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Research Article

A multi-scaled analysis of avian response to habitat amount and fragmentation in the Canadian dry mixed-grass prairie

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Abstract

Previous research has suggested that ducks and songbirds may benefit from prairie landscapes that consist primarily of contiguous grasslands. However, the relative importance of landscape-level vs. local characteristics on mechanisms underlying observed patterns is unclear. We measured effects of grassland amount and fragmentation on upland and wetland songbird and duck density and nest success, and on some nest predators, across 16 landscapes in southern Alberta, Canada. We compared these landscape-level effects with local-scale responses, including distance to various edges and vegetation characteristics. We also evaluated several statistical approaches to comparing effects of habitat characteristics at multiple spatial scales. Few species were influenced by grassland amount or fragmentation. In contrast, distance to edge and local vegetation characteristics had significant effects on densities and nest success of many species. Previous studies that reported effects of landscape characteristics may have detected patterns driven by local mechanisms. As a corollary, results were very sensitive to statistical model structure; landscape level effects were much less apparent when local characteristics were included in the models.

Introduction

Conservation of the wetlands and uplands of the North American dry mixed-grass prairie region is critical. Temperate grasslands have undergone some of the highest rates of habitat conversion of any biome world-wide, while being afforded the least protection (Hoekstra et al. 2005). Over fifty percent of grassland bird species in midland North America declined dramatically between 1966 and 1993 (Herkert 1995); wetland-dependent birds are also at risk, due to climate change and development pressures (Gibbs 2000; Schindler 2001). Threats to these species include the loss and fragmentation of native grasslands, however, the mechanism influencing population declines is not known. Few studies have examined effects of grassland fragmentation on avian populations in mixed-grass prairie (Johnson and Igl 2001; Davis 2004) or on wetland species (Naugle et al. 2001). In particular, there is a need for more research on the concurrent effects of habitat fragmentation on nest success, predation rates, and predator distributions at multiple spatial scales (McGarigal and Cushman 2002; Stephens et al. 2003).

Both ducks and songbirds may be sensitive to grassland amount and fragmentation (Austin et al. 2001; Bakker et al. 2002; Phillips et al. 2003). Some non-game wetland species distributions may also vary with amount and arrangement of grassland habitat (Naugle et al. 2001; Fletcher and Koford 2002). However, there exists little information about effects of upland habitat context on wetland species (Naugle et al. 2001). Nest success, which influences population trends (Donovan and Thompson 2001; Hoekman et al. 2002), is reportedly higher for prairie songbirds in landscapes with greater amounts of grassland (Bergin et al. 2000) and in large patches of remnant prairie (Herkert et al. 2003). Grassland amount and fragmentation may, therefore, have significant conservation implications for upland and wetland prairie birds.

However, landscape-scale patterns may result from finer-scale mechanisms. Edge effects have been proposed as a mechanism to explain landscape-level patterns (e.g., Johnson and Igl 2001); however, their effect is local, as habitat edges only influence those individuals nearest to the habitat edge, rather than all individuals within a landscape. It is therefore necessary to conduct research at multiple spatial scales to infer mechanisms (Wiens 1989; Stephens et al. 2003). Furthermore, it is important that statistical models include both landscape and local variables, to distinguish whether landscape or local habitat structure influences landscape-level patterns in density or nest success.

Here, we use available data to address three objectives: (1) to measure effects of amount and fragmentation of grasslands on duck and songbird densities and nest success, (2) to compare the importance of landscape-scale effects with effects of neighbourhood (distance to edge) and local vegetation characteristics, and (3) to determine the extent to which statistical model structure influences the apparent importance of landscape-level variables. Like many landscape-scale analyses (e.g., Villard et al. 1999), the data analyzed in this study were collected primarily for other purposes: in this case, an evaluation of local habitat management strategies for ducks and songbirds. However, data such as these can contain a wealth of information relevant to landscape ecology (Holland et al. 2004), and are rich sources for exploratory analyses.

Methods

Landscapes

All study sites were located in southern Alberta, Canada (Latitude 50 32 03/Longitude 111 54 57), within native dry mixed-grass prairie fields that also contained managed wetlands. Upland vegetation was dominated by needle-and-thread (*Stipa comata*) and blue grama grass (*Bouteloua gracilis*), with some silver sagebrush (*Artemisia cana*). Emergent wetland vegetation was dominated by cattail (*Typha latifolia*), spikerush (*Eleocharis palustris*), and great bulrush (*Scirpus acutus*). Some fields were grazed by cattle, but as effects of grazing on these species were minimal (Koper 2004), and to minimize over-parameterization, this factor was not considered here. Surveys were conducted seasonally from 2000 to 2002.

