1994, Helzer and Jelinski 1999).

For the next set of analyses, I included vegetation variables in abundance and occurrence models to determine whether their inclusion explained additional variation not accounted for by patch size. Point-counts were treated as a repeated measure within pastures, and I modeled the relationship between songbird abundance and patch-level features using Poisson regressions and GEEs with an exchangeable correlation structure (PROC GENMOD). I used a Poisson distribution for abundance models, because it characterizes count data (Stokes et al. 2000). However, there was not a sufficient number of non-zero observations of Grasshopper Sparrows (*A. savannarum*) and Brown-headed Cowbirds, so I modeled species occurrence using a binomial distribution and logit link function (PROC GENMOD). Covariates of interest for all analyses included vegetation height (centimeters); litter depth (millimeters); distance to nearest shrub (meters); density of live grass, standing dead vegetation, forbs, and shrubs (number of contacts); bare ground (yes or no); distance to nearest edge (meters); patch size (hectares); and ratio of edge to interior habitat (hereafter "edge:area"; calculated by dividing perimeter length [kilometers] by area [hectares]). I included area $\times$ shrub distance, edge distance $\times$ shrub distance, and edge:area $\times$ shrub distance interaction terms because some grassland birds may be less (or more) likely to occur on small patches that have a high density of shrubs within, or around the perimeter of the patch (Johnson 2001). Shrub distance, edge distance, and patch size were log

transformed, and edge:area was arcsine transformed. I combined decimeter height intervals three and four for live grass and standing dead vegetation because of the low number of contacts and high correlation ($r > 0.7$) among height intervals and combined all decimeter intervals for shrubs and forbs for the same reasons. Thus, a total of 12 vegetation variables were considered in my analyses.

I first analyzed each variable one at a time for each species to determine whether responses to vegetation and patch-level metrics were consistent across years. Although relationships with patch size were consistent across years (except for Savannah Sparrow), responses to vegetation variables were inconsistent; therefore, I analyzed years separately for each species, except Grasshopper Sparrow and Brown-headed Cowbird, because of low sample-sizes for those two species.

I employed a backward-elimination procedure to sequentially remove variables with the largest P -value based on likelihood-ratio tests (TYPE3 option) and used Akaike's Information Criterion, corrected for overdispersion and small sample sizes (QAIC_c; Burnham and Anderson 1998) to identify the most parsimonious model(s). Main effect variables included in any interaction term were not removed during the backward-elimination procedure unless the interaction term had already been eliminated. I calculated a variance inflation factor by dividing the deviance value by the deviance degrees of freedom from the full model and used that as a correction factor to determine QAIC_c scores. I considered models within two QAIC_c units ($\Delta\text{QAIC}_c < 2$) of the best model as competing models (Burnham and Anderson 1998; Appendix). QAIC_c weights were calculated according to Burnham and Anderson's (1998) procedure and represent the likelihood that that particular model is the best model for the data. Because edge:area was strongly correlated with patch size in 1996 ($r = -0.83$) and 1997 ($r = -0.91$), I identified the best models by first including patch size in the models and then comparing QAIC_c scores of those models with scores from the same models using the edge:area in place of patch size.

RESULTS

Bird surveys.—A total of 190 point-counts (97 in 1996 and 93 in 1997) were conducted on 89 different pastures: 52 in 1996 and 37 in 1997, ranging in size from 8 to 1,650 ha (median = 63.2) and 14 to 6,475 ha (median = 82.6), respectively. Thirty species were recorded inside point-count circles, and 91 species were recorded on the pastures overall. The following analyses are restricted to the nine species that were recorded on >15% of the pastures: Horned Lark (*Eremophila alpestris*), Sprague's

Pipit, Savannah Sparrow, Clay-colored Sparrow (*Spizella pallida*), Baird's Sparrow, Grasshopper Sparrow, Chestnut-collared Longspur (*Calcarius ornatus*), Western Meadowlark (*Sturnella neglecta*), and Brown-headed Cowbird (Table 1). Baird's Sparrow was the most frequently encountered and abundant species recorded within point-counts; Western Meadowlarks were recorded on the most pastures (Table 1).

Area sensitivity and vegetation structure.— Occurrence of five species was significantly related to patch size (Table 2). Sprague's Pipits, Baird's Sparrows, Grasshopper Sparrows, and Chestnut-collared Longspurs were found to be area-sensitive, in that their probability of occurrence increased with patch size. Sprague's Pipits did not occur on pastures of <29 ha, and Grasshopper Sparrows did not occur on pastures of <15 ha. Clay-colored Sparrows, Baird's Sparrows, Western Meadowlarks, and Brown-headed Cowbirds were not recorded on the smallest pasture (8 ha). Minimum size requirements were greater for Grasshopper Sparrows and Sprague's Pipits (134 and 145 ha, respectively) than for Baird's Sparrows and Chestnut-collared Longspurs (25 and 39 ha, respectively) (Fig. 1). However, Grasshopper Sparrows and Sprague's Pipits also occurred least frequently and had greater variation in size requirements than the other species (Tables 1 and 2). Occurrence of Savannah Sparrows was inversely related to patch size in 1996, and Western Meadowlarks and Clay-colored Sparrows tended to occur more often on smaller patches, but the relationships were not statistically significant (Table 2).

Poisson-regression models including patch and vegetation parameters support the above results, in that patch size was included in the best model for Sprague's Pipits, Baird's Sparrows, and Chestnut-collared Longspurs in each year. However, comparison of models with patch size and edge:area revealed that the latter variable was a better predictor of abundance in nearly every case (Table 3 and Appendix). Abundance of those three species declined with increasing proportion of edge to interior habitat. Edge:area was also included in the best model for Horned Larks and Clay-colored Sparrows in 1997 and Brown-headed Cowbirds for the two years combined. Horned Lark abundance increased as the edge:area ratio and the distance to nearest shrubs decreased.

TABLE 1. Summary of occurrence and abundance of the most common grassland songbirds recorded in southern Saskatchewan, 1996 and 1997.

