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MIXED-GRASS PRAIRIE PASSERINES EXHIBIT WEAK AND VARIABLE RESPONSES TO PATCH SIZE

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A .—Much of our current understanding of the demographic e ects of habitat fragmentation on bird populations is derived from studies of passerines in forests and tallgrass prairie surrounded by woody vegetation. We quantified grassland bird density, nest survival, and productivity in 41 native mixed-grass prairie pastures during 1997–2000 in southern Saskatchewan, Canada. Pastures ranged in size from 18 ha to 11,600 ha and were typically surrounded by agriculture (i.e., ranching and annual cropping). Grassland passerines did not respond strongly or uniformly to patch size. Sprague's Pipit (*Anthus spragueii*) was the only species whose density increased with pasture size. Patch size had minimal influence on nest survival of Sprague's Pipit or Clay-colored Sparrow (*Spizella pallida*); whereas nest survival increased with patch size for Savannah Sparrow (*Passerculus sandwichensis*) and declined for Baird's Sparrow (*Ammodramus bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta* de type prairie herbacée indigène en 1997–2000 dans le sud de la Saskatchewan, Canada. Les pâturages avaient une taille qui variait de 18 à 11 600 ha et ils étaient généralement entourés par des activités agricoles (i.e. élevage et cultures annuelles). Les passereaux répondaient faiblement et de manière non uniforme à la taille des parcelles d'habitats. *Anthus spragueii* a été la seule espèce dont la densité augmentait avec la taille des prairies. La taille des parcelles avait une influence minimale sur la survie des couvées d'*Anthus spragueii* et de *Spizella pallida*, alors que la survie des couvées augmentait avec la taille des parcelles pour *Passerculus sandwichensis* et déclinait chez *Ammodramus bairdii*, *Calcarius ornatus* et *Sturnella neglecta*. Les facteurs temporelles (i.e. l'âge, la date et l'année de la couvée) étaient des prédicateurs plus importants de la survie des couvées que la taille des parcelles. Des analyses exploratoires ont indiqué que les e ets sur la survie des couvées de la distance à la bordure, de la forme des pâturages et du paysage étaient aussi peu probables que les e ets de taille des parcelles. Néanmoins, les e ets de bordure sur *Calcarius ornatus* pourraient être issus de facteurs qui agissent à l'échelle du paysage, puisque la survie des couvées diminuait avec la distance à la bordure dans les paysages avec des quantités croissantes de cultures. Nos résultats indiquent que les parcelles de 18 ha de prairies herbacées jouent un rôle important dans la conservation de plusieurs espèces de passereaux de prairie actuellement en déclin. Mais, la conservation d'*Anthus spragueii* dépend probablement du maintien de plus larges étendues de prairies indigènes.

H been cited as the most important factor threatening biological diversity (Noss 1991; but see Fahrig 2003). Consequences of habitat fragmentation include a reduction in the size of remaining habitat patches, increased isolation of remaining habitat patches, and reduced amount of core habitat because of the increased ratio of edge to interior habitat (Temple and Cary 1988, Wiens 1995). Thus, in fragmented landscapes, habitat interior species may experience lower reproductive success because they are forced to nest near habitat edges, where they are more susceptible to nest predators and brood parasites (Gates and Gysel 1978, Winter et al. 2000). Much of our current understanding of the demographic e ects of habitat fragmentation on birds is derived from passerine studies in forests (Thompson et al. 2002) and tallgrass prairie (Johnson and Temple 1986, 1990; Winter and Faaborg 1999; Winter et al. 2000). Few fragmentation studies have been conducted in the northern mixed-grass prairie region, where annual precipitation is lower than that found in tallgrass prairie regions (Bragg and Steuter 1996). Hence, the habitat surrounding patches of mixed-grass prairie is typically similar in structure to the prairie patch itself (e.g., rangeland and cropland), whereas patches of tallgrass prairie are frequently surrounded by habitat that di ers in structure, such as woodlands or shrublands (Johnson and Temple 1986, Winter et al. 2000). Fragmentation e ects documented in grassland patches surrounded by woody cover likely di er from grasslands that are similar in structure to the surrounding vegetation. Winter et al. (2000) found that nest success of tallgrass prairie passerines declined with increasing proximity to wooded edges, but not to roads or agricultural fields.