Amount and fragmentation of grassland was estimated using a digital land-use map derived from Landsat TM images collected between 1993 and 1995 (Prairie Farm Rehabilitation Administration 2002), and ArcGIS 8.2. The data had a resolution of 30 m (but were digitally re-sampled to 25 m). There was little habitat conversion in this region between the time these data were collected and our bird surveys (M. Stromsmoe, pers. comm.). Grasslands at the landscape scale were defined as native or non-native permanent cover, and were distinguished from forage, which is used for hay or silage production (Prairie Farm Rehabilitation Administration 2002). Updated Road Network (URN) maps, accurate to within 10 m (confidence level 90%) were used to indicate locations of most roads (Centre for Topographic Information 2000). Some additional wetlands, and roads adjacent to canals, were added to the map manually. Distances of nests and point-count plots to roads, wetlands, and cropland/forage were measured using Hawth's Tools (Beyer 2003).

Preliminary analyses of point count data collected in 2000 indicated that densities of songbird, shorebird and raptor species were more strongly correlated with landscape characteristics measured at a 5-km radius (7854 ha), than characteristics measured at smaller landscape extents (Koper 2004). Therefore to select independent landscape sites for these analyses, we imposed 5 km-radii landscapes centred on each of 34 study sites located in dry mixed-grass prairie fields under management agreements with Ducks Unlimited Canada, ensuring consistency in habitat and management structure (Koper 2004). In two cases where fields were adjacent and small (<100 ha), we centred the landscapes over both fields. We then discarded sites that overlapped, resulting in 18 independent sites. Two sites had few (<2) upland point counts and few (<2) duck or songbird nests, yielding 16 landscapes for this study, consisting of 22–95% grassland (Table 1).

There were too few landscapes to generate fragmentation indices using GAMs (see below). We therefore randomly selected 82 additional, non-overlapping sites across a digital map of the dry mixed-grass prairie habitat of southern Alberta to generate regional distributions. We used the resultant 100 sites (82 + 18) for deriving GAM residuals and comparing fragmentation indices. Analyses of avian response were restricted to the original 16 sites.

The Modifiable Areal Unit Problem (MAUP), whereby landscape analyses are sensitive to extent and grain size, can cause spurious results in GIS-based landscape analyses. We avoided such problems by using the same extent and grain size for all sites, and by using the original, non-aggregated digital maps at the resolution the data were collected (Jelinski and Wu 1996). The mapping resolution was much finer than the patchiness within these sites, and the level of patchiness to which prairie birds are sensitive (Davis 2004), making them appropriate for our objectives (McGarigal et al. 2002). Habitat variables differed between scales, so differences between scales cannot be attributed to MAUP effects. We also used a combination of landscape metrics to describe the sites, minimizing problems unique to each index (Li and Wu 2004). Sites were categorized into habitat types that were relevant to both management and our study species (Davis et al. 1999).

Selecting landscape variables

Because we included only 16 sites in avian analyses, we restricted models to include only four landscape-scale variables. We note that while this results in a high variable to sample ratio (4:16), we used log-likelihood theory to select among competing models, rather than conventional hypothesis testing, which minimizes related concerns

Table 1. Landscapes used in avian landscape ecology study in southern Alberta, 2000–2002.

Site name	# Upland point count plots	# Wetland point count plots	Years surveyed	# Songbird nests	# Duck nests	Distance to closest landscape (km)[a]	Distance to farthest landscape (km)[a]
ACHDA 4	10	3	2000–2002	12	10	12.7	122.4
Bobby Hale	9	4	2000–2002	6	4	11.8	144.7
Contra Costa	20	3	2000–2002	8	0	15.2	77.1
Kinbrook	9	2	2001–2002	5	1	10.1	98.7
Kitsim Deferred	15	3	2001–2002	12	31	10.2	109.8
Lomond Canals	16	3	2000–2002	17	16	12.8	127.9
Lore Lake	4	2	2000–2002	10	6	11.8	135.6
Murray Lake	4	1	2001–2002	0	0	31.4	137
Newell Backflood	5	2	2000–2002	4	2	10.2	103.1
North Lake	14	3	2000–2001	8	9	12.8	116
Pheasant Hatchery	2	1	2000–2002	5	1	10.1	101.0
Reservoir H	9	4	2000–2002	9	2	22.0	98.8
Rolling Hills Spillway	6	3	2000–2001	1	5	23.3	76.2
San Diego	14	3	2000–2002	1	2	12.1	111.6
Tilley West	12	3	2001	15	6	16.2	92.0
Vauxhall	15	3	2001	0	0	12.4	99.3
Total	164	43		113	95		
Total plots × Years studied	322	95					

[a] Measured from centre.

(Quinn and Keough 2002: 52; see *Statistical analyses* for further explanation). The variables were, (1) amount of grassland (Fahrig 1998, 2003), (2) total length of wetland edge (to control for variation in duck densities), (3) an interaction term between amount of grassland and the fragmentation parameter described below, as effects of fragmentation may vary with habitat amount (Fahrig 1998; Flather and Bevers 2002), and (4) one grassland fragmentation variable. We used the following criteria to select between fragmentation variables provided by FRAGSTATS 3.3: (a) theoretically reasonable, (b) no requirement for arbitrary or species-specific input data, (c) interpretable, and (d) not correlated with other variables. As a result, we selected the Landscape Shape Index (LSI) to represent fragmentation (Koper 2004). LSI was calculated as the length of grassland edge divided by the minimum length of edge that would surround the amount of grassland in a landscape if the grassland were clumped in a maximally compact patch (McGarigal et al. 2002). Parameter estimates derived using the LSI index are assumed to be robust to choice of landscape grain size, as this index shows consistent and robust scaling relationships (Wu 2004). The range of values among the sites we used for these analyses was 1.13 to 20.09. The number of point counts and nests per site are provided in Table 1.