Species	Pastures recorded (%)			Point-counts recorded (%)			Mean ($\pm$ SE) singing males per point-count		
	1996	1997	Overall	1996	1997	Overall	1996	1997	Overall
	(n = 52)	(n = 37)	(n = 89)	(n = 97)	(n = 93)	(n = 190)			
Horned Lark	63	43	55	48	31	40	0.48 $\pm$ 0.05	0.31 $\pm$ 0.05	0.40 $\pm$ 0.04
Sprague's Pipit	42	54	47	34	52	43	0.34 $\pm$ 0.05	0.52 $\pm$ 0.05	0.43 $\pm$ 0.03
Clay-colored Sparrow	81	40	64	72	31	52	0.72 $\pm$ 0.05	0.31 $\pm$ 0.05	0.52 $\pm$ 0.04
Savannah Sparrow	58	59	58	41	49	45	0.41 $\pm$ 0.05	0.49 $\pm$ 0.05	0.45 $\pm$ 0.04
Baird's Sparrow	54	65	58	61	71	66	0.61 $\pm$ 0.05	0.71 $\pm$ 0.05	0.66 $\pm$ 0.03
Grasshopper Sparrow	25	49	35	21	39	23	0.21 $\pm$ 0.04	0.39 $\pm$ 0.05	0.29 $\pm$ 0.03
Chestnut-collared Longspur	42	76	56	53	74	63	0.53 $\pm$ 0.05	0.74 $\pm$ 0.05	0.63 $\pm$ 0.03
Western Meadowlark	71	73	72	60	54	57	0.60 $\pm$ 0.05	0.54 $\pm$ 0.05	0.57 $\pm$ 0.04
Brown-headed Cowbird	31	32	31	21	25	29	0.21 $\pm$ 0.04	0.25 $\pm$ 0.04	0.23 $\pm$ 0.03

TABLE 2. Results of weighted logistic-regression analyses modeling occurrence of grassland songbirds as a function of patch size. Minimum size requirements (ha; 50% of maximum predicted probability) are provided for area-sensitive species.

Species	Intercept	Parameter (estimate $\pm$ SE)	Wald chi-square statistic	Minimum size (95% CI)
Horned Lark	-0.667	0.048 $\pm$ 0.083	0.33, $P = 0.56$	—
Sprague's Pipit	-2.627	0.421 $\pm$ 0.093	20.40, $P < 0.0001$	145 (69–314)
Clay-colored Sparrow	0.950	-0.158 $\pm$ 0.105	2.27, $P = 0.13$	—
Savannah Sparrow (1996)	1.556	-0.409 $\pm$ 0.191	4.57, $P = 0.032$	—
Savannah Sparrow (1997)	-0.199	0.029 $\pm$ 0.124	0.05, $P = 0.82$	—
Baird's Sparrow	-1.575	0.421 $\pm$ 0.110	14.64, $P = 0.0001$	25 (14–33)
Grasshopper Sparrow	-2.483	0.285 $\pm$ 0.097	8.57, $P = 0.003$	134 (23–544)
Chestnut-collared Longspur	-1.859	0.441 $\pm$ 0.132	11.16, $P = 0.0008$	39 (18–56)
Western Meadowlark	1.009	-0.134 $\pm$ 0.083	2.58, $P = 0.11$	—
Brown-headed Cowbird	-1.297	0.019 $\pm$ 0.112	0.03, $P = 0.86$	—

Clay-colored Sparrows and Brown-headed Cowbirds were more abundant in irregular-shaped patches with greater density of shrubs (Table 3). Western Meadowlark abundance in 1996 and the occurrence of Grasshopper Sparrows were both positively associated with patch size, but those relationships interacted with shrub distance. Grasshopper Sparrow occurrence and Western Meadowlark abundance were greater on larger pastures with a lower density of shrubs (Table 3).

Distance to edge of patch also influenced abundance of Horned Larks and Savannah Sparrows, but the relationships were opposite in the two years (Table 3). The relationship between edge distance and Clay-colored Sparrow abundance and Brown-headed Cowbird occurrence depended on the density of shrubs (Table 3). Clay-colored Sparrow abundance increased with shrub density and distance to edge, and occurrence of Brown-headed Cowbirds was greater farther from the habitat edge but in pastures with more dispersed shrubs (i.e. greater distance to shrubs; Table 3).

Vegetation structure was not strongly correlated with patch size (Table 4) and explained additional variation not accounted for by patch size, edge:area, or distance to the habitat edge (Table 3). Horned Lark abundance was greater in pastures with short vegetation, as indicated by their positive association with density of live grass (1 dm; Table 3). Similarly, Chestnut-collared Longspur abundance increased in pastures with lower densities of standing dead vegetation and tall grass. However, the relationship between Chestnut-collared Longspur abundance and vegetation height was not consistent between

years (Table 3). Sprague's Pipit abundance decreased with increasing density of forbs, and Baird's Sparrows were more abundant in pastures with fewer shrubs but greater density of taller vegetation (Table 3). Similarly, Western Meadowlarks were more abundant in pastures with greater density of tall dead vegetation (Table 3). Savannah Sparrow abundance was influenced primarily by vegetation structure, but no consistent trends emerged; their abundance appeared to be negatively influenced by density of grass near the ground and >30 cm from the ground (i.e. live grass1 and live grass3–4) in 1996, but was positively associated with taller grass in 1997 (Table 3). Occurrence of Grasshopper Sparrows appeared to be influenced mostly by vegetation of intermediate height and density, in that they were negatively associated with density of tall live and dead grass, and grass close to the ground (Table 3). Occurrence of Brown-headed Cowbirds was influenced by amount of residual vegetation, being positively associated with density of standing dead vegetation within 10 cm of the ground and negatively associated with density of standing dead vegetation at greater heights (Table 3).