Studies conducted in arid and semiarid prairies have relied on artificial nests to examine fragmentation e ects on grassland birds (Pasitschniak-Arts and Messier 1995, Howard et al. 2001) and, thus, may not reflect predation rates or pa erns of real nests (Paton 1994, Davison and Bollinger 2000). Because of the lack of information concerning fragmentation e ects on the demography of mixed-grass prairie birds, conservation programs have assumed that the response of grassland birds to habitat fragmentation in mixed-grass prairie is similar to that observed in tallgrass prairie (Fitzgerald et al. 1999).

Our primary objectives were to determine whether grassland bird density, nest survival, and productivity are influenced by patch size. We focused on the six most common nesting passerines on mixed-grass prairie in Saskatchewan: Sprague's Pipit (*Anthus spragueii*), Clay-colored Sparrow (*Spizella pallida*), Savannah Sparrow

(*Passerculus sandwichensis*), Baird's Sparrow (*Ammodramus bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*).

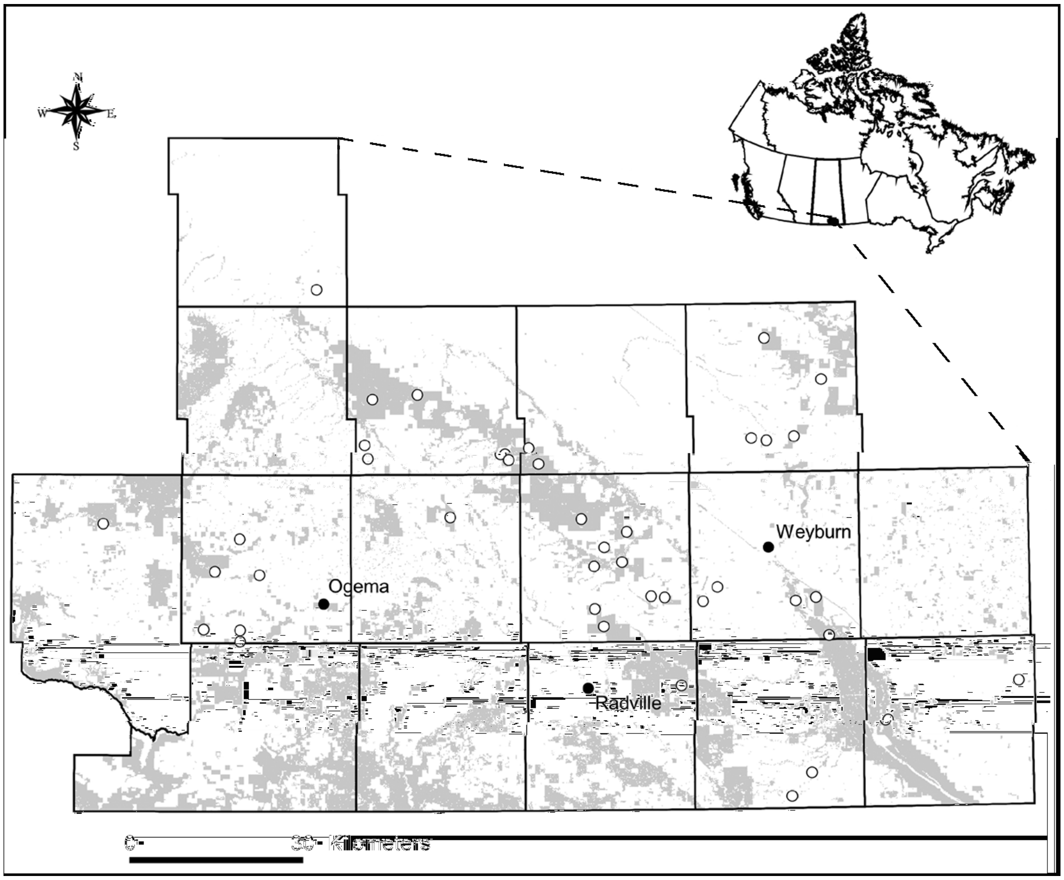
M

Study area and sites.—We conducted the study on native pastures in southern Saskatchewan along the border of the Mixed and Moist-mixed Grassland ecoregions from 1997 to 2000. The moist-mixed grassland represents the northern extent of the open grasslands in Saskatchewan and borders the Aspen Parkland ecoregion to the north. This region is characterized by semi-arid conditions and dark brown soils, whereas the mixed grassland is the driest region of Saskatchewan and is characterized by brown soils. Because of the low moisture levels, trees are scarce and shrubs are restricted to mesic areas (Ecological Stratification Working Group 1995). In our study, native pastures were typically surrounded by cropland and were bordered by roads on at least one side. Pastures were flat to gently rolling, and vegetation consisted predominantly of *Stipa* spp., June grass (*Koeleria macrantha*), thickspike wheatgrass (*Elymus lanceolatus*), western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), sedges (*Carex* spp.), lesser spikemoss (*Selaginella densa*), sage (*Artemisia* spp.), and various other forbs. The most common shrubs were western snowberry (*Symphoricarpos occidentalis*) and rose (*Rosa* spp.). Aspen (*Populus tremuloides*) was rare on the pastures and was typically associated with riparian areas and farmsteads.

The study area comprised 12 rural municipalities (RMs) totalling ~10,500 km^2. Amount of native grassland remaining in an RM ranged from 1% to 28%, with 17% remaining in the study area overall (Fig. 1). We selected study sites from patches of native mixed-grass prairie identified from 1:20,000 aerial photographs in 1997 and 1998, and classified 1995 Landsat thematic mapper imagery in 1999 and 2000. We identified a pool of potential patches from each of three size categories (<65, 65–256, and >256 ha) in each year of the study to ensure that patch sizes were evenly distributed among years and that a wide range of patch sizes was considered for the study. A subset of patches was randomly selected from each size category. Patches not selected were set aside for consideration in subsequent years (but see below). We visited grassland patches identified from aerial photographs and satellite images before the field season to determine their suitability. We retained pastures only if they had never been cultivated, were in fair to excellent range condition (Task Group on Unity in Concepts and Terminology 1995), and had experienced