To avoid collinearity in the statistical models (Quinn and Keough 2002), we needed to remove the significant linear correlation between grassland amount and LSI (R^2 (adjusted) = 0.694, $p < 0.0001$), and a more subtle curvilinear trend between wetland edge and grassland cover (R^2 (adjusted) = $0.122, p = 0.005$). We modelled the relationship between LSI and grassland cover, and wetland edge and grassland cover, using generalized additive models (GAMs; Quinn and Keough 2002) in R 1.8.1 (R Foundation for Statistical Computing 2003), which applies a non-parametric smoothing function to the data. We then used the residuals as the indices of LSI and wetland edge, respectively. We note that this procedure favours finding effects of amount of grassland over effects of fragmentation or amount of wetland edge. Therefore, we do not try to distinguish between the effects of habitat amount and fragmentation. Prior to all other analyses, we examined a correlation matrix to ensure that variables used in the models were not highly correlated ($r < 0.6$).

Bird density and nest success surveys

Five minute, 100-m point-count plots were conducted to measure richness and densities of duck (n = 6) and songbird (n = 11) species, and densities of two common nest predators: gulls (California *Larus californicus* and ring-billed *L. delawarensis*), and Richardson's ground squirrels (*Citellus richardsoni*) (Table 1). Plot centres were at least 300-m apart and were stratified by distance to road and wetland (Koper 2004). Wetland surveys only included wetland or pond habitats within the 100-m plot, and ignored upland habitats. Surveys were conducted between sunrise and 1000 h, in dry conditions or very light rain, and when wind speeds were less than 20 km/h. Surveys were conducted 4–5 ×/year, between 20 May and 5 July. Preceding statistical analyses, data were averaged across surveys within years. Wetland plots were located up to 3941 m from cropland/forage, and 2350 m from roads, while upland plots were up to 1855 m from water, 4127 m from cropland/forage, and 2250 m from roads.

We located duck and songbird nests both systematically and incidentally, between 4 May and 7 August of each year. Only upland nests were included in analyses. Within each site, 1 or 2, 300×300-m plots were searched for nests using ropes dragged by hand; and 1, 100×2000-m plot adjacent to wetlands was searched using ATV-pulled cable-chain drags. This method flushes incubating parents, thereby alerting the researchers to the presence of nests, while the rope or chain passes above the eggs and does not cause damage (Winter et al. 2003). Nests were marked with bamboo poles and pin-flags 10 m south and west of each nest. Nests were monitored every 4–7 days until hatching, and for songbird nests, every 2–4 days thereafter to determine fate. Successful nests were defined as having at least one duck egg hatched, or at least one songbird hatchling fledged. As we had no more than 56 nests per species, we pooled nests across duck species and songbird species (Table 1), to increase sample sizes (Flaspohler et al. 2001).

Vegetation

Vegetation at point-count plots and at nests was measured using methods developed by Wiens

(1969). For point-count plots, samples were taken at random distances from the centre along each cardinal direction. For nests, samples were taken at the nest and at a random location within 50 m. At each vegetation sampling station, crossed metre sticks were placed and a metal rod dropped vertically at each corner (and at the North edge of each nest). Where the pole touched the ground, litter depth, vegetation height and density (the number of blades of live vegetation contacting the pole) were recorded. Percent bare ground was estimated for each quarter of the square created by the metre sticks. Emergent wetland vegetation was sampled by measuring percent bare ground, vegetation height, average width of the wetland fringe, and percent of dead vegetation ((number of contacts with dead vegetation/total number of contacts with vegetation) $*$ 100), at every metre, along 3 transects per wetland.

Statistical analyses

We used generalized linear mixed-effects (glme; Gaussian, Poisson or binomial) models (S-plus 6.2, Insightful 2001; R 1.8.1) to compare effects of habitat characteristics on (a) richness and density of songbirds and ducks, and (b) density of nest predators, at three spatial scales: *landscape* (amount and fragmentation of grasslands, an interaction term, and length of wetland edge), *neighbourhood* (distances to cropland/forage, roads, and wetlands), and *local vegetation* (upland and nests: height and density of native grasses, litter depth, and percent bare ground; wetland: height, percent dead, percent bare ground, and width of the wetland fringe) (Table 2). Measures of model fit such as R^2 are not yet available for glme models, due to the complexity of the hierarchical model structure (Pendergast et al. 1996). A few recently developed tests show promise, but are not yet available for use with commercial statistical packages such as S-plus and R (Zheng 2000; Jiang 2001). However, the relative fit of alternate models can be compared using information theory (Burnham and Anderson 1998). Our application of this approach for selecting best-fitting models is described below.