DISCUSSION

Area sensitivity.—My results show that prairie fragment size influences occurrence of some mixed-grass prairie passerines but not others. Sprague's Pipits, Baird's Sparrows, Grasshopper Sparrows, and Chestnut-collared Longspurs were found to be area-sensitive, in that they were more likely to occur on larger pastures. Horned Larks, Clay-colored

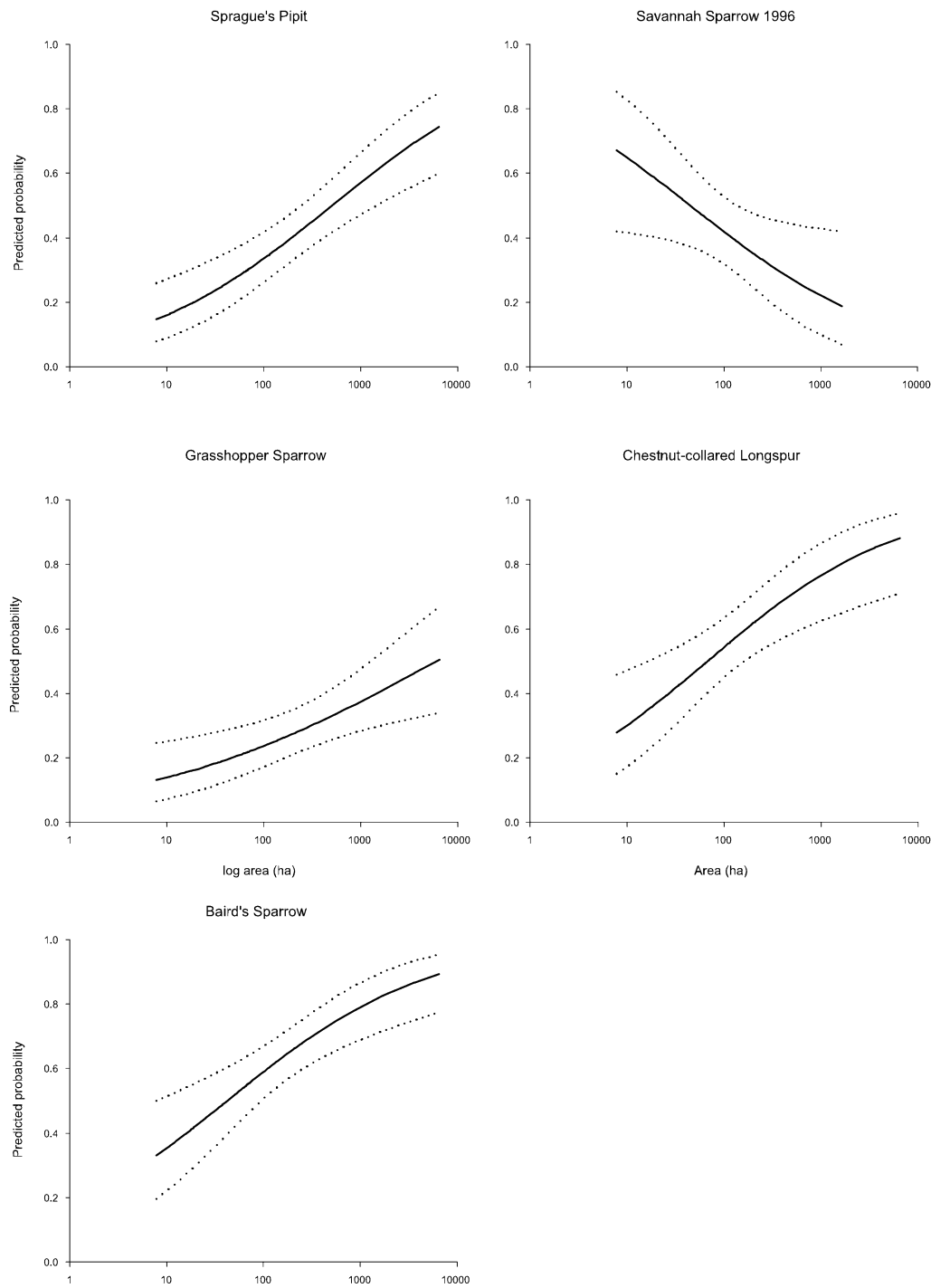


FIG. 1. Incidence curves for grassland songbirds exhibiting a significant relationship between occurrence and patch size, 1996 and 1997. Solid line represents the predicted probability of occurrence at a particular patch size, and dotted lines represent 95% confidence intervals. Years are combined for all species except Savannah Sparrow, for which patch size interacted with year and was significant only for 1996.

TABLE 3. The most parsimonious models (lowest QAIC_c value) quantifying relationships between grassland songbird abundance and occurrence, patch size and shape, edge distance, and vegetation structure, 1996 and 1997. Model parameters in the global model include patch size; edge-to-area ratio; distance to edge; density of standing dead vegetation; density of live grass, forbs, and shrubs; bare ground; vegetation height; litter depth; distance to nearest shrub; and interaction terms (patch size $\times$ shrub distance, edge distance $\times$ shrub distance, and edge:area $\times$ shrub distance). Numbers associated with vegetation parameters indicate decimeter intervals where vegetation contacted the sampling pole (e.g. live grass3–4 = density of live grass within the third and fourth decimeter). Parameters are given in order of importance. Competing models (Δ QAIC_c < 2) and the best patch-size model for those species models where edge:area ratio was a better predictor are found in the Appendix.

Year	Model parameters	QAIC _c	Δ QAIC _c	W_i^a
Horned Lark				
1996	Live grass1(+), live grass2(–), standing dead2(–), edge distance(+)	97.0	0.00	0.22
1997	Edge:area(–), standing dead1(–), shrub distance(–), edge:area $\times$ shrub distance(+), live grass1(+)	99.9	0.00	0.24
Sprague's Pipit				
1996	Edge:area(–), forbs(–), bare ground(+)	101.4	0.0	0.24
1997	Patch size(+), forbs(–), shrub distance(+)	88.0	0.0	0.35
Clay-colored Sparrow				
1996	Shrub distance(–), live grass2(+)	92.7	0.0	0.38
1997	Shrub distance(–), edge distance(+), edge $\times$ shrub distance(–), edge:area(+)	97.9	0.00	0.34
Savannah Sparrow				
1996	Live grass1(–), bare ground(–), live grass3–4(–), edge distance(–)	95.1	0.00	0.48
1997	Live grass3–4(+), standing dead2(–)	98.3	0.0	0.22
Baird's Sparrow				
1996	Edge:area(–), live grass(–)	103.1	0.0	0.25
1997	Edge:area(–), shrubs(–)	87.8	0.0	0.43
Grasshopper Sparrow				
Both years	Patch size(+), live grass3–4(–), shrub distance(+), patch size $\times$ shrub distance(–)	189.9	0.0	0.31
Chestnut-collared Longspur				
1996	Standing dead1(–), shrubs(–), vegetation height(+), standing dead3–4(–), edge:area(–)	103.6	0.0	0.25
1997	Vegetation height(–), edge:area(–)	89.8	0.0	0.45
Western Meadowlark				
1996	Shrub distance(+), patch size(+), patch size $\times$ shrub distance(–), bare ground(+), standing dead3–4(+)	100.2	0.0	0.38
1997	Standing dead2(–), standing dead3–4(+), shrub distance(–)	86.9	0.0	0.32
Brown-headed Cowbird				
Both years	Edge distance(+), shrub distance(+), edge distance $\times$ shrub distance(–), standing dead1(+), standing dead2(–), edge:area(+), edge:area $\times$ shrub distance(+), litter depth(+)	202.4	0.0	0.36

^a W_i = QAIC weights.