light to moderate grazing intensity the previous year. These criteria were chosen to reduce confounding effects of vegetation on pasture size, to increase the likelihood of high-priority species (i.e., Baird's Sparrow and Sprague's Pipit) breeding on the pastures, and to ensure a similar bird community among sites. Ultimately, we were restricted to working in pastures where landowners permitted access to their land. These criteria often resulted in some pastures not being included in the study, particularly pastures <256 ha. Subsequently, some sites were located opportunistically while in the field. Overall, 41 native prairie pastures (12 small, 12 medium, and 17 large), ranging in size from 18 ha to 11,600 ha, were included in the study. Although pastures tended to be square or rectangular in shape, small patches were more irregularly shaped, because the ratio of edge to interior habitat decreased with increasing pasture size (Pearson's $r = -0.82$, $P < 0.001$). Agriculture and Agri-Food Canada's Prairie Farm Rehabilitation Administration managed nine pastures, whereas the remaining pastures were privately managed. All pastures were actively grazed, but four study plots were located in paddocks that did not contain cattle during the field season. Vegetation structure and species composition in these plots were indistinguishable from sites where cattle were present.

Habitat patch delineation and landscape composition.—We ground-truthed a 3.2-km buffer around each study plot and made corrections on 1:20,000 air photographs and township-level site maps derived from classified satellite imagery. These corrections were then used to update the imagery in ARCVIEW, version 3.1 (Environmental Systems Research Institute, Redlands, California). Habitat patches were defined as areas of contiguous native prairie. Changes in land use, such as cropland, seeded pasture and hayland, wooded riparian areas, and ditched roads, delineated native-prairie patches.

Density and demography.—We established a 14–16 ha study plot near the center of each



F . 1. Study area and location of pastures in Saskatchewan Rural Municipalities where nest searching was conducted, 1997–2000. Clear circles represent study sites, and solid black dots are locations of nearest towns. Remaining grassland habitat is represented in grey.

pasture and partitioned it into 50-m grids with bamboo stakes (~50 cm in length) and surveyor flags. Because of the shape and size of one pasture, we could only fit a 9-ha study plot into it. The 50-m grid within each study plot allowed us to map habitat features (e.g., shrubs) and more accurately record the location of territorial males detected during spot-mapping surveys (Robbins 1970). The entire area of each study plot was surveyed five or six times from 2 June to 15 August on days with no precipitation and with wind speed <20 km h^{-1}. Surveys were conducted mostly during the morning (0700–1030 hours CST), though a few surveys were conducted during the late a ernoon and early evening periods under favorable conditions. A trained observer recorded all bird observations within 50 m on a site map containing landmark features (e.g., shrubs, wetlands, fence lines, etc.) plo ed in relation to the grid points. Birds flying over the plot were noted but not included in any analyses. One observer conducted surveys in 1997–1999, and a second observer conducted surveys in 2000. The result of each day's survey was plo ed on a composite map to delineate clusters of territorial males recorded in each of the surveys.

