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Management and Conservation

Songbird Abundance in Native and Planted Grassland Varies With Type and Amount of Grassland in the Surrounding Landscape

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ABSTRACT Agriculture and wildlife conservation programs have converted vast amounts of cropland into grasslands planted with exotic species. Understanding how landscape context influences avian use of native and planted grasslands is essential for developing effective conservation strategies in agricultural landscapes. Our primary objective was to determine the extent to which the amount and type of grassland in the surrounding landscape influences the abundance of grassland songbird species on native and planted grassland parcels in southern Saskatchewan and Alberta, Canada. Bird abundance was more strongly influenced by the amount and type of grassland within 400 m of breeding parcels than at larger spatial scales. Grassland specialists responded similarly to habitat and landscape type over both years and provinces. Sprague's pipit (*Anthus spragueii*) and Baird's sparrow (*Ammodramus bairdii*) were most common in native grassland parcels surrounded by native grassland and were more likely to occur in planted grasslands surrounded by native grassland. Bobolinks (*Dolichonyx oryzivorus*) were most common in planted grassland parcels, but their abundance increased with the amount of native grassland surrounding these parcels. Our findings indicate that the suitability of planted grasslands for these species is influenced by their proximity to native grassland. Grassland generalists showed mixed responses to habitat and landscape type over the 2 years (Le Conte's sparrow [*Ammodramus leconteii*] and between provinces (Savannah sparrow [*Passerculus sandwichensis*] and western meadowlark [*Sturnella neglecta*]). Management to benefit grassland specialists should therefore consider the landscape context when seeding cultivated land to non-native grassland and conserve extant native grassland. © 2013 The Wildlife Society.

KEY WORDS Alberta, cropland conversion, grassland songbirds, habitat selection, landscape composition, mixed-grass prairie, native grassland, planted grassland, Saskatchewan.

Seeding cropland to perennial grasslands is a common strategy used by wildlife conservation agencies to increase the amount of habitat available to grassland species (Arnold et al. 2007). Agricultural programs targeting conservation have converted large amounts of cultivated lands to grasslands planted with exotic grass and forb species (Johnson and Schwartz 1993, McMaster and Davis 2001). Although these programs likely benefit some avian species, grassland specialists like Sprague's pipit (*Anthus spragueii*) and Baird's sparrow (*Ammodramus bairdii*) rarely use these habitats and are associated primarily with native mixed-grass prairie (Johnson and Schwartz 1993, McMaster and Davis 2001). Populations of these and other species dependent on grasslands have undergone widespread declines in North America, presumably because of loss and degradation of grassland habitat (Askins et al. 2007). Identifying habitat requirements of grassland birds is an important step towards protecting, managing, and

restoring their habitat. Research has increased our understanding of bird habitat requirements and has guided management of existing grasslands and creation of grasslands using native and non-native plants (Madden et al. 2000, Davis 2004, Winter et al. 2006). Although some songbirds occupy planted hayfields and pastures (Dale et al. 1997, Sutter and Brigham 1998, Davis et al. 1999), the conditions under which this occurs are poorly understood.

Abundance of birds may be influenced by local factors such as patch size, edge habitat, and vegetation structure of grasslands (Johnson and Igl 2001, Koper and Schmiegelow 2006a, Fisher and Davis 2010). Demographic responses to these factors may vary over time and space, due in part to changes in management, moisture levels, and size of regional populations (Johnson and Igl 2001, Davis 2004, Winter et al. 2005). However, species may also be influenced by factors extending beyond the size and structure of habitat patches (Brotons et al. 2005, Ribic et al. 2009). The landscape surrounding habitat patches may influence the movement of individuals between patches (Bender and Fahrig 2005). Landscape-level effects may also arise from individuals

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substituting or supplementing resources in a habitat patch with those found in the surrounding landscape (Dunning et al. 1992, Brotons et al. 2005) or through numerical and behavioral changes in predator populations (Phillips et al. 2003) that in turn influence reproduction and habitat selection (Martin 1993, 1998). Furthermore, species abundance may increase in preferred breeding habitats in landscapes where suitable habitat is scarce (McMaster et al. 2005, Shaffer et al. 2006). Agriculture and wildlife conservation programs typically have not considered the surrounding landscape matrix when providing incentives to landowners to convert cropland to perennial grasslands (Weber et al. 2002). Understanding how landscape composition influences the use of native and planted grasslands is essential for developing effective conservation strategies in agricultural landscapes. We examined how landscape composition influences the abundance of mixed-grass prairie habitat specialists and generalists in native and planted grasslands. Our objectives were to assess 1) whether the amount and type of grassland in the landscape influences the abundance of grassland passerines on native and planted grasslands, 2) the scale at which passerines respond to landscape composition and whether landscape scales currently used in waterfowl conservation planning are relevant to songbirds, and 3) the extent of temporal and spatial variation in the response of passerines to habitat and composition of grassland landscapes.

STUDY AREA

In 2006, we delineated 5,600 km² centered on the Last Mountain Lake National Wildlife Area (51°2'N, 105°15'W) in Saskatchewan (SK), Canada. We used a geographic information system to randomly select township sections (256 ha; McKercher and Wolfe 1986) within the area and assigned them as the northwest corner of a 41-km² square polygon. We assigned each landscape to 1 of 3 landscape treatments: ≥50% cropland (hereafter crop landscape), <40% cropland dominated by intact native grassland (hereafter native landscape), and ≤40% cropland dominated by planted grassland (hereafter planted landscape). We continued this process until we obtained at least 10 replicates of each landscape and then randomly selected 3 replicates of each treatment for inclusion into the study (Table 1). We used these sites again in 2007 (Fig. 1). We used the same procedure to select additional landscapes in southeastern Alberta (AB), Canada. In 2006, we randomly selected 6 landscapes within 7,000 km² centered on Stettler, AB (52°19'0" N—112°43'0" W; Fig. 1). In 2007, we selected 9 different landscapes from 5,000 km² north of Bassano, AB (50°47'12" N; 112°27'41" W; Fig. 1). We selected 41-km² landscapes to align with waterfowl studies and waterfowl conservation priorities at this spatial scale in these regions (Emery et al. 2011). Each study region was characterized by a gently rolling topography with a mosaic of native and planted grassland, cropland, wetlands, and riparian areas. Mean annual precipitation ranged from 434 mm in SK to 348 mm and 481 mm near the Bassano and Stettler study sites, respectively.