Our study design was hierarchical: landscape variables were replicated at the level of the site

Table 2. Suite of models used to describe density and nest success of ducks and songbirds at landscape, neighbourhood, and local scales in southern Alberta, 2000–2002.

Model	*n*		1	2	3	4	5	6	7	8
				Landscape						Global
Random[a]		Site and Year	Y	Y	Y	Y	Y	Y	Y	Y
Landscape	16	Grassland cover (GC)		Y			Y	Y		Y
	16	LSI		Y			Y	Y		Y
	16	Wetland edge		Y			Y	Y		Y
	16	GC*LSI		Y			Y	Y		Y
Neighbourhood	322	Distance to water[b]			Y		Y		Y	Y
	322 (upland) or 95 (wetland)	Distance to crop/forage			Y		Y		Y	Y
	322 (upland) or 95 (wetland)	Distance to road			Y		Y		Y	Y
Local		*Upland*[b]								
	322	Height				Y		Y	Y	Y
	322	Density				Y		Y	Y	Y
	322	% bare				Y		Y	Y	Y
	322	Litter				Y		Y	Y	Y
		Wetland[c]								
	95	Height				Y		Y	Y	Y
	95	% bare				Y		Y	Y	Y
	95	% dead				Y		Y	Y	Y
	95	Width				Y		Y	Y	Y

n indicates the sample sizes from which degrees of freedom were calculated in each model (see description of mixed models, above).

[a] Density models.

[b] Upland density and nest success models.

[c] Wetland density models.

(n = 16), while neighbourhood and local variables were nested within landscapes and were replicated at the level of the point-count plot (n = 322 (upland) or 95 (wetland)). Different variables within the same mixed-effects model are therefore evaluated against different degrees of freedom (Pinheiro and Bates 2000). Random variables were included in mixed models, allowing us to model the covariance among point-counts located within the same site. Random variables in the mixed model were site and year, to control for similar response of birds within sites and within years. Year was nested within site for most analyses, but blue-winged teal (*Anas discors*), gadwall (*Anas strepera*), marsh wren (*Cistothorus palustris*) and red-winged blackbird (*Agelaius phoeniceus*) models did not converge, so site-year groups were used as the random variable instead. Prior to analyses, we ensured that independent variables, among and within spatial scales, were not correlated ($r < 0.6$).

We used a modified logistic regression approach to compare effects of these habitat variables on songbird and duck nest success (Dinsmore et al. 2002) using PROC NLMIXED within SAS 8.0.2 (SAS Institute Inc. 2001). The modification to logistic regression involves estimating the daily survival probability by taking the inverse link function to the power of the interval between nest visits (in days), instead of using the inverse link function itself. Logistic models of nest success that include random variables have not yet been developed (for further discussion see Dinsmore et al. 2002) so we excluded the random variables from these analyses. It is possible that removing the random variables would result in a less conservative test. However, any bias introduced by excluding the random variables would be consistent among the candidate models within the AIC*c* model suite (see below), so was unlikely to influence our results.

To determine whether including local and neighbourhood variables in a model influenced the apparent importance of landscape-level variables, we compared results of three models for each analysis: (a) the best of eight candidate models selected using an information-theoretic approach (Akaike's information criterion modified for small sample sizes: AIC*c*) (Table 2; Burnham and Anderson 1998), (b) the model that only included the landscape-scale variables (the 'landscape-only' model), and (c) the global model, which included local, neighbourhood and landscape variables. The eight candidate models consisted of a null model (model 1), models that included independent variables at local, neighbourhood or landscape scales (models 2–4), models that included variables at 2 of the 3 spatial scales (models 5–7), and the global model, within which all other models were nested. The AIC*c* approach was taken to maximize model parsimony (Burnham and Anderson 1998). We report parameter estimates of only best-fitting models, but where Δ AIC*c* values of second-best models were low (<2), we also discuss these alternate models, as the low Δ AIC*c* indicates that the model describes the data relatively well compared with the best-fitting model (Burnham and Anderson 1998). In addition, the global model was compared with the landscape model and the hypothesis-testing approach, for which we used p-values (calculated using glme or logistic regression) to indicate whether variables exhibited a significant effect. The latter approach allowed us to examine whether models including only landscape-level variables could be misleading. However, most of our data interpretation is based on AIC*c*-selected models.

To explore biological parameters that might explain the pattern of species responses to landscape characteristics, we tabulated life history characteristics and conservation status for our study species, and compared these against response to landscape characteristics.

Results

Effects of model structure

Model structure had a strong effect on the apparent importance of landscape-level variables. Landscape variables were included in AIC*c*-selected models in only 4 of 27 analyses, and results from global models were similar to those from AIC*c*-selected models. In contrast, 12 of 27 landscape-only models had p-values < 0.05 (Tables 3–6), which would have been interpreted as indicating that many species were influenced by landscape-level variables, had we not compared these results to models that also included local effects. For example, the landscape-only model for upland songbird abundance suggested that abundance was higher in landscapes with more grassland ($\beta = 0.0003$, $p = 0.011$).