Nest searching and monitoring were carried out from early May to early August. Between 0730 and 1400 hours, we systematically located nests by flushing adult birds using a weighted 25-m nylon rope with aluminium and tin cans a ached every 0.5 m, pulled between two people. Each study plot was systematically searched five or six times during the breeding season. We also located nests fortuitously while walking on pastures conducting other activities. Nests were marked with surveyor flags and bamboo stakes 5 m away and inspected every 2–5 days until the young fledged or the nesting attempt ended. We candled eggs (Lokemoen and Koford 1996) to determine hatching dates to allow increased accuracy of survival rates. Nest attempts were considered successful if at least one nestling of the parental species survived to fledging age (i.e., left the nest). Cues such as adult(s) uttering alarm calls nearby, minimal nest disturbance, and presence of feces and feather scales in the nest were used, along with nestling age, to determine whether nests were successful. Twelve pastures–study plots were searched in 1997 and 1998, 10 in 1999, and 7 in 2000.

Data analysis.—We used SAS, versions 8 or 9 (SAS Institute 1999), for all analyses. All means are presented along with standard errors, except where noted. We used an information-theoretic approach (Burnham and Anderson 1998) to determine whether pasture size influenced density of singing males, clutch size, nest survival, and productivity (number of young fledged per nest) of six grassland passerines. Pasture size was log transformed for all analyses. For density models, we used generalized linear models (PROC GENMOD) with a log link and modeled the number of territories delineated in the study plot as a random variable with a Poisson distribution. The size of the study plot (log transformed) was used as an offset function. Covariates of interest included pasture size, shape (ratio of edge habitat [km] to patch area [ha]), year, and size * year and shape * year interactions. Patch shape was included because Davis (2004) found it to be a good predictor of relative abundance and occurrence for grassland passerines in this region. Because pasture size and shape were correlated (Pearson's $r = 0.76$), we considered them separately, which resulted in 10 models (including a null and a global model) being examined overall. Variance inflation factors for global models were as high as 3.3, which indicated that the data were overdispersed. Therefore, we used Akaike's Information Criterion (AIC) corrected for overdispersion and small sample size ($QAIC_c$; Burnham and Anderson 1998) to select the model that best fit the data. We calculated $QAIC_c$ weights (W_i) on the basis of all candidate models following Burnham and Anderson (1998); these represent the likelihood that a particular model is the best given the data and the candidate models considered. The same 10 models were examined to determine whether clutch size varied as a function of patch size. We modeled the relationship between clutch size and covariates using generalized estimating equations (GEE). We treated clutch size as a random Poisson-distributed variable and modeled the relationships using a log-link function with an exchangeable correlation structure to account for lack of dependence among nests within a pasture. Because GEE is not a full likelihood-modeling method, we used a quasi-likelihood-based information criterion (QICu; Pan 2001) to select the most-parsimonious models.

We used the logistic-exposure method (Shaffer 2004) to determine whether nest survival varied as a function of patch size. Before modeling nest survival and patch size, we first evaluated time-specific effects of nest age and date, because these have been shown to influence survival of grassland passerine nests (Grant et al. 2005). *A priori* models that we considered included linear effects of age and date, quadratic effects of age and date, cubic effect of age, a null model (constant survival), and a global model. We considered models with and without year effects for a total of 21 models. Quadratic models included both linear (x) and quadratic (x^2) terms; whereas cubic models included linear, quadratic, and cubic terms (x^3). We used the effective sample size (Rotella et al. 2004) to calculate AIC_c and considered the model with the lowest AIC_c score to be the best-fitting model. We attempted to account for variation in survival among pastures (i.e., site effects) by nesting sites within years and including site as a class variable in our models. However, we could not quantify site effects in this manner for four of the six species because small sample sizes precluded model convergence. Models failed to converge regardless of whether we modeled site effects as fixed or random for all species, except Baird's Sparrow and Chestnut-collared Longspur. We compared time-specific nest survival models with and without site effects for these two species and observed similar patterns. Therefore, we present results of the simpler analysis (i.e., ignoring site effects) for all six species.