The 6 landscapes in AB, 2006, were comprised of 2 replicates of each of the 3 landscape treatments, although results of

Table 1. Landscape composition (%) of 41-km² landscapes and percent grassland comprised of native and planted vegetation in Alberta (AB) and Saskatchewan (SK), 2006 and 2007. Landscape treatments sharing the same study site number indicate parcels used in both years.

Landscape type—study site	Landscape composition			Grassland	
	Planted	Native	Cropland	Native	Planted
AB 2006					
Cropland-1	14	8	78	38	62
Cropland-2	22	2	77	7	93
Cropland-3	44	2	54	3	97
Planted-1	69	6	25	8	92
Native-1	32	62	6	66	34
Native-2	30	47	23	61	39
AB 2007					
Cropland-4	12	14	74	54	46
Cropland-5	13	18	69	57	43
Cropland-6	14	19	67	58	42
Native-3	1	83	16	99	1
Native-4	22	43	35	66	34
Native-5	17	76	7	82	18
Planted-2	62	36	2	63	37
Planted-3	42	18	40	31	69
Planted-4	67	19	14	22	78
SK 2006					
Cropland-1	20	13	67	39	61
Cropland-2	29	20	50	41	59
Cropland-3	40	10	50	20	80
Native-1	42	44	14	51	49
Native-2	19	81	0	81	19
Native-3	32	36	32	53	47
Planted-1	64	17	19	21	79
Planted-2	38	31	31	45	55
Planted-3	43	25	32	37	63
SK 2007					
Cropland-1	21	13	66	39	61
Cropland-2	29	19	52	39	61
Cropland-3	37	8	55	17	83
Native-1	42	49	9	53	47
Native-2	19	81	0	81	19
Native-3	33	36	31	52	48
Planted-1	64	17	19	20	80
Planted-2	42	30	29	42	58
Planted-3	43	25	31	37	63

our ground-truthing revealed that 1 planted grassland landscape more closely met the definition of a cropland landscape and was considered that in our analyses (Table 1). Land cover was determined from 2000 Landsat TM imagery (Prairie Farm Rehabilitation Administration 2002). We visited each landscape to verify habitat types and update existing land use information. Within each of the landscapes, we randomly selected 65-ha parcels of native and planted grassland to conduct surveys. We chose these parcels, also known as quarter-sections, as our sampling unit because they represented the typical unit of land management and ownership in prairie Canada (McKercher and Wolfe 1986). The number of parcels in each landscape for each year ranged from 4–18 in SK and 6–19 in AB; ≥80% of the landscapes had >10 parcels sampled.

Native grassland parcels had ≥75% cover of native grass species and were not previously cultivated, except for small portions of some parcels that may have been cultivated in the past. Native grasslands were grazed by domestic cattle and were characterized by speargrasses (*Stipa* spp.), June grass (*Koeleria cristata*), wheatgrasses (*Agropyron* spp.), blue gramma grass (*Bouteloua gracilis*), club moss (*Selaginella*

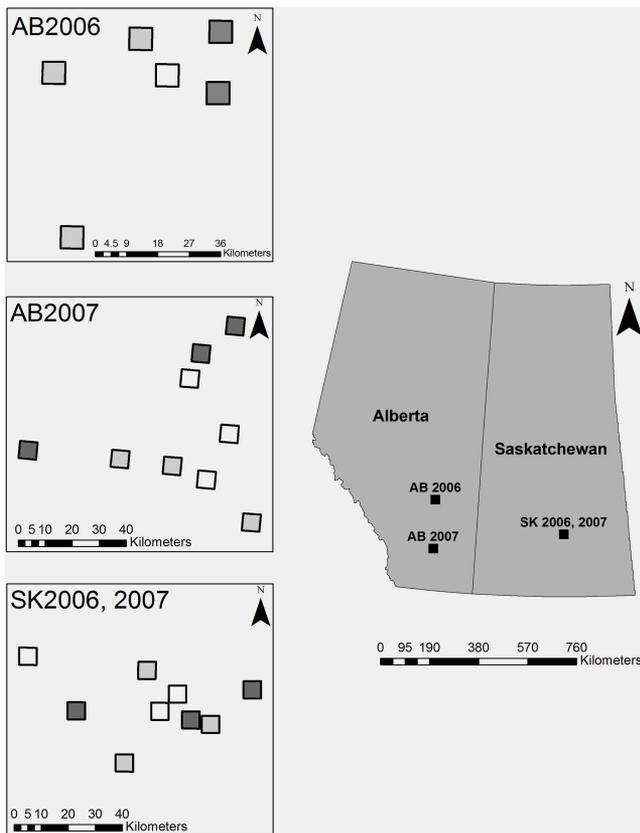


Figure 1. Locations of study areas and landscape treatments in Saskatchewan (SK) and Alberta (AB), Canada in 2006 and 2007. The same landscapes were surveyed in 2006 and 2007 in SK, whereas different landscapes were used in AB in 2006 and 2007. Light gray squares represent cropland landscape treatments, dark gray squares are native grassland landscapes, and white squares represent planted grassland landscapes.

densa), pasture sage (*Artemisia frigida*), and a variety of other forbs. Saline areas were characterized by salt tolerant grasses such as salt grass (*Distichlis stricta*) and foxtail barley (*Hordeum jubatum*). Small patches of smooth brome (*Bromus inermis*), crested wheatgrass (*Agropyron cristatum*), Kentucky bluegrass (*Poa pratensis*), and quack grass (*Agropyron repens*) had invaded some pastures. Western snowberry (*Symphoricarpos occidentalis*), rose (*Rosa* spp.), and wolf willow (*Eleagnus commutata*) were sparsely distributed throughout the regions along with small patches of trembling aspen (*Populus tremuloides*).