Sparrows, Savannah Sparrows, Brown-headed Cowbirds, and Western Meadowlarks appeared to be area-insensitive, in that their occurrence was independent of pasture size. Furthermore, Western Meadowlarks and Clay-colored Sparrows showed signs of inverse area-sensitivity (Donovan and Lamberson 2001), in that their occurrence tended to decline with pasture size.

Several studies have examined area sensitivity in Grasshopper Sparrows, but only

one study has examined area sensitivity in Baird's Sparrows, and no such study has considered Sprague's Pipits or Chestnut-collared Longspurs. Thus, few comparisons between studies can be made for the latter species. Johnson (2001) summarized and critiqued studies that examined area sensitivity in grassland birds. He reviewed six studies that quantified area sensitivity in Grasshopper Sparrows, all of which showed the species to be area-sensitive.

TABLE 4. Vegetation variables in native mixed-grass are not strongly correlated (Pearson's *r*) with patch size (log), 1996 and 1997.

Vegetation structure	1996			1997		
	Mean ± SD	Range	<i>r</i>	Mean ± SD	Range	<i>r</i>
Vegetation height (cm)	12.4 ± 4.9	3.7–30.0	0.03	18.5 ± 11.2	1.7–45.8	0.31
Litter depth (mm)	4.8 ± 4.7	0.0–40.0	–0.02	5.2 ± 6.9	0.0–43.8	–0.17
Standing dead vegetation 1 dm (number of contacts)	3.6 ± 2.8	0.0–14.8	0.05	3.7 ± 2.2	0.2–12.5	0.37
Standing dead vegetation 2 dm (number of contacts)	0.6 ± 0.9	0.0–4.7	–0.06	0.7 ± 0.9	0.0–4.5	0.07
Standing dead vegetation 3–4 dm (number of contacts)	0.1 ± 0.4	0.0–2.2	–0.08	0.1 ± 0.2	0.0–1.0	0.09
Live grass 1 dm (number of contacts)	2.1 ± 1.0	0.0–5.0	0.10	1.0 ± 0.6	0.0–2.5	0.05
Live grass 2 dm (number of contacts)	0.7 ± 0.6	0.0–2.8	0.06	0.3 ± 0.4	0.0–2.2	–0.14
Live grass 3–4 dm (number of contacts)	0.1 ± 0.3	0.0–1.7	0.05	0.03 ± 0.1	0.0–0.7	–0.03
Forbs (number of contacts)	0.5 ± 0.5	0.0–2.3	–0.03	0.2 ± 0.2	0.0–1.2	0.15
Shrubs (number of contacts)	0.1 ± 0.2	0.0–1.3	–0.10	0.1 ± 0.3	0.0–1.9	–0.23
Shrub distance (m)	16.0 ± 18.1	0.0–100	–0.24	12.9 ± 12.4	0.0–66.5	–0.02
Bare ground (number of contacts)	0.2 ± 0.3	0.0–1.1	0.01	0.3 ± 0.3	0.0–1.1	0.17

However, Johnson (2001) concluded that the results of three of the studies were somewhat questionable, because of methodological or analytical problems (see also Horn et al. 2000). One of the studies (Johnson and Igl 2001) found that the Grasshopper Sparrow's preference for larger grassland patches varied regionally.

Minimum size requirement of Grasshopper Sparrows in the present study was 134 ha, but the confidence interval ranged between 23 and 544 ha. Vickery et al. (1994) determined the minimum size requirement for Grasshopper Sparrows in Maine to be 100 ha, whereas much smaller size requirements were found in Illinois (10–30 ha; Herkert 1994) and Nebraska (8–12 ha; Helzer and Jelinski 1999). Those results are likely a function of regional abundance of Grasshopper Sparrows, which were uncommon in my Saskatchewan study area and in Maine (relatively large size requirements) and common in Illinois and Nebraska (relatively small size requirements). Thus, the area sensitivity exhibited by Grasshopper Sparrows in my study may be a local phenomenon and not be evident in other regions where differences in landscape composition or regional abundance exist. If area-sensitive species were distributed in an "ideal free" manner (Fretwell and Lucas 1970), then individuals of those species would be expected to exhibit large size requirements if regional

abundance were low because of the availability of suitable habitat. However, if suitable habitat were saturated when abundance was high, then apparent size requirements would be low or not detectable. That other studies using different techniques have found Grasshopper Sparrows to be area-sensitive in various parts of their range (Johnson 2001, Perkins et al. 2003) suggests that Grasshopper Sparrows are indeed area-sensitive, though the actual size requirements of the species are uncertain.

My finding that Baird's Sparrow occurrence increases with patch size is consistent with the work of Johnson and Igl (2001), who found that the species was area-sensitive in two of three counties analyzed. In addition, McMaster and Davis (2001) found that occurrence of Baird's Sparrow was positively associated with size of fields enrolled in Canada's Permanent Cover Program.

Although no studies have examined area sensitivity in Sprague's Pipits or Chestnut-collared Longspurs, Davis (2003) found that Sprague's Pipit density consistently increased with pasture size in each year of the study, whereas density of Chestnut-collared Longspurs was positively associated with patch size in two of the four years. Further support for Sprague's Pipits' affinity for large patches of native grassland comes from Breeding Bird Survey (BBS) data. Regional trend estimates indicate

that Sprague's Pipit populations are declining at the periphery of their range but are stable to increasing in southwestern Saskatchewan, southeastern Alberta, and northern Montana (Sauer et al. 2002)—areas where large tracts of contiguous grassland still exist. In addition, Davis et al. (unpubl. data) found that the amount of grassland within an 800-m-radius circle was the strongest predictor of Sprague's Pipit occurrence in southern Saskatchewan. Although I found direct support for area sensitivity in Sprague's Pipits, the specific patch-size requirements of the species is uncertain for the same reasons indicated in the case of Grasshopper Sparrows.