Table 3. AIC*c*-selected models describing effects of habitat characteristics on duck distributions in southern Alberta, 2000–2002.

Model Family	Duck richness 4 Poisson	Blue-winged Teal 7 Poisson	Lesser Scaup 7 Poisson	Mallard (L) 2 Gaussian
Amount grassland (AG) (ha)				-2×10^{-5} *0.862*
LSI				−0.582
				0.028
Length wetland edge (m)				-3×10^{-6}
				0.524
AG ∗ LSI				0.0001
				0.057
Distance to crop/forage (km)		−0.501	−0.435	
		0.040	0.239	
Distance to road (km)		−0.746	−0.966	
		0.140	*0.141*	
Height (cm)	−0.008	−0.058	−0.085	
	0.136	*0.0001*	*0.0001*	
Dead veg. (%)	−0.003	−0.020	0.010	
	0.469	*0.049*	*0.413*	
Width wetland fringe (m)	−0.006	−0.030	−0.036	
	0.129	*0.106*	*0.112*	
Bare ground (%)	0.006	−0.102	−0.023	
	0.674	*0.014*	*0.622*	

Estimate is shown above *p*. *n* of landscape variables = 16, *n* of other variables = 95. Results for random effects Site and Year are not shown, but confidence intervals did not include 0. G or L indicate that the global or landscape model included landscape-level variables with $p < 0.05$. Null models fit best for duck abundance, Gadwall (L), Northern Pintail and Northern Shoveler.

However, landscape variables were not included in the AIC*c*-selected model. Similarly, grassland amount was not significant in the global model ($\beta = 0.00007$, $p = 0.497$). The effect of landscape amount may have been driven by the higher abundance found farther from cropland/forage ($\beta = 0.414$, $p < 0.0001$) and roads ($\beta = 0.477$, $p = 0.008$).

Because AIC*c*-selected models are less sensitive than global models to spurious significant effects resulting from including many variables in a single model (Burnham and Anderson 1998), we restrict the following interpretation of results to AIC*c*-selected models.

Effects of grassland amount and fragmentation on richness and density

Species generally responded more strongly to local and neighbourhood characteristics than to landscape characteristics (Figure 1). Mallards had higher densities in landscapes with less fragmented grasslands, and the effect was stronger in landscapes with less grassland (Table 3). In addition, the Δ AIC*c* value for the landscape-only model for gadwall was low relative to the top-ranked model (1.4), indicating that gadwall may also select sites with greater amounts of, and less fragmented, grassland cover.

Densities of both chestnut-collared longspurs (*Calcarius ornatus*) and western meadowlarks (*Sturnella neglecta*) were significantly influenced by factors at landscape, neighbourhood, and local levels (Table 4). Densities of the other five upland songbird species reflected stronger effects of local vegetation and distance to other habitats than to grassland cover and fragmentation (Table 4).

Red-winged blackbird densities were higher in landscapes with more fragmented grassland, and were influenced by distance to road and local vegetation (Table 5). A low Δ AIC*c* value for the landscape-only model (0.23) suggests that common yellowthroats (*Geothlypis trichas*) may also select landscapes with less grassland cover and higher fragmentation.

Table 4. AIC*c*-selected models describing effects of habitat characteristics on upland songbird distributions in southern Alberta, 2000–2002.

	Songbird richness (G)	Songbird abundance (L)	Brown-Headed Cowbird (G, L)	Chestnut-collared Longspur (L)	Horned Lark (L)	Savannah Sparrow	Sprague's Pipit (L)	Vesper Sparrow (L)	Western Meadowlark (G, L)
Model	3	3	7	8	7	4	3	3	
Family	Gaussian	Gaussian	Gaussian (logged)	Gaussian	Gaussian	Gaussian	Gaussian (logged)	Gaussian (logged)	Gaussian
Amount grassland (AG) (ha)				0.0003 *0.006*					-5×10^{-5} *0.042*
LSI				0.137 *0.515*					− 0.027 *0.559*
Length wetland edge (m)				-8×10^{-7} *0.807*					2×10^{-6} *0.027*
AG ∗ LSI				-6×10^{-5} *0.294*					1×10^{-5} *0.267*
Distance to water (km)	−0.061 *0.691*	0.069 *0.783*	−1.505 *0.0001*	0.543 *0.0003*	0.520 *0.001*		0.753 *0.004*	−0.610 *0.043*	−0.147 *0.034*
Distance to crop/forage (km)	0.281 *0.0001*	0.414 *0.0001*	−0.185 *0.156*	0.136 *0.080*	0.030 *0.610*		0.608 *0.001*	−0.268 *0.011*	0.012 *0.666*
Distance to road (km)	0.257 *0.019*	0.477 *0.008*	−0.066 *0.779*	0.457 *0.0001*	0.135 *0.157*		0.033 *0.863*	−0.990 *0.0001*	−0.107 *0.020*
Height (dm)			−0.051 *0.135*	−0.008 *0.582*	−0.005 *0.712*	0.026 *0.019*			0.018 *0.014*
Density (number contacts)			0.066 *0.009*	−0.022 *0.061*	−0.006 *0.592*	0.042 *0.0001*			0.004 *0.435*
Litter depth (mm)			0.010 *0.394*	−0.011 *0.036*	−0.012 *0.021*	0.012 *0.004*			0.005 *0.070*
Bare ground (%)			−0.0002 *0.985*	−0.005 *0.231*	0.006 *0.092*	−0.003 *0.280*			−0.001 *0.552*

Estimate is shown above *p*. *n* of landscape variables = 16, *n* of other variables = 95. Results for random effects Site and Year are not shown, but confidence intervals did not include 0. G or L indicate that the global or landscape model included landscape-level variables with $p < 0.05$.