Planted grassland parcels contained $\geq 75\%$ cover of exotic grasses and forbs and were typically grazed, hayed, or both. These sites had been cultivated before being seeded with introduced perennial grasses and forbs including: crested wheat grass, brome grass, or bluegrass, and occasionally alfalfa (*Medicago* spp.) or sweet clover (*Melilotus* spp.). Grasslands were not hayed until after our avian surveys were completed. Cropland was cultivated land that was seeded to annual crops, most commonly wheat, flax, or canola.

METHODS

Avian Surveys

Surveyors conducted up to 3, 5-minute, 100-m radius point counts in each parcel within each landscape treatment per

year. Point count centers were separated by ≥ 400 m and were ≥ 100 m from parcel boundaries to reduce the probability of double-counting birds and to ensure that only birds within the surveyed parcels were counted. We conducted point counts from 0500 to 0930 CST on days with winds < 30 km/hr and no precipitation or extreme temperatures. We surveyed for birds at each point count station once between mid-May and early July. Observers recorded detections of 6 species: Sprague's pipit; Baird's, Savannah (*Passerculus sandwichensis*), and Le Conte's (*Ammodramus leconteii*) sparrows; western meadowlark (*Sturnella neglecta*); and bobolink (*Dolichonyx oryzivorus*). All avian survey protocols were approved by the University of Regina (#06-02) and Canadian Wildlife Service (#2006PNR001) animal care committees.

We used removal (Farnsworth et al. 2002) and distance (Buckland et al. 2001) sampling to adjust counts for potential detection biases. Surveyors recorded the distance at which each bird was first observed and assigned it to a distance category: 0–20 m, 20–30 m, 30–40 m, 40–50 m, 50–75 m, and 75–100 m. We selected categories a priori based on previous studies (Rotella et al. 1999) and accuracy of distance estimation abilities of surveyors during training. We used DISTANCE 5.0 (Thomas et al. 2010) to model detection probabilities of each species-observer combination. We divided our 5-minute point count into 3 equal intervals of 100 seconds and recorded the number of new detections of individuals in each interval. We used Program MARK v.4.3 (White and Burnham 1999) and Huggins (1989) closed-capture models to model detection based on removal sampling. We included the effects of habitat type, observer, and date as covariates to potentially explain differences in detection probability.

Statistical Analysis

We used an information theoretic approach (Burnham and Anderson 2002) to determine the relationship between bird abundance and landscape composition and habitat type. We combined planted hayfields and pastures because we could not locate or gain access to hayfield sites in 3 cropland landscapes. We considered landscape composition at 2 scales: the original 41-km² landscape treatments and a smaller landscape defined as a 400-m buffer surrounding the parcel. We used the smaller scale covariate to account for situations where local landscape differed greatly from the larger 41-km² landscape and for those parcels near the edge of the 41-km² landscapes. We also considered 800-m radius landscapes, but found that landcover types were highly correlated with 400-m landscapes ($r > 0.97$). Furthermore, 400-m landscape models consistently had smaller Akaike's Information Criterion corrected for small sample sizes (AIC_c) values. We present only results from the 400-m models but acknowledge that grassland birds may be influenced by landscapes within 800 m of the parcel. We calculated the proportion of native (native400) and planted (planted400) grassland surrounding each parcel. We first determined whether effects of habitat type (native or planted grassland parcel), local landscape (native400 and planted400), and 41-km² landscape (landscape type; crop, native, and planted)

treatments on bird abundance varied by year (we note that year effects in AB may also be attributed to site effects because the two are confounded). We conducted these analyses to assess temporal variation in bird responses to habitat and landscape covariates and to determine whether years could be pooled for subsequent analyses. We treated the parcel as the experimental unit and modeled the maximum number of singing males detected in a given point count per parcel using generalized linear mixed models (SAS v.9.2 Institute Inc., Cary, NC, PROC GLIMMIX; Littell et al. 2006) with a Poisson distribution, log link, and Laplace approximation. We included a random effect of the individual 41-km² landscape (landscape identifier) nested within landscape treatment (landscape type) and an interactive effect of landscape identifier \times habitat type nested within landscape type for Baird's sparrow in SK. We simplified models to landscape identifier nested within landscape type for all other species analyses because more complex models would not converge.

We initially considered 10 models to determine whether the effects of habitat type, landscape type, native400, and planted400 on songbird abundance depended upon the year we conducted surveys: null, year, year + habitat type, year + landscape type, year + native400, year + planted400, year \times habitat type, year \times landscape type, year \times native400, and year \times planted400. We identified the best fitting and most parsimonious candidate models using AIC_c (Burnham and Anderson 2002). We combined years for subsequent analyses for those species 1) where an interactive effect of year did not perform better (greater AIC_c values) than models with an additive effect of year or those without a year effect or 2) if the interactive effect of year indicated that the direction of the response was the same in both years but stronger in one. Rankings of the 10 models for each species revealed that models containing landscape type effects (i.e., cropland, native grassland, and planted grassland at the 41 km² scale) were consistently poor models for all species but Le Conte's sparrow. Therefore, we considered 11 models containing main, additive, and interactive effects of landscape type, habitat type, and native400 and a null model for Le Conte's sparrow. For other species, we compared 4 models containing main, additive, and interactive effects of habitat type and native400 and a null model. Native400 and planted400 were inversely correlated ($r = -0.70$) and therefore not included in the same model (Burnham and Anderson 2002). For species where native400 was included in the best model, we examined whether substituting native400 with planted400 affected the fit of the model (i.e., extent to which the AIC_c value changed). All means are based on model predictions and presented \pm standard error except where indicated. We use 85% confidence intervals to discriminate between informative and uninformative parameters and graphically present results only if 85% confidence intervals do not include zero (Arnold 2010).

RESULTS

We conducted 356 point counts on 130 parcels and 376 point counts on 136 parcels in SK in 2006 and 2007, respectively.

In AB, we surveyed 199 point counts on 75 parcels in 2006 and 296 point counts on 104 parcels in 2007. Savannah sparrow was the most common species recorded in both native and planted grasslands (Appendix A). Baird's sparrow and Sprague's pipit occurred up to 5 times more frequently in native parcels, whereas bobolink occurred almost exclusively in planted grassland parcels (Appendix A).