Horned Larks and Brown-headed Cowbirds were not strongly influenced by patch size in the present study. Only one other study (Skagen et al. unpubl. data) has examined area sensitivity in Horned Larks. Although Brown-headed Cowbirds have been shown to be more abundant in fragmented forests of the eastern and midwestern U.S. (Faaborg et al. 1995), only Johnson and Igl (2001) have examined area sensitivity of those birds in grasslands. Skagen et al. (unpubl. data) had results consistent with mine: they found that Horned Lark density was unrelated to patch size in shortgrass-prairie pastures (range = 7–505 ha) in northeastern Colorado. In contrast to the work of Johnson and Igl (2001), who found that Brown-headed Cowbirds were more common in small CRP fields, my results suggest that cowbird occurrence is not influenced by patch size. Such contrasting results are likely a function of differences in land use between study areas, given that regional abundance is likely comparable (Sauer et al. 2002). Cattle and shrubs were consistent components of the native pastures examined in the present study, whereas Johnson and Igl (2001) conducted their study on ungrazed CRP fields where potential perch sites were restricted to field edges. Thus, cowbird abundance may have been lower in large CRP fields, because cowbirds likely concentrated their activities near edge habitat rather than in the interior of large fields. In contrast, shrub distances were not strongly correlated with patch size in the present study. Hence, availability of perches in different-sized patches may have made pastures equally attractive to cowbirds.

Savannah Sparrow, Clay-colored Sparrow, and Western Meadowlark abundances were

independent of patch size, though those species tended to occur more often in smaller pastures. These results are generally consistent with those of Johnson and Igl (2001), except that they found Clay-colored Sparrow occurrence and abundance to be higher in larger patches. As with Johnson and Temple's (1986) findings, the apparent inverse area-sensitivity exhibited by this species here may be a function of the proportion of the patch covered by shrubs. The attractiveness of shrubs, particularly western snowberry, to Clay-colored Sparrows is well documented (Knapton 1978, Arnold and Higgins 1986). As Johnson and Igl (2001) suggested, Clay-colored Sparrows may be attracted to small pastures if shrub invasion occurs along the periphery of the patch, such that smaller pastures have a disproportionately greater coverage of shrubs and subsequently more attractive habitat than large pastures. The weak correlation between shrub distance and patch size does not appear to support that hypothesis, but shrub effects cannot be discounted (see below).

Influence of patch-level characteristics and vegetation structure.—Poisson regression models incorporating patch-level characteristics and vegetative features revealed several trends: (1) patch size was included in the best model for species identified as area-sensitive (see above) and indicated that abundance increased with pasture size in both years; (2) edge:area was typically a better predictor of abundance of area-sensitive species than patch size; (3) neither patch size nor edge:area was included in the best models for species identified as area-insensitive (see above) in at least one of the two years; (4) vegetation structure explained additional variation in abundance not accounted for by patch-level effects; and (5) vegetative features that were important predictors of abundance in one year were not always important the next year, and in some cases a species' response to a variable in one year was the opposite of that found in the second year.

Although effects of patch size on grassland bird abundance and occurrence have received considerable attention in recent years (Herkert 1994, Vickery et al. 1994, Walk and Warner 1999, Johnson and Igl 2001), only Helzer and Jelinski (1999) have assessed the influence of patch shape (i.e. edge:area). Those authors found that edge:area was a better predictor of grassland bird occurrence than patch size—a result

consistent with the present study—though how they arrived at their conclusion is not clear, given the high correlation between patch size and edge:area ($r = -0.97$; Helzer and Jelinski 1999). In addition, those authors did not account for changes in vegetation structure associated with patch size or edge:area and suggested that this likely influenced their results for some area-sensitive species. Regardless, the results of the present study and of Helzer and Jelinski's (1999) are consistent with previous studies that have documented detrimental effects of edge habitat. Grassland species may be less abundant in patches with a greater amount of edge habitat because of low reproductive success attributable to increased predation and brood parasitism near habitat edges (but see Davis 2003), in particular wooded edges (Johnson and Temple 1990, Winter et al. 2000). Although agricultural edges may not have the same deleterious effects as wooded edges (Pasitschniak-Arts and Messier 1995, Winter et al. 2000, Davis 2003), roadside edges may be avoided by some mixed-grass prairie songbirds (Sutter et al. 2000).

As was stated above, vegetation structure influences the attractiveness of grassland patches to songbirds. In fact, observed patterns of area sensitivity may be influenced by vegetation structure if vegetation varies with patch size or shape. For example, if small pastures are heavily grazed, then species associated with relatively tall, dense vegetation (e.g. Baird's Sparrow) will likely appear to be area-sensitive, and species that are attracted to short, sparse vegetation (e.g. Horned Lark) will not. However, the patterns found here are likely not influenced by vegetation structure, given the criteria I used to select pastures and because no vegetation parameters were strongly correlated with patch size.

Conclusion.—The results of the present study underscore the need to conserve large tracts of mixed-grass prairie. In addition, the results have implications for setting conservation priorities regarding not only the size of grassland patches, but also their shape. Grassland patches that have a higher proportion of interior habitat relative to edge habitat are more attractive to area-sensitive species. Furthermore, Perkins et al. (2003) found that grasslands with a high interior core-to-edge ratio tended to act as source habitats, as compared with edge areas. Hence, restoration programs could play a role in enhancing the attractiveness and reproductive potential of irregular-shaped

grassland patches by focusing efforts on increasing patch size and minimizing the amount of edge habitat. Agricultural programs, such as CRP in the U.S. (Johnson and Schwartz 1993) and the Permanent Cover Program in Canada (McMaster and Davis 2001), could assist grassland conservation efforts in the same way. It should also be noted that several species were insensitive to patch size or shape. Thus, small patches of native prairie also play a role in conservation of grassland birds and should not be overlooked in the pursuit of conserving large tracts of native grassland, particularly given that nest success does not appear to be correlated with patch size in these species (Davis 2003).