After we identified the best time-specific model, we compared it with four patch-size models, along with a null and a global model. Patch-size models included a linear effect of size, additive effects of size and year, interaction between size and year, and the best time-specific model with pasture size included. This allowed us to determine whether patch size explained additional variation not accounted for by time-specific e ects. We initially employed GEE to account for potential dependence among nests within a pasture, but found li le evidence of correlation among nests ($r < 0.02$).

We a empted to quantify the relationship between the number of young fledged per nest and pasture size using GEE, but our models failed to converge. Instead, we used multiple linear regression (PROC GLM) to determine whether pasture size influenced the mean number of young fledged per nest a empt. Pastures were used as sample units to avoid pseudoreplication (Hurlbert 1984). We used the square root of the number of nests in each pasture as a weighting factor to account for unequal samples among pastures. Covariates of interest included pasture size, year, and a size * year interaction. We fit four models using combinations of these variables along with a null model and selected the model with the lowest AIC_c as our best model. We performed the same analysis on the number of young fledged per successful nest.

Our *a priori* hypotheses centered on patch-level e ects. However, it has been suggested that landscape e ects are an important factor governing processes at the patch level (Thompson et al. 2002, Fahrig 2003). Thus, we conducted exploratory analyses to investigate the importance of landscape composition on survival of grassland passerine nests. We compared four types of models: (1) nest, (2) patch, (3) landscape, and (4) nest and patch-level interactions within landscapes. Time-specific variables from the best time-specific model were included in all models, resulting in a total of 17 models examined overall. The nest-level model included distance to edge, and patch-level models comprised patch size and shape. We were unsure at what scale landscape influences nest survival of grassland passerines, so we considered three scales: 0.8-, 1.6-, and 3.2-km radius bu er from the center of the study plot. Proportion of cropland in the landscape was calculated for each bu er size, because cropland is the dominant cover type in the landscape (along with grassland) and the primary cover type fragmenting extant prairie patches in this region. We used 3.2 km as our largest radius because predators are the primary cause of reproductive failure in grassland species in this area (Davis 2003), with small mammals being the dominant predators (Pietz and Granfors 2000, Grant et al. 2006). Thus, it seems unlikely that spatial scales >3.2 km are appropriate when examining landscape e ects on grassland passerine nest survival in this region.

R

Density.—Patch size or shape was the best predictor of density for only Sprague's Pipit (Table 1). Additive e ects of year and pasture size best explained variation in Sprague's Pipit density, with density increasing with pasture size in each of the four years (slope = 0.11 ± 0.04). Although the year model received the most support for Western Meadowlark, pasture size and shape likely influenced density of Western Meadowlarks, because $\Delta QAIC_c$ scores were within 0.7 units of the best model and both models received substantially more weight than the null model (Table 1). However, standard errors were relatively large for models comprising additive e ects of year and shape or year and size (slopes = 0.05 ± 0.04).

Clutch size.—Clutch size did not vary with pasture size, pasture shape, or year for any of the six species. In every case, the null model received the most support (i.e., lowest $QAIC_c$ score) and was within 1.5 $QAIC_c$ units of the next best supporting model.

Nest survival and productivity.—Model selection results indicated that there was li le support for constant daily nest survival rates (Table 2). Age e ects were included in all of the top models with nest survival of four species best explained by a cubic e ect of age. Sprague's Pipit nest survival decreased with age, whereas the e ect of age was dependent on date for Clay-colored Sparrow (Table 2). Nest survival of Baird's Sparrow, Chestnut-collared Longspur, and Western Meadowlark was highest during early to mid-incubation and lowest 5–7 days a er hatching (Fig. 2). Savannah Sparrow nest survival decreased during late incubation and shortly a er hatch but stabilized a few days before fledging (Fig. 2). In addition to age e ects, nest survival also varied by date and among years for most species (Table 2), though unconditional standard errors were large in relation to model-averaged parameter estimates in most cases.