Our point count data for all species violated the assumption that detection was 100% at the point count center (Appendices B and C). In nearly all cases, observers did not record birds within the 0–20 m distance category (Appendix D) and the majority of χ^2 goodness-of-fit tests indicated that detection curves did not fit the data ($P \leq 0.05$; Appendices B and C), suggesting evasive movements by the birds (Thomas et al. 2010). With the exception of western meadowlark and Sprague's pipit, no species showed any effect of habitat type, observer, or season (early vs. late) on detection probability based on removal analyses (Appendix E). Detection probability during early surveys (13 June or earlier) was 0.80 for western meadowlark and 0.97 for Sprague's pipit and detection of both species was 0.99 for late surveys (14 June or later). We chose to use unadjusted raw counts for all species because of 1) the violation of distance sampling assumptions 2) a lack of any strong relationships between the covariates we examined and detection probability, and 3) no systematic bias in the number and type of fields or landscapes surveyed by each observer over time.

Sprague's pipit abundance was best explained by habitat type in SK and habitat type \times native400 in AB (Table 2). Mean pipit abundance was greater in native than planted grassland in SK (0.28 ± 0.09 vs. 0.06 ± 0.03 , respectively) and AB (0.70 ± 0.12 vs. 0.28 ± 0.07 , respectively). Although we identified habitat type \times native400 as the best model for Alberta, the additive model was more parsimonious given the similar AIC_c values and large standard error for the interaction term ($\beta = -1.74 \pm 1.07$) versus the additive terms ($\beta = 0.902 \pm 0.35$ and 0.674 ± 0.38 for habitat type and native400, respectively). Sprague's pipit abundance on native parcels increased more sharply as the amount of native grassland in the landscape increased than on planted grassland parcels (Fig. 2). Replacing native400 with planted400 indicated that the amount of planted grassland in the landscape had little effect on pipit abundance in AB ($\Delta AIC_c = 2.6$).

The top model explaining variation in Baird's sparrow abundance in AB and SK was native400 \times habitat type (Table 2). In both provinces, Baird's sparrow abundance in native and planted grassland parcels increased with the amount of native grassland in the landscape but the increase was more pronounced albeit variable on planted grassland parcels (Fig. 2). Overall, abundance was similar in native and planted grassland in both SK (0.35 ± 0.14 vs. 0.28 ± 0.11 , respectively) and AB (0.58 ± 0.15 vs. 0.52 ± 0.16 , respectively). Replacing native400 with planted400 resulted in weaker models ($\Delta AIC_c = 2.3$ and 22.5 for SK and AB, respectively).

Table 2. Models examining effects of year (2006, 2007), habitat type (native and planted grassland), and proportion of native grassland within 400 m of the habitat parcel (native400) on grassland bird abundance in Saskatchewan (SK) and Alberta (AB). The number of parameters (K), log-likelihood (LL), and Akaike's Information Criterion corrected for small sample size (AIC_c) are presented. Only the top 90% confidence set of models (i.e., model weights [w_i] sum to ≥ 0.90) whose weights are greater than the null model are presented.

Species	Model	K	$-2LL$	AIC_c	ΔAIC_c	w_i		
Sprague's pipit	SK	Habitat type	3	257.5	263.6	0.0	0.57	
		Native400 \times habitat type	5	255.3	265.5	1.9	0.22	
AB	Native400 + habitat type	Native400 + habitat type	4	257.5	265.7	2.1	0.21	
		Null	2	271.1	275.2	11.6	0.00	
		Native400 \times habitat type	5	305.3	315.6	0.0	0.41	
		Native400 + habitat type	4	307.7	315.9	0.3	0.36	
		Habitat type	3	311.0	317.2	1.6	0.19	
Baird's sparrow	SK	Null	2	344.7	348.8	33.2	0.00	
		Native400 \times habitat type	6	413.8	426.1	0.0	0.50	
AB	Native400 + habitat type	Native400	4	420.2	428.4	2.3	0.16	
		Native400 + habitat type	5	418.2	428.4	2.3	0.16	
		Habitat type	4	420.6	428.8	2.7	0.13	
		Null	3	424.7	430.8	4.7	0.05	
		Native400 \times habitat type	5	314.6	324.9	0.0	0.96	
Savannah sparrow	SK	Null	2	381.1	385.2	60.3	0.00	
		Native400 \times habitat type	5	1,152.7	1,163.0	0.0	0.81	
AB	Native400 + habitat type	Null	2	1,163.8	1,167.8	4.8	0.07	
		Habitat type	3	653.7	659.8	0.0	0.41	
		Native400 + habitat type	4	651.9	660.1	0.3	0.35	
		Native400 \times habitat type	5	651.7	662.0	2.2	0.13	
		Native400	3	656.2	662.3	2.5	0.11	
Bobolink	SK	Null	2	671.9	676.0	16.2	0.00	
		Native400 + habitat type	4	345.8	354.0	0.0	0.56	
Le Conte's sparrow	SK	Habitat type	3	349.6	355.7	1.7	0.24	
		Native400 \times habitat type	5	345.8	356.1	2.1	0.20	
		Null	2	413.7	417.7	63.7	0.00	
		Landscape type	4	401.5	409.6	0.0	0.44	
		Landscape type + habitat Type	5	401.2	411.4	1.8	0.18	
AB	Native400 + year	Landscape type + native400	5	401.4	411.7	2.1	0.16	
		Landscape type + native400 + habitat type	6	401.2	413.5	3.9	0.06	
		Null	2	410.3	414.4	4.8	0.04	
		Native400 \times year	6	131.7	144.2	0.0	0.30	
		Habitat type \times year	6	131.9	144.4	0.2	0.27	
		Year	4	137.8	146.1	1.9	0.12	
		Null	3	141.1	147.3	3.1	0.06	
		2006	Native400	3	131.5	137.8	0.0	0.49
		2007	Null	2	135.2	139.4	1.6	0.22
		Habitat type	3	57.5	63.9	0.0	0.41	
2006	Native400	Native400	3	57.7	64.0	0.1	0.37	
		Habitat type + native400	4	57.3	65.9	2.0	0.15	
		Null	2	63.2	67.4	3.5	0.07	
Western meadowlark	SK	Null	2	319.3	323.3	0.0	0.42	
		Habitat type	2	245.6	249.7	0.0	0.37	
AB	Native400	Native400	2	246.1	250.2	0.5	0.29	
		Habitat type + native400	3	244.8	250.9	1.2	0.20	
		Habitat type \times native400	4	243.7	251.9	2.2	0.12	
		Null	1	253.5	255.5	4.8	0.02	

Variation in Savannah sparrow abundance was best described by an interactive effect of habitat type and native400 in SK and by habitat type in AB (Table 2). In SK, Savannah sparrow abundance was similar on native (4.5 ± 0.4) and planted grassland (4.7 ± 0.4) parcels, but abundance on native parcels increased as native grassland in the surrounding landscape increased, whereas abundance on planted grassland parcels decreased (Fig. 2). Replacing native400 with planted400 resulted in a weaker model ($\Delta AIC_c = 6.3$). In AB, Savannah sparrow abundance was

greater in planted (3.4 ± 0.3) than native grassland (2.2 ± 0.2) parcels.