Patch-level factors, such as size and shape, are not the only considerations for conservation of grassland birds and their habitat. My results show that vegetative features at the local scale also influence settling patterns of grassland birds. Physiognomic features, such as density of live and residual vegetation, vegetation height, and shrub density influence the attractiveness of grassland patches. Moreover, responses of grassland birds to vegetation structure may vary, depending on growing conditions in a particular year or site. For example, Chestnut-collared Longspur abundance was positively related to vegetation height in 1996, but inversely related in 1997 when vegetation was taller; Savannah Sparrows exhibited a similar response to the density tall live grass. In addition, factors influencing grassland birds at larger spatial scales, such as diversity of land-cover types (Ribic and Sample 2001), edge density (Fletcher and Koford 2002), and proportion of grassland in the landscape (Bakker et al. 2002, Davis et al. unpubl. data) may also be important considerations for conservation of grassland birds.

ACKNOWLEDGMENTS

I am grateful to C. Penner and R. Waple for their assistance in the field. I thank D. C. Duncan for helpful suggestions on the initial design of the study and D. H. Johnson and L. M. Armstrong for providing statistical advice. I benefited greatly from the GIS expertise of D. MacDonald and L. Strauss and from comments by R. M. Brigham, D. H. Johnson, P. Vickery, and an anonymous reviewer on an earlier draft of this manuscript. Financial support was provided in part by the Saskatchewan Wetland Conservation Corporation (now Saskatchewan Watershed Authority), National Fish and Wildlife Foundation, Canadian Wildlife

Service (CWS), Saskatchewan Environment (Fish and Wildlife Branch), and the Endangered Species Recovery Fund (World Wildlife Fund Canada, CWS, and government of Canada Millenium partnership fund). I thank the private landowners and staff of the Prairie Farm Rehabilitation Administration pastures for giving me access to their pastures and for being model stewards of our remaining native prairie.

LITERATURE CITED

- ABOUGUENDIA, Z. M. 1990. A practical guide to planning for management and improvement of Saskatchewan rangeland: Range plan development. Saskatchewan Research Council Report, no. E-2520-1-E-90.
- ARNOLD, T. W., AND K. F. HIGGINS. 1986. Effects of shrub coverages on birds of North Dakota mixed-grass prairies. *Canadian Field-Naturalist* 100:10-14.
- BAKKER, K. K., D. E. NAUGLE, AND K. F. HIGGINS. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. *Conservation Biology* 16:1638-1646.
- BURKE, D. M., AND E. NOL. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk* 115: 96-104.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. *Model Selection and Inference: A Practical Information-theoretic Approach*. Springer-Verlag, New York.
- DAVIS, S. K. 2003. Habitat selection and demography of mixed-grass prairie songbirds in a fragmented landscape. Ph.D. dissertation, University of Regina, Saskatchewan.
- DAVIS, S. K., AND D. C. DUNCAN. 1999. Grassland songbird occurrence in native and crested wheatgrass pastures of southern Saskatchewan. *Studies in Avian Biology* 19:211-218.
- DONOVAN, T. M., AND R. H. LAMBERSON. 2001. Area-sensitive distributions counteract negative effects of habitat fragmentation on breeding birds. *Ecology* 82:1170-1179.
- FAABORG, J., M. BRITTINGHAM, T. DONOVAN, AND J. BLAKE. 1995. Habitat fragmentation in the temperate zone. Pages 357-380 *in* *Ecology and Management of Neotropical Migratory Birds* (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.
- FLETCHER, R. J., JR., AND R. R. KOFORD. 2002. Habitat and landscape associations of breeding birds in native and restored grasslands. *Journal of Wildlife Management* 66:1011-1022.
- FRETWELL, S. D., AND H. L. LUCAS, JR. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16-36.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- HAMMERMEISTER, A., D. GAUTHIER, AND K. MCGOVERN. 2001. Saskatchewan's Native Prairie: Statistics of a Vanishing Ecosystem and Dwindling Resource. Native Plant Society of Saskatchewan, Saskatoon.
- HELZER, C. J., AND D. E. JELINSKI. 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecological Applications* 9:1448-1458.
- HERKERT, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications* 4:461-471.
- HOBSON, K. A., AND E. BAYNE. 2000. Effects of forest fragmentation by agriculture on avian communities in the southern boreal mixed woods of western Canada. *Wilson Bulletin* 112:373-387.
- HORN, D. J., R. J. FLETCHER, JR., AND R. R. KOFORD. 2000. Detecting area sensitivity: A comment on previous studies. *American Midland Naturalist* 144:28-35.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monograph* 54:187-211.
- HUTTO, R. L., S. M. PLETSCHE, AND P. HENDRICKS. 1986. A fixed-radius point count method for non-breeding and breeding season use. *Auk* 103:593-602.
- JOHNSON, D. H. 2001. Habitat fragmentation effects on birds in grasslands and wetlands: A critique of our knowledge. *Great Plains Research* 11: 211-231.
- JOHNSON, D. H. 2002. The importance of replication in wildlife research. *Journal of Wildlife Management* 66:919-932.
- JOHNSON, D. H., AND L. D. IGL. 2001. Area requirements of grassland birds: A regional perspective. *Auk* 118:24-34.
- JOHNSON, D. H., AND M. D. SCHWARTZ. 1993. The conservation reserve program: Habitat for grassland birds. *Great Plains Research* 3:273-295.
- JOHNSON, R. G., AND S. A. TEMPLE. 1986. Assessing habitat quality for birds nesting in fragmented tallgrass prairies. Pages 245-249 *in* *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates* (J. Verner, M. L. Morrison, and C. J. Ralph, Eds.). University of Wisconsin Press, Madison.
- JOHNSON, R. G., AND S. A. TEMPLE. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *Journal of Wildlife Management* 54: 106-111.
- KNAPTON, R. W. 1978. Breeding ecology of the Clay-colored Sparrow. *Living Bird* 17:137-157.
- MCMASTER, D. G., AND S. K. DAVIS. 2001. An evaluation of Canada's Permanent Cover

Program: Habitat for grassland birds? *Journal of Field Ornithology* 72:195–210.

PASITSCHNIAK-ARTS, M., AND F. MESSIER. 1995. Risk of predation on waterfowl nests in the Canadian prairies: Effects of habitat edges and agricultural practices. *Oikos* 73:347–355.

PERKINS, D. W., P. D. VICKERY, AND W. G. SHRIVER. 2003. Spatial dynamics of source–sink habitats: Effects on rare grassland birds. *Journal of Wildlife Management* 67:588–599.