Patch size was included in the top candidate models for each species and included in the best model for four species (Table 3). Nest survival for Baird's Sparrow, Chestnut-collared Longspur, and Western Meadowlark was inversely correlated with pasture size, T 2. Selection results for models explaining variation in nest survival as a function of time-specific e ects for six mixed-grass prairie passerines. Models include the best model (lowest AIC_c value), candidate models within two ΔAIC_c units from the best model, and null (constant survival) models. Number of parameters (*K*) and AIC_c weights (W_i) for each model are provided. Global models include linear, quadratic, and cubic e ects of age; linear and quadratic e ects of date; age * date interactions; year; and combinations. Twenty-one models were considered (*n* = e ective sample size and actual number of nests used in analyses [e.g., 793 and 65]).

Species	Model	*K*	AIC_c	ΔAIC_c	W_i
Sprague's Pipit	(–)Age, year	5	289.8	0.0	0.42
(*n* = 793 and 65)	Age^2, year	6	291.7	1.9	0.16
	(–)Age, year, (+)date	6	291.9	2.1	0.15
	Null	1	306.3	16.5	0.00
Clay-colored Sparrow	Age * date	4	248.8	0.0	0.57
(*n* = 543 and 69)	Null	1	290.8	6.0	0.03
Savannah Sparrow	(+)Date, age^3, year	8	288.3	0.0	0.22
(*n* = 688.5 and 75)	(+)Date, (–)age, year	6	288.5	0.2	0.20
	(+)Date, (–)age, age * date, year	10	290.0	1.7	0.09
	(+)Date, (–)age	3	290.1	1.8	0.09
	(+)$Date^2$, age^3, year	9	290.3	2.0	0.08
	(+)Date, age^3	5	290.3	2.0	0.08
	Null	1	303.9	15.6	0.00
Baird's Sparrow	Age^3, year	7	686.8	0.0	0.25
(*n* = 1,576 and 164)	Age^3, (+)date	5	687.2	0.4	0.20
	Age^3, (+)date, year	8	687.6	0.8	0.16
	Age^3	4	687.7	0.9	0.15
	Age^3, $date^2$	6	688.4	1.6	0.11
	Age^3, $date^2$, year	9	688.6	1.8	0.10
	Null	1	717.2	30.4	0.00
Chestnut-collared Longspur	Age^3, year	7	1630.6	0.0	0.38
	Age^3, year, (+)date	8	1631.8	1.2	0.21
(*n* = 3,615.5 and 379)	Age^3	4	1632.0	1.4	0.19
	Null	1	1650.6	20.0	0.00
Western Meadowlark	Age^3, (+)date	5	337.4	0.0	0.49
(*n* = 783 and 80)	Age^3, $date^2$	6	338.5	1.1	0.28
	Null	1	349.1	11.7	0.00

D

Overall, we found limited support for patch-size e ects on density, clutch size, nest survival, and productivity for most mixed-grass prairie passerines in our study. In addition, the grassland species in the present study exhibited both positive and negative responses to patch size, and patch-size response varied among years for some species.

Density.—Species with greater densities on larger habitat patches are termed area-sensitive. Although factors influencing area-sensitivity have not been explored in most grassland systems (but see Winter et al. 2000), previous research has found that several grassland bird species are found more o en and in higher abundance in relatively large parcels of remnant grassland habitat (Vickery et al. 1994, Johnson and Igl 2001, Davis 2004). Sprague's Pipit was the only species whose density consistently increased with pasture size over the four years of the study, supporting a separate study where Davis (2004) found Sprague's Pipits to be area-sensitive.

Pasture size had li le influence on the density of five of the six species in our study. Pa erns of area-sensitivity appear to vary spatially for grassland birds. For example, Johnson and Igl (2001) found evidence of area-sensitivity for grassland passerines in some regions, but did not find support for the same