Bobolink abundance in SK was most influenced by habitat type and native400 (Table 2). Abundance was greater in planted (0.60 ± 0.12) than native (0.03 ± 0.01) grassland and abundance tended to increase on planted grassland parcels with increased native grassland in the surrounding landscape ($\beta = 1.28 \pm 0.64$; Fig. 2). Replacing native400 with planted400 suggested that bobolink abundance was not influenced by the amount of planted grassland in the

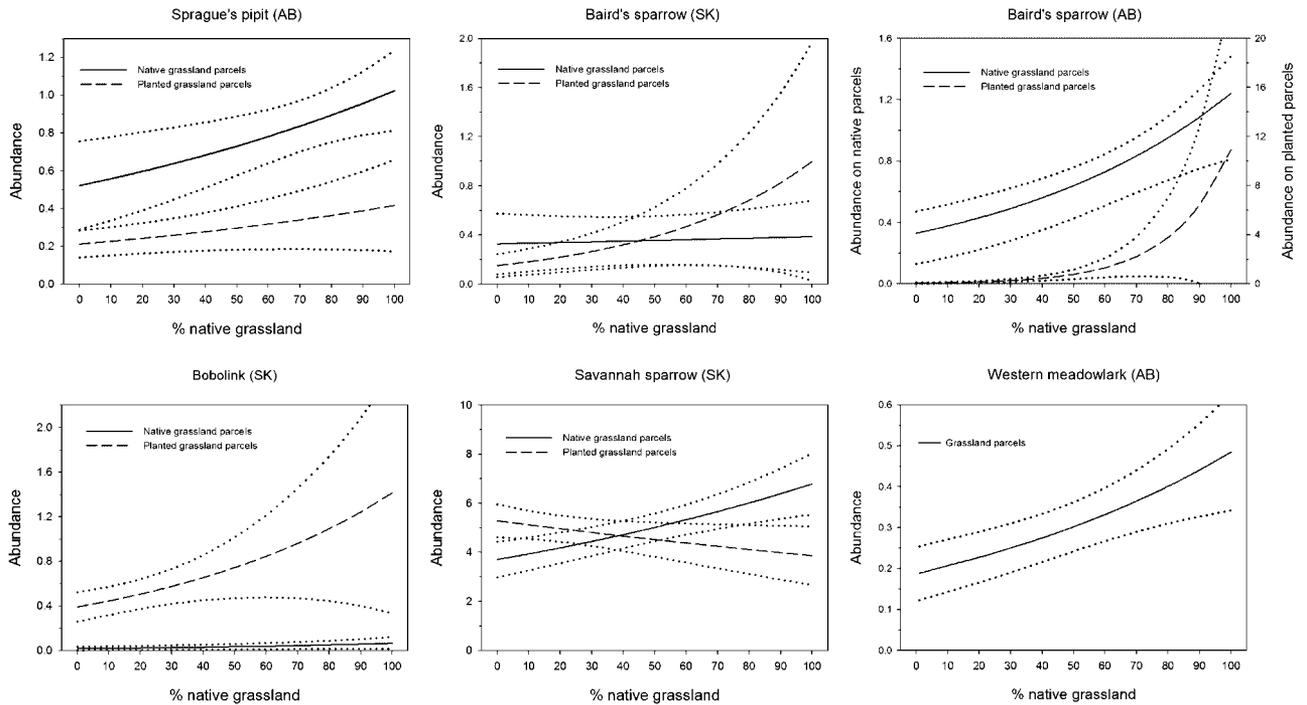


Figure 2. Mean abundance of grassland passerines in 65-ha native and planted grassland parcels varies as a function of the amount of native or planted grassland within 400 m of the parcel in Saskatchewan (SK) and Alberta (AB), 2006 and 2007. Dotted lines represent 85% confidence limits.

landscape ($\Delta AIC_c = 3.8$). We had too few bobolink detections in AB to analyze (Appendix A).

We analyzed years separately for Le Conte's sparrow in AB because abundance was most influenced by an interactive effect of year with both habitat type and native400 (Table 2). Abundance was best explained by NATIVE400 in 2006 (Table 2) with abundance increasing with the amount of native grassland within 400 m of the parcel ($\beta = 1.79 \pm 1.05$). Habitat type ranked as the best model for 2007 with abundance greater in planted (0.16 ± 0.08) than native (0.03 ± 0.02) grassland (Table 2). In SK, Le Conte's sparrow was most influenced by landscape type (Table 2). Abundance was greater in native grassland-dominated landscapes (0.37 ± 0.06) compared to planted grassland-dominated landscapes (0.12 ± 0.08). Abundance in cropland-dominated landscapes (0.30 ± 0.07) was not substantially different than the other 2 landscape types as 85% confidence intervals overlapped.

Habitat type and the amount of native grassland in the landscape had little influence on western meadowlark abundance in SK (Table 2). Variation in meadowlark abundance was best explained by habitat type in AB with abundance being greater in native (0.41 ± 0.07) than planted grassland (0.18 ± 0.05). Meadowlark abundance also increased with the amount of native grassland surrounding grassland parcels ($\beta = 0.95 \pm 0.35$; Fig. 2).