PETERJOHN, B. G., AND J. R. SAUER. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey, 1966–1996. *Studies in Avian Biology* 19:27–44.

RIBIC, C. A., AND D. W. SAMPLE. 2001. Associations of grassland birds with landscape factors in southern Wisconsin. *American Midland Naturalist* 146:105–121.

RIEMER, G., T. HARRISON, L. HALL, AND N. LYNN. 1997. The native prairie stewardship program. Pages 111–116 *in* *Caring for the Home Place: Protected Areas and Landscape Ecology* (P. Jonker, J. Vandall, L. Baschak, and D. Gauthier, Eds.). University Extension Press, University of Saskatchewan, Saskatoon.

ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic States. *Wildlife Monographs*, no. 103.

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.

SAMSON, F. B., AND F. L. KNOPF. 1994. Prairie conservation in North America. *BioScience* 44:418–421.

SAS INSTITUTE. 1999. *SAS/STAT User’s Guide*, version 8. SAS Institute, Cary, North Carolina.

SAUER, J. R., J. E. HINES, AND J. FALLON. 2002. *The North American Breeding Bird Survey: Results and Analysis 1966–2001*, version 2002.1. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.

STOKES, M. E., C. S. DAVIS, AND G. G. KOCH. 2000. *Categorical Data Analysis Using the SAS System*, 2nd ed. SAS Institute, Cary, North Carolina.

SUTTER, G. C., S. K. DAVIS, AND D. C. DUNCAN. 2000. Grassland songbird abundance along roads and trails in southern Saskatchewan. *Journal of Field Ornithology* 71:110–116.

VICKERY, P. D., M. L. HUNTER, JR., AND S. M. MELVIN. 1994. Effects of habitat area on the distribution of grassland birds in Maine. *Conservation Biology* 8:1087–1097.

WALK, J. W., AND R. E. WARNER. 1999. Effects of habitat area on the occurrence of grassland birds in Illinois. *American Midland Naturalist* 141:339–344.

WILSON, S. D., AND J. W. BELCHER. 1989. Plant and bird communities of native prairie and introduced Eurasian vegetation in Manitoba, Canada. *Conservation Biology* 3:39–44.

WINTER, M., AND J. FAABORG. 1999. Patterns of area sensitivity in grassland-nesting birds. *Conservation Biology* 13:1424–1436.

WINTER, M., D. H. JOHNSON, AND J. FAABORG. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. *Condor* 102:256–266.

ZANETTE, L., P. DOYLE, AND S. M. TREMONT. 2000. Food shortage in small fragments: Evidence from an area-sensitive passerine. *Ecology* 81: 1654–1666.

Associate Editor: M. Brittingham

APPENDIX. Competing models and the best-size model quantifying relationships between grassland songbird abundance and occurrence, patch size and shape, edge distance, and vegetation structure, 1996 and 1997. Model parameters in the global model include patch size; edge-to-area ratio; distance to edge; density of standing dead vegetation; density of live grass, forbs, and shrubs; bare ground; vegetation height; litter depth; distance to nearest shrub; and interaction terms (patch size × shrub distance, edge distance × shrub distance, and edge:area × shrub distance). Numbers associated with vegetation parameters indicate decimeter intervals where vegetation contacted the sampling pole (e.g. live grass3–4 = density of live grass within the third and fourth decimeter). Parameters are given in order of importance.

Year	Model parameters	QAIC _c	ΔQAIC _c	W _i ^a
Horned Lark				
1996	Live grass1(+), live grass(–), standing dead2(–), edge distance(+)	97.0	0.00	0.22
	Live grass1(+), live grass2(–), standing dead2(–)	97.3	0.3	0.19
	Live grass1(+), live grass2(–), standing dead2(–), edge distance(+), bare ground(–)	97.6	0.6	0.17
	Live grass1(+)	98.1	1.1	0.13
	Live grass1(+), live grass2(–), standing dead2(–), edge distance(+), bare ground(–), litter depth(–)	98.2	1.2	0.12
	Live grass1(+), live grass2(–)	98.7	1.7	0.09

APPENDIX. Continued.

Year	Model parameters	QAIC _c	ΔQAIC	W _i ^a
1997	Edge:area(-), standing dead1(-), shrub distance(-), edge:area × shrub distance(+), live grass1(+)	99.9	0.00	—
	Edge:area(-), standing dead1(-), shrub distance(-), edge:area × shrub distance(+), live grass1(+), edge distance(-), edge × shrub distance(+)	100.6	0.7	0.17
	Edge:area(-), standing dead1(-), shrub distance(-), edge:area × shrub distance(+), live grass1(+), edge distance(-), edge distance × shrub distance(+), shrubs(-)	101.1	1.1	0.13
	Edge:area(-), standing dead1(-)	101.1	1.2	0.13
	Edge:area(-), standing dead1(-), shrub distance(-), edge:area × shrub distance(+)	101.3	1.4	0.12
1997	[Size model:] standing dead1(-), patch size(+), shrub distance(-), patch size × shrub distance(+), live grass1(+)	101.9	2.0	—
Sprague's Pipit				
1996	Edge:area(-), forbs(-), bare ground(+)	101.4	0.0	0.24
	Edge:area(-), forbs(-), bare ground(+), live grass2(-), vegetation height(+)	101.6	0.2	0.22
	Edge:area(-), forbs(-), bare ground (+), live grass2(-)	102.0	0.6	0.17
	Edge:area(-), forbs(-), bare ground (+), live grass2(-), vegetation height(+), shrub distance(-)	102.6	1.3	0.13
	Edge:area(-), forbs(-)	103.2	1.8	0.10
1996	[Size model:] patch size(+), bare ground(+), live grass2(-), vegetation height(+)	111.1	10.3	—
1997	Patch size(+), forbs(-), shrub distance(+)	88.0	0.0	0.35
	Patch size(+), forbs(-)	89.3	1.3	0.19
	Patch size(+)	89.3	1.3	0.18
	Patch size (+), forbs(-), shrub distance(+), standing dead3-4(-)	89.9	1.9	0.13
Clay-colored Sparrow				
1996	Shrub distance(-), live grass2(+)	92.7	0.0	0.38
	Shrub distance(-)	93.1	0.4	0.32
	Shrub distance(-), live grass2(+), litter depth(-)	94.4	1.7	0.16
1997	Shrub distance(-), edge distance(+), edge distance × shrub distance(-), edge:area(+)	97.9	0.00	0.34
	Shrub distance(-), edge distance(+), edge distance × shrub distance(-), edge:area(+), live grass3-4(+)	98.1	0.2	0.31
	Shrub distance(-), edge distance(+), edge distance × shrub distance(-), edge:area(+), live grass3-4(+), forbs(-)	99.9	2.0	0.12
1997	[Size model:] shrub distance(-), edge distance(+), edge distance × shrub distance(+), live grass3-4(+), forbs(-), patch size(-)	103.5	5.6	—
Savannah Sparrow				
1996	Live grass1(-), bare ground(-), live grass3-4(-), edge distance(-)	95.1	0.00	0.48
	Live grass1(-), bare ground(-), live grass3-4(-), edge distance(-), forbs(-)	96.6	1.6	0.22
1997	Live grass3-4(+), standing dead2(-)	98.3	0.0	0.22
	Live grass3-4(+), standing dead2(-), standing dead1(+), shrub distance(+), edge distance(+), edge distance × shrub distance(-)	98.9	0.6	0.16
	Live grass3-4(+), standing dead2(-), standing dead1(+)	99.0	0.7	0.15
	Live grass3-4(+), standing dead2(-), standing dead1(+), shrub distance(+), edge distance(+)	99.4	1.1	0.13
	Live grass3-4(+)	99.8	1.5	0.10
	Live grass3-4(+), standing dead2(-), standing dead1(+), shrub distance(+), edge distance(+), edge distance × shrub(-), distance(-), patch size(+)	100.3	2.0	0.08