Table 5. AIC*c*-selected models describing effects of habitat characteristics on wetland songbird distributions in southern Alberta, 2000–2002.

	Songbird richness	Songbird abundance	Common Yellowthroat (G, L)	Marsh Wren	Red-winged Blackbird (L)	Yellow-headed Blackbird (L)
Model	4	4	3	3	(8)	4
Family	Gaussian	Gaussian	Gaussian	Poisson	Poisson	Gaussian (logged)
Amount grassland (AG) (ha)					−0.0001	
					0.292	
LSI					0.765	
					0.007	
Length wetland edge (m)					5×10^{-6}	
					0.190	
AG ∗ LSI					−0.0001	
					0.043	
Distance to crop/forage (km)			−0.104	0.427	−0.117	
			0.086	*0.100*	*0.572*	
Distance to road (km)			−0.205	1.275	−0.864	
			0.110	*0.033*	*0.002*	
Height (cm)	0.016	0.136			0.044	0.044
	0.010	*0.0002*			*0.0001*	*0.001*
Dead veg. (%)	0.006	0.021			−0.005	−0.004
	0.098	*0.306*			*0.285*	*0.550*
Width wetland fringe (m)	0.006	0.024			0.012	0.001
	0.065	*0.153*			*0.0001*	*0.856*
Bare ground (%)	0.0003	0.202			−0.027	0.081
	0.984	*0.012*			*0.239*	*0.004*

Estimate is shown above *p*. *n* of landscape variables = 16, *N* of other variables = 95. Results for random effects Site and Year are not shown, but confidence intervals did not include 0. G or L indicates that the global or landscape model included landscape-level variables with $p < 0.05$.

Effects of grassland amount and fragmentation on nest success and nest predators

Gulls densities were apparently independent of the habitat characteristics we measured. Richardson's ground squirrel densities were only influenced by distances to other habitats (water $\beta = 0.061$, $p = 0.677$, crop/forage $\beta = -0.288$, $p < 0.0001$, and road −0.287, $p = 0.008$).

Local vegetation characteristics, and distance to water and cropland/forage, had a greater effect on duck nest success than grassland amount and fragmentation (Table 6). There was no effect of grassland amount or fragmentation on songbird nest success (Table 6). This indicates that removing the random variables from the models did not increase the apparent importance of grassland amount and fragmentation.

Species that responded to landscape characteristics tended to have relatively large territory sizes (Table 7). The exception to this pattern was the northern pintail (*Anas acuta*). Other life-history characteristics, and conservation status, were not consistently associated with response to landscape characteristics (Table 7).

Discussion

Effects of model structure

The apparent importance of amount and fragmentation of grassland varied substantially, depending on the other variables included in candidate models. In most cases, landscape-only models suggested stronger effects of grassland amount and fragmentation than either global models (including landscape, neighbourhood and vegetation variables) or AIC*c*-selected models. This suggests that landscape-level patterns may not result from landscape-level mechanisms. Some of the effects of habitat amount and fragmentation in previous studies may have resulted from effects of distance to edge, but many

Table 6. AIC*c*-selected models describing effects of habitat characteristics on nest success in southern Alberta, 2000–2002.

	Ducks $n = 95$ (L)	Songbirds $n = 113$
Model	7	4
Family	binomial	binomial
Distance to water (km)	1.600 *0.096*	
Distance to crop/forage (km)	−0.510 *0.004*	
Distance to road (km)	0.220 *0.632*	
Height (dm)	0.002 *0.153*	0.0006 *0.523*
Density (number contacts)	0.022 *0.490*	−0.083 *0.114*
Litter depth (mm)	−0.011 *0.079*	−0.005 *0.545*
Bare ground (%)	−0.010 *0.664*	−0.010 *0.438*

Estimate is shown above p. G or L indicates that the global or landscape model included landscape-level variables with $p < 0.05$. Landscape variables did not affect nest success.

landscape-scale studies have been unable to distinguish between local- and landscape-scale effects (Greenwood et al. 1995; Bender et al. 1998; Villard et al. 1999; and others). In this study, apparent influences of habitat *amount* on songbird abundance in landscape-only models were in fact driven by distance to edge, although edge effects are generally associated with fragmentation rather than habitat amount.