DISCUSSION

Habitat type and both the amount and type of grassland in the landscape matrix influenced the abundance of grassland passerines in both provinces. Furthermore, abundance was more strongly influenced by the amount and type of grass-

land within 400 m of the breeding parcel than at the 41-km² scale for all but Le Conte's sparrow in SK. Our results corroborate Koper and Schmiegelow's (2006b) contention that management strategies at scales useful for prairie-nesting waterfowl conservation may not be successful for songbird conservation in these landscapes. Passerine abundance appears to be influenced by landscape composition at scales of 200–1,600 m from breeding sites (Brotons et al. 2005, Cunningham and Johnson 2006, Ribic et al. 2009), spatial scales smaller than those influencing prairie-nesting waterfowl (Horn et al. 2005, Stephens et al. 2005). Predation is the primary factor affecting reproductive success in grasslands for waterfowl (Greenwood et al. 1995, West and Messmer 2004) and songbirds (Winter 1999, Davis 2003) and is an influential driver of habitat selection in birds (Martin 1993, 1998). However, predators on waterfowl such as striped skunk (*Mephitis mephitis*) and red fox (*Vulpes vulpes*) are likely influenced by landscape composition at larger spatial scales (Phillips et al. 2003) than the small mammalian predators of ground-nesting passerines (Pietz and Granfors 2000, Renfrew and Ribic 2008, Davis et al. 2012). The precise scale at which landscape composition is most influential on passerine abundance is difficult to determine from our data because landscape composition at the 400-m scale was strongly correlated with that at the 800-m scale and landscape composition between 400-m and 1,600-m scales are also highly correlated in our region (Davis et al. 2006). Nevertheless, models including grassland composition at the 400-m scale always outperformed models at the 800-m scale.

Songbirds varied in their response to habitat type and the amount and type of grassland in the surrounding landscape.

However, most species responded similarly to habitat and landscape type over the 2 years and in both provinces. Sprague's pipit was more common in native grasslands in SK and AB and abundance increased with the amount of native grassland in the landscape. Baird's sparrow abundance also increased with the amount of native grassland in the landscape in both provinces and years. These species' affinity for native grassland is well documented (Robbins and Dale 1999, Madden et al. 2000, Green et al. 2002) and the positive influence of the amount of native grassland surrounding native grassland parcels is consistent with findings that these species are area-sensitive (Davis 2004). However, Sprague's pipit did occur on planted grassland parcels in our study and they are known to occupy planted grasslands that are structurally similar to native grassland in other parts of their range (Davis and Duncan 1999, Davis et al. 1999, Madden et al. 2000). Baird's sparrows also occupy planted grasslands in other parts of their range (Green et al. 2002) and their abundance was similar in native and planted grasslands in our study. Sprague's pipit and Baird's sparrow may be more likely to occupy planted grasslands in native grassland landscapes because they are able to subsist on resources within planted grassland patches or supplement resources with those from the surrounding native grassland matrix (Dunning et al. 1992, Brotons et al. 2005). However, the extent to which either of these species place their territories near, or partly within planted grasslands, or whether they leave their territories to acquire resources elsewhere is unknown. Despite some pipits occupying planted grasslands, the lower abundance of this species in planted grassland parcels suggests that planted grasslands may be lower quality habitat (Lloyd and Martin 2005). A lower survival rate of post-fledging pipits in planted parcels compared to native provides further evidence that planted grasslands may be lower quality habitat for this threatened species (Fisher and Davis 2011).

In contrast to Baird's sparrow and Sprague's pipit, Savannah and Le Conte's sparrows, bobolink, and western meadowlark breed in a variety of native and planted grasslands (Martin and Gavin 1995, Lowther 2005, Davis and Lanyon 2008, Wheelwright and Rising 2008). Savannah sparrows were equally abundant in planted and native grasslands in SK and more abundant in planted grassland in AB. In SK, Savannah sparrow abundance increased in native grassland parcels when surrounded by native grassland in the landscape and increased in planted grassland parcels when surrounded by planted grassland. These results would be expected for an area-sensitive species, but previous research suggests that this grassland generalist is not influenced by patch size or landscape composition in the northern mixed-grass prairie (Johnson and Igl 2001, Davis 2004, Davis et al. 2006, Koper and Schmiegelow 2006a).

The effect of habitat type and amount of grassland in the surrounding landscape on Le Conte's sparrow abundance in AB depended upon the year surveys were conducted. In 2006, we found abundance was most strongly and positively influenced by the amount of native grassland within 400 m of the parcel, whereas in 2007, abundance was greatest in planted grassland parcels. Although abundance of Le Conte's

sparrows may fluctuate substantially among years (Igl and Johnson 1995), we cannot ascertain whether these results are a function of year- or geographic-specific factors since we used different study areas in each year. In SK, Le Conte's sparrows were most abundant in native-dominated landscapes, despite the species' affinity for planted grassland (Igl and Johnson 1995, McMaster and Davis 2001, Lowther 2005). However, Le Conte's sparrows are often associated with low-lying, moist grasslands (Lowther 2005) and distance to lakes and wetlands was shorter for point counts within native grassland-dominated landscapes (134 ± 4.5 m) compared to point counts in cropland (210 ± 14.3 m) and planted grassland (161 ± 8.2 m) landscape treatments. Thus, greater Le Conte's sparrow abundance in native-dominated grassland landscapes may have been attributed to a greater density of mesic sites.

Similar to Savannah and Le Conte's sparrows, we found inconsistent relationships between habitat and landscape type and abundance of western meadowlark in the 2 provinces. Meadowlarks occupy a variety of grassland habitats (Owens and Myres 1973, Davis and Lanyon 2008) and do not appear to be influenced by patch size (Knick and Rotenberry 1995, Davis 2004, Davis et al. 2006). However, the response of meadowlarks to the amount of grassland habitat surrounding a habitat patch and the type of grassland matrix may vary among regions (Johnson and Igl 2001). For example, Haroldson et al. (2006) found abundance to be influenced by the amount of planted grassland in the landscape and Owens and Myres (1973) found little difference in occurrence between survey routes containing 99% native grassland versus routes containing 66% cropland, whereas we found meadowlark abundance increased with the amount of native grassland within 400 m of grassland parcels in AB only.