APPENDIX. Continued.

Year	Model parameters	QAIC _c	ΔQAIC	W _i ^a
Baird's Sparrow				
1996	Edge:area(-), live grass1(-)	103.1	0.0	0.25
	Edge:area(-), live grass1(-), shrub distance(-), edge:area × shrub distance(+), forbs(+)	104.2	1.1	0.14
	Edge:area(-), live grass1(-), shrub distance(-), edge:area × shrub distance(+), forbs(+), live grass3-4(+)	104.4	1.3	0.13
	Edge:area(-), live grass1(-), shrub distance(-), edge:area × shrub distance(+)	104.5	1.4	0.13
	Edge:area(-), live grass1(-), shrub distance(-)	104.9	1.8	0.10
1996	[Size model:] patch size(+), live grass1(-)	110.7	7.6	—
1997	Edge:area(-), shrubs(-)	87.8	0.0	0.43
	Edge:area(-), shrubs(-), shrub distance(-)	88.3	0.5	0.33
1997	[Size model:] patch size(+), shrubs(-), forbs(+), shrub distance(-)	88.2	0.4	—
Grasshopper Sparrow				
Both	Patch size(+), live grass3-4(-), shrub distance(+), patch size × shrub distance(-)	189.9	0.0	0.31
	Patch size(+), live grass3-4(-), shrub distance(+), patch size × shrub distance(-), standing dead3-4(-), litter depth(+)	191.5	1.6	0.14
	Patch size(+), live grass3-4(-), shrub distance(+)	191.5	1.6	0.14
	Patch size(+), live grass3-4(-), shrub distance(+), patch size × shrub distance(-), standing dead3-4(-)	191.5	1.6	0.14
	Patch size(+), live grass3-4(-), shrub distance(+), patch size × shrub distance(-), standing dead3-4(-), litter depth(+), live grass1(-)	191.6	1.7	0.13
Chestnut-collared Longspur				
1996	Standing dead1(-), shrubs(-), vegetation height(+), standing dead3-4(-), edge:area(-)	103.6	0.0	0.25
	Standing dead1(-), shrubs(-), vegetation height(+), standing dead3-4(-), edge:area(-), edge distance(-)	103.6	0.0	0.25
	Standing dead1(-), shrubs(-), vegetation height(+), standing dead3-4(-), edge:area(-), edge distance(-), live grass1(+)	103.9	0.3	0.22
1996	[Size model:] standing dead1(-), shrubs(-), vegetation height(+), standing dead3-4(-), patch size(+)	105.8	2.2	—
1997	Vegetation height(-), edge:area(-)	89.8	0.0	0.45
	Vegetation height(-), edge:area(-), live grass3-4(-)	91.6	1.8	0.18
1997	[Size model:] vegetation height(-), patch size(+)	91.8	2.0	—
Western Meadowlark				
1996	Shrub distance(+), patch size(+), patch size × shrub distance(-), bare ground(+), standing dead3-4(+)	100.2	0.0	0.38
	Shrub distance(+), patch size(+), patch size × shrub distance(-), bare ground(+), standing dead3-4(+), vegetation height(-)	101.2	1.0	0.24
1997	Standing dead2(-), standing dead3-4(+), shrub distance(-)	86.9	0.0	0.32
	Standing dead2(-)	87.7	0.8	0.22
	Standing dead2(-), standing dead3-4(+)	87.8	0.9	0.21
	Standing dead2(-), standing dead3-4(+), shrub distance(-), forb(-)	88.5	1.6	0.15
Brown-headed Cowbird				
Both	Edge distance(+), shrub distance(+), edge distance × shrub distance(-), standing dead1(+), standing dead2(-), edge:area(+), edge:area × shrub distance(+), litter depth(+)	202.4	0.0	0.36
	Edge distance(+), shrub distance(+), edge distance × shrub distance(-), standing dead1(+), standing dead2(-), edge:area(+), edge:area × shrub distance(+), litter depth(+), standing dead3-4(-)	202.4	0.0	0.36
	Edge distance(+), shrub distance(+), edge distance × shrub distance(-), standing dead1(+), standing dead2(-), edge:area(+), edge:area × shrub distance(+), litter depth(+), standing dead3-4(-), live grass1(+)	204.3	1.9	0.14

APPENDIX. Continued.

Year	Model parameters	QAIC _c	ΔQAIC	W _i ^a
	[Best size model:] edge distance(+), shrub distance(+), edge distance × shrub distance(-), standing dead1(+), standing dead2(-), patch size(-), patch size × shrub distance(+), standing dead3-4(-), live grass1(+), litter depth(+)	218.0	15.6	-

^a W_i = QAIC weights.