These results challenge the ability of some previous studies (e.g. Villard et al. 1999; Flather and Bevers 2002; see review in Fahrig 2003) to clearly distinguish between effects of habitat amount and habitat fragmentation. Whereas adjusting indices of fragmentation using residuals (from fragmentation regressed on habitat amount) results in statistical independence of variables, the variable representing habitat amount may still correlate with fragmentation and thus reflect effects of fragmentation not captured by the specific fragmentation variables included in models.

Effects of grassland amount and fragmentation on species richness and density

Most species we studied were not significantly influenced by landscape-level variables. Previous studies have found that landscape factors significantly influence distributions of some grassland birds, although responses are species- and scale-specific (O'Connor et al. 1999; Ribic and Sample 2001; Bakker et al. 2002). Mallards, and possibly gadwalls, were the only duck species that responded to landscape characteristics, consistent

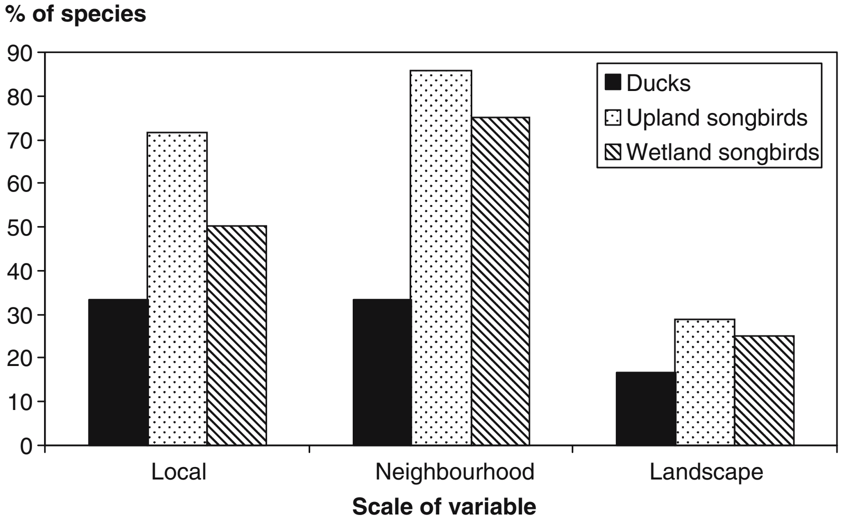

Figure 1. The percent of avian species whose AIC*c*-selected model included local, neighbourhood and/or landscape variables in southern Alberta, 2000–2002. $n = 6$ duck species, 7 upland songbird species, and 4 wetland songbird species.

Table 7. Relationship between life history characteristics and landscape context on avian species in prairie landscapes of southern Alberta, 2000–2002.

Species	Landscape effect	Guild[a]	Trend[b]	Territory size (ha)[c]	Generalist Specialist[d]	Clutch size[e]	Reference
Chestnut-collared longspur	YES	US	D	L (0.25–4)	S	3–5	Hill and Gould 1997
Mallard	YES	D	S	L (9.2–70)	G	8.7A	Drilling et al. 2002
Red-winged blackbird	YES	WS	S	M (0.2–2.9)	G	3.3A	Yasukawa and Searcy 1995
Western meadowlark	YES	US	D	L (3–7)	G	4.8A	Lanyon 1994
Brown-headed cowbird	MAYBE[f]	US	I	L (4–20)	G	40/yr	Lowther 1993
Common Yellowthroat	MAYBE	WS	S or D	M (0.16–0.93)	G	4A	Guzy and Ritchison 1999
Gadwall	MAYBE	D	I	L (27–100+)	S	8–12	Leschack et al. 1997
Blue-winged teal	NO	D	S	S (0.37–0.69)	S	10A	Rohwer et al. 2002
Horned lark	NO	US	S or D	S (0.3–1.4)	G	2–5	Beason 1995
Lesser scaup	NO	D	S (low)	S	G	8–10	Austin et al. 1998
Marsh Wren	NO	WS	S or I	S (0.05–0.3)	S	4–6	Kroodsma and Verner 1997
Northern pintail	NO	D	D	L (480–900)	G	6.9A	Austin and Miller 1995
Northern shoveler	NO	D	I	S (HR = 6–36)	G	10.1A	Dubowy 1996
Savannah sparrow	NO	US	S or I	S (< 0.5)	S	2–6	Wheelwright and Rising 1993
Sprague's pipit	NO	US	D	S (0.1–1)	S	4.4	Robbins and Dale 1999
Vesper sparrow	NO	US	D	N/A	G	3–5	Jones and Cornelys 2002
Yellow-headed blackbird	NO	WS	S or I	S (< 0.4)	G	3.2–4	Twedt and Crawford 1995

[a] US = upland songbird, D = duck, WS = wetland songbird.

[b] Regional population is D = decreasing, S = stable, I = increasing

[c] L = large (relative to other species in the same guild), M = medium, S = small

[d] G = generalist (uses a variety of upland habitats), S = specialist (primary upland habitat used is native grassland)

[e] A = average

[f] AIC of landscape or global model is < 2 but > 0.

with other studies (Artmann et al. 2001; Naugle et al. 2001). This is noteworthy as the majority of research on effects of amount of grassland on ducks has focussed on mallards (e.g., Greenwood et al. 1995; Artmann et al. 2001). Our results suggest that other duck species may not respond similarly.