Bobolinks were almost exclusively detected in planted parcels, but abundance increased with the amount of native grassland in the surrounding landscape. However, the amount of planted grassland in the landscape had little influence on bobolink abundance despite area sensitivity being documented for this species in other regions (Ribic et al. 2009). Herkert (1994) found that the minimum patch size requirement of bobolink was approximately 50 ha suggesting that our surveyed parcels (65 ha) likely met the species' needs. Native grassland surrounding planted parcels may increase the quality of planted parcels and thus attract more males (Brotons et al. 2005). Alternatively, if native grassland in the surrounding landscape is largely unsuitable (e.g., vegetation too short and sparse), it may cause more individuals to occupy planted grasslands (Brotons et al. 2005, McMaster et al. 2005).

MANAGEMENT AND IMPLICATIONS

Our results suggest that seeding cultivated land with exotic grasses and forbs will benefit grassland songbird generalists more so than grassland specialists. Conservation programs in the Northern Great Plains should focus on the preservation and enhancement of native grassland to sustain or enhance populations of grassland specialists. However, converting

cropland to non-native grassland near existing parcels of native grassland may be a useful conservation strategy in cropland-dominated landscapes. We caution against the use of invasive species in planted seed-mixes since they disrupt ecosystem function (Christian and Wilson 1999) and reduce habitat suitability for grassland specialists (Wilson and Belcher 1989, Davis and Duncan 1999). Conservation practitioners should also consider the amount and type of warm and cool season grasses and forbs in seed mixes (McCoy et al. 2001, Thompson et al. 2009), management type (Johnson 1997, McMaster and Davis 2001), and frequency (Luscier and Thompson 2009) when creating habitat for grassland species. We acknowledge that further work is required to determine whether the numerical responses to habitat type and landscape composition by grassland birds in our study reflect similar changes in vital rates, but we believe that enough information currently exists to take action with limited adverse consequences until more demographic information is available.

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Appendix A. Raw maximum abundance \pm standard error per parcel and frequency of occurrence (%) per point count of grassland birds in native and planted grassland parcels in southern Saskatchewan (SK) and southeastern Alberta (AB), 2006 and 2007. Sample sizes in parentheses indicate the number of grassland parcels sampled in each habitat type in each province ($n = \text{SK/AB}$).

Species/province	Native grassland ($n = 120/96$)	Planted grassland ($n = 146/83$)
Sprague's pipit		
SK	0.3 \pm 0.05 (27)	0.1 \pm 0.02 (9)
AB	0.8 \pm 0.07 (68)	0.2 \pm 0.05 (20)
Savannah sparrow		
SK	5.5 \pm 0.22 (99)	5.0 \pm 0.18 (97)
AB	2.1 \pm 0.15 (86)	3.6 \pm 0.19 (96)
Baird's sparrow		
SK	0.6 \pm 0.08 (41)	0.3 \pm 0.07 (20)
AB	1.0 \pm 0.11 (58)	0.2 \pm 0.07 (10)
Le Conte's sparrow		
SK	0.5 \pm 0.06 (41)	0.3 \pm 0.05 (28)
AB	0.2 \pm 0.06 (10)	0.3 \pm 0.07 (17)
Western meadowlark		
SK	0.3 \pm 0.04 (72)	0.2 \pm 0.04 (68)
AB	0.4 \pm 0.07 (31)	0.2 \pm 0.04 (17)
Bobolink		
SK	0.04 \pm 0.02 (4)	0.5 \pm 0.08 (31)
AB	0 (0)	0.04 \pm 0.02 (2)

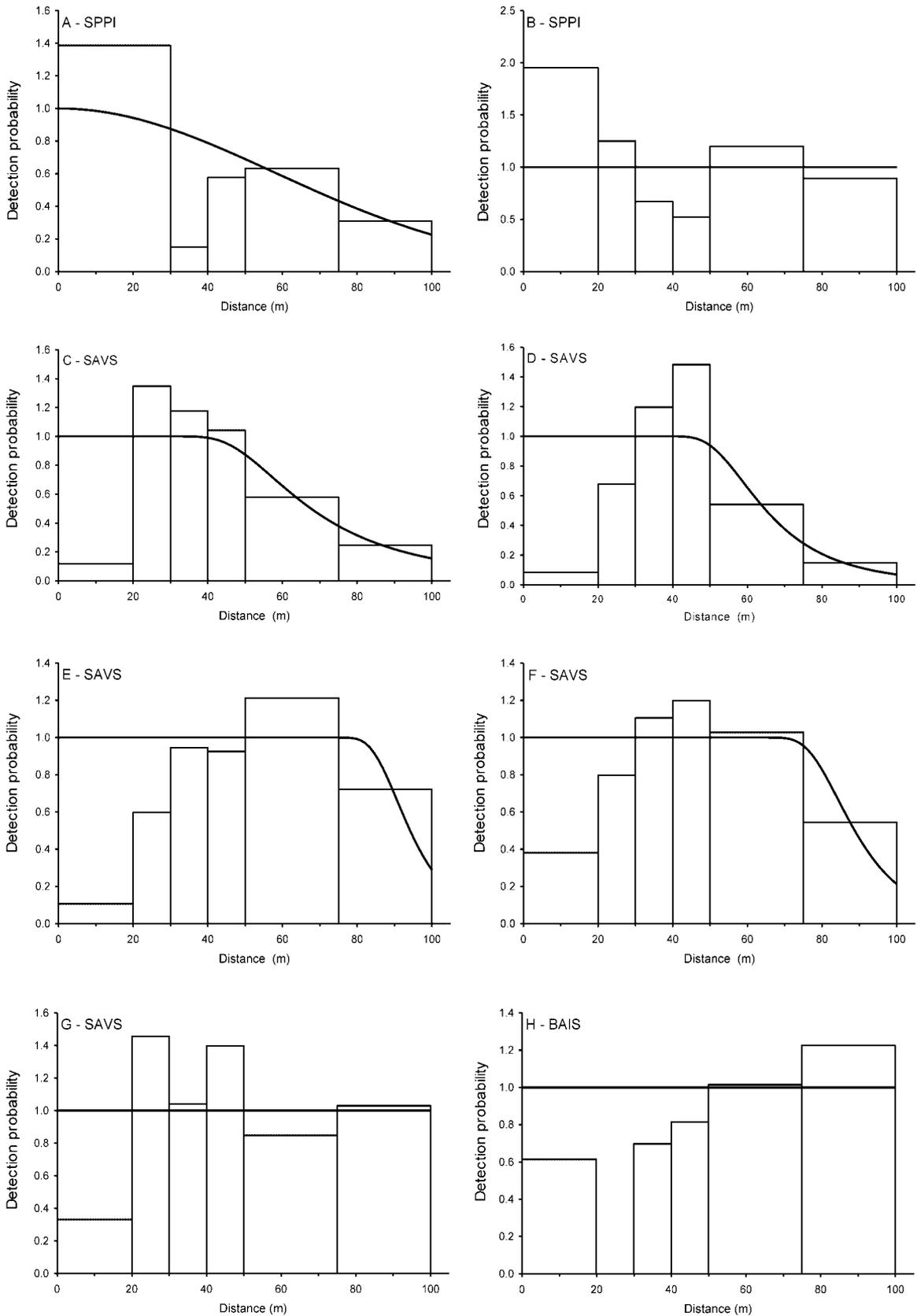
Appendix B. Sampling effort and model selection of detection functions for species and observer (Obs) combinations resulting from grassland bird surveys in 2006 and 2007 in Saskatchewan, Canada. Included is the top model (HR SP, hazard rate—simple polynomial; HR Cos, hazard rate-cosine; U Cos, uniform cosine; U SP, uniform—simple polynomial; NA, not applicable), number of detections used to generate the detection function (N), detection probability (P) with 95% lower (P LCL) and upper (P UCL) confidence limits, goodness-of-fit statistic (χ^2 GOF P), and whether the detection function violated the assumption that $P = 1.0$ in the first distance interval.

Species	Obs	Year	Top model	N	P	P LCL	P UCL	χ^2 GOF P	$P < 1.0$ in first interval?
Savannah sparrow	A	2006	HR SP	796	0.54	0.49	0.59	0	Yes
	B	2006	HR SP	589	0.49	0.45	0.53	0	Yes
	C	2007	HR Cos	823	0.88	0.81	0.96	0	Yes
	D	2007	HR Cos	682	0.8	0.72	0.89	0	Yes
Sprague's pipit	A	2006	NA	18					
	B	2006	NA	13					
	C	2007	NA	11					
Baird's sparrow	D	2007	NA	15					
	A	2006	NA	36					
	B	2006	U-Cos	41	1	1	1	0.057	Yes
	C	2007	U-Cos	46	1	1	1	0.08	Yes
Bobolink	D	2007	U-SP	41	1	1	1	0.517	Yes
	A	2006	NA	25					
	B	2006	NA	25					
	C	2007	NA	25					
Western meadowlark	D	2007	NA	25					
	A	2006	NA	19					
	B	2006	NA	12					
	C	2007	U-Cos	42	1	1	1	0.049	Yes
D	2007	NA	11						

Appendix C. Sampling effort and model selection of detection functions for species and observer (Obs) combinations resulting from grassland bird surveys in 2006 and 2007 in Alberta, Canada. Included is the top model (HR SP, hazard rate—simple polynomial; U SP, uniform—simple polynomial; U Cos, uniform cosine; HN Cos, half-normal cosine; NA, not applicable), number of detections used to generate the detection function (N), detection probability (P) with 95% lower (P LCL) and upper (P UCL) confidence limits, goodness-of-fit statistic (χ^2 GOF P), and whether the detection function violated the assumption that $P = 1.0$ in the first distance interval.

Species	Obs	Year	Top model	N	P	P LCL	P UCL	χ^2 GOF P	$P < 1.0$ in first interval?
Savannah sparrow	E	2006	HR SP	411	0.74	0.65	0.85	0.029	Yes
	F	2006	U SP	235	1	1	1	0.592	Yes
	G	2007	HR SP	359	0.71	0.62	0.82	0	Yes
	H	2007	U Cos	151	1	1	1	0.180	Yes
Sprague's pipit	E	2006	HN Cos	50	0.52	0.34	0.78	0.097	No
	F	2006	NA	31					
	G	2007	NA	23					
Baird's sparrow	H	2007	U SP	64	1	1	1	0.363	No
	E	2006	NA	28					
	F	2006	NA	17					
Bobolink	G	2007	U SP	92	1	1	1	0	Yes
	H	2007	U SP	57	1	1	1	0.031	Yes
	E	2006	NA	1					
Western meadowlark	F	2006	NA	0					
	G	2007	NA	5					
	H	2007	NA	1					
	E	2006	NA	14					
Western meadowlark	F	2006	NA	5					
	G	2007	NA	20					
	H	2007	NA	36					

Appendix D. Example histograms of grassland songbird detections as a function of distance (m) from various observers (A–H) and the estimated detection probability function (solid line) from grassland bird surveys in 2006 and 2007 in Saskatchewan and Alberta, Canada. Although some models fit the data (goodness-of-fit $\chi^2 P > 0.05$) and show no evasive movements (observers A, B), others indicate that detection probability is < 1.0 within the first interval (observers C–H). Species included are Sprague’s Pipit (SPPI), Savannah sparrow (SAVS), and Baird’s Sparrow (BAIS).



Appendix E. Detection probability (P) of 6 species from grassland bird surveys in 2006 and 2007 in Saskatchewan (SK) and Alberta (AB) based on removal sampling. We only used detections that were <100 m from the point count center. The p(.) model represents constant detection probability with no covariate effects, and p(date) is a model that included survey date.

Species	Study area	Top model	P
Baird's sparrow	SK	p(.)	0.857
	AB	p(.)	0.901
Savannah sparrow	SK	p(.)	0.757
	AB	p(.)	0.876
Le Conte's sparrow	SK	p(.)	0.887
	AB	na ^a	
Western meadowlark	SK	p(date)	Early = 0.803, late = 0.989
	AB	p(.)	0.603
Sprague's pipit	SK	p(.)	0.946
	AB	p(date)	Early = 0.974, late = 0.999
Bobolink	SK	p(.)	0.724
	AB	na	

^a Sample size was <30, therefore we did not conduct detection analyses.