Densities of chestnut-collared longspurs, western meadowlarks, and red-winged blackbirds were influenced by landscape, neighbourhood, and local-level characteristics. Our results contradict previous studies on chestnut-collared longspurs and western meadowlarks (Bakker et al. 2002; Davis 2004), but are consistent with studies on red-winged blackbirds and Savannah sparrows (*Passerculus sandwichensis*) (Fletcher and Koford 2002; Davis 2004).

Species may respond to habitat characteristics at spatial scales that are correlated with home range and territory size (Wiens 1989; Söderström and Pärt 1999). With the exception of northern pintails, a species with a very large home range that did not respond to landscape characteristics, our results are consistent with this hypothesis. This suggests that the spatial scale that influences species densities is regulated by species behaviour and perception of their environment. While population declines may result from habitat loss and fragmentation, the lack of a trend between conservation status and response to landscape characteristics suggests that mechanisms are local.

Effects of grassland amount and fragmentation on nest success and nest predators

We also found little effect of landscape characteristics on nest success of ducks or songbirds. In contrast, other studies in grasslands (Greenwood et al. 1995; Herkert et al. 2003) and agro-ecosystems (Bergin et al. 2000) have found higher nest success in landscapes with greater proportions of grassland or in larger patches, although this varies by species. However, our power to detect landscape effects was relatively low, due to small sample sizes and pooling nests across species. Nevertheless, our results suggest that landscape-level effects are not strong, and that local habitat management is important for ensuring adequate reproduction of these species.

Results related to nest success are consistent with the lack of landscape-level effects influencing densities of nest predators in this study, but inconsistent with meta-analyses that reported greater effects of landscape-level than local habitat characteristics on both nest success (Phillips et al. 2003; Stephens et al. 2003) and predator distributions (Chalfoun et al. 2002). Because proportions of grassland on the landscapes we studied were relatively high (22–95%), predator communities may not have been altered as dramatically as they have been in other regions.

Comparison among scales

Different species responded to habitat characteristics at different spatial scales. However, AIC*c*-selection generally suggested that local vegetation and neighbourhood were more important determinants of avian densities and nest success than landscape characteristics, while landscape-only models suggest that these local mechanisms sometimes result in landscape-level patterns. Grassland loss and fragmentation may affect prairie bird species through abundance of roads and grassland edges on the landscape, but mechanisms are local and not strongly influenced by general characteristics of the surrounding landscape. Other research in grassland systems has also found greater effects of distance to edge on nest success than patch size (Winter and Faaborg 1999) and larger effects of local vegetation characteristics than landscape characteristics (Hughes et al. 1999; but see Vander Haegen et al. 2000).

Given the importance of landscape characteristics reported in other studies (e.g., Villard et al. 1999; Bakker et al. 2002; Stephens et al. 2003), our results merit consideration. Although many grassland birds have higher densities in grasslands than in cropland or forage, they also use the surrounding matrix, for example for foraging (Knick and Rotenberry 1995; Davis et al. 1999). Use of the matrix will significantly alter effects of habitat amount and fragmentation (Wiens 1994). Alternatively, if effects of habitat loss are nonlinear (e.g. With and Crist 1995), we may have observed few effects because all of our sites had more than 20% habitat remaining on the landscape. Effects of habitat fragmentation may increase with habitat loss, particularly below 20 or 30% habitat remaining (With and Crist 1995; Fahrig 1998; but see Fahrig 2003). However, an additional explanation for the relative infrequency of landscape effects observed in our study is that we were able to clearly separate effects of landscape characteristics from neighbourhood and local vegetation characteristics.

Recommendations for future research

Our exploratory landscape-level analyses provided insight into potential effects of grassland loss and fragmentation on ducks and songbirds, and suggest relationships that merit more directed studies. A greater number of landscape sites, and sampling of multiple grassland patches and habitat types within each site, would provide stronger tests of whether amount and fragmentation of grasslands influences ducks and songbirds. Moreover, landscape-level research must focus on determining whether landscape-level patterns result from landscape-level mechanisms, or more local ones (Bender et al. 1998; McGarigal and Cushman 2002). One way to evaluate this is to conduct studies at multiple spatial scales (Wiens 1989; Stephens et al. 2003) and to ensure that models including only landscape-scale variables are compared to more complex models. We recommend use of an information-theoretic approach to determine suitable and parsimonious models, rather than analyzing models with too few or too many variables, both of which may lead to erroneous conclusions.

Our results suggest that densities of some ducks and wetland songbirds may be influenced by loss and fragmentation of grasslands, and more research on these species is warranted (Naugle et al. 2001). Grassland songbirds, however, may be less strongly influenced by habitat amount and fragmentation than forest songbirds (e.g., Villard et al. 1999; but see e.g., Bakker et al. 2002), and declines in these species may result from local rather than landscape-level mechanisms. Nevertheless, the influence of landscape context cannot be determined without additional studies that evaluate the importance of landscape attributes in the context of multiple spatial scales.

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