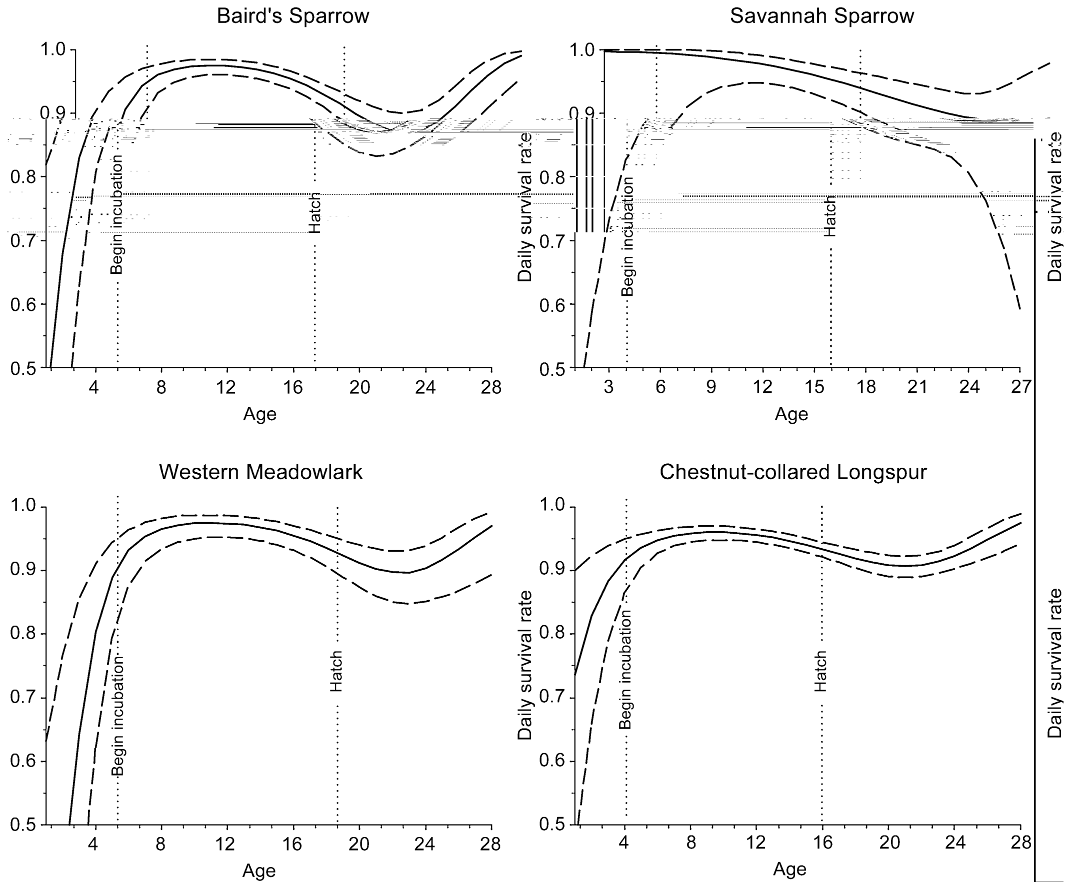


FIG. 2. Cubic age effects best explain variation in nest survival for four grassland passerines in southern Saskatchewan. Dates were held at their median value for Savannah Sparrow and Western Meadowlark, and years were held at a value of 0.25 for each of the four years for Baird's Sparrow and Chestnut-collared Longspur models. Ages for the onset of incubation and hatching are provided for each species. Dashed lines are 95% confidence limits.

species in other regions. Similarly, we found no evidence for patch-size effects for Baird's Sparrow and Chestnut-collared Longspur, yet Davis (2004) found these species to be area-sensitive and most common in pastures >25 ha and >39 ha, respectively. These differences may be attributable to variation in regional abundance or landscape composition, but may also arise from the present study having only three pastures <40 ha. Some species appear to be influenced more by local vegetation characteristics within the patch (Davis 2004) or by encroaching vegetation along the periphery of the patch (Johnson and Igl 2001) than by factors at larger spatial scales (Knick and Rotenberry 1995).

Nest survival and productivity.—Although it is unclear whether habitat fragmentation or habitat loss is the primary driver (Fahrig 2003), demographic studies conducted in fragmented landscapes have typically shown that birds breeding in small parcels of habitat experience lower nest success than those breeding in larger fragments. This has been documented for forest (Donovan et al. 1995, Hoover et al. 1995; but see Tewksbury et al. 1998, Fauth 2000) and tallgrass prairie birds (Winter and Faaborg 1999, Winter et al. 2000). Patch size was included in the best model for four of the six species in our study. Survival of Savannah Sparrow nests exhibited a positive association with pasture size, whereas survival of Baird's Sparrow, Chestnut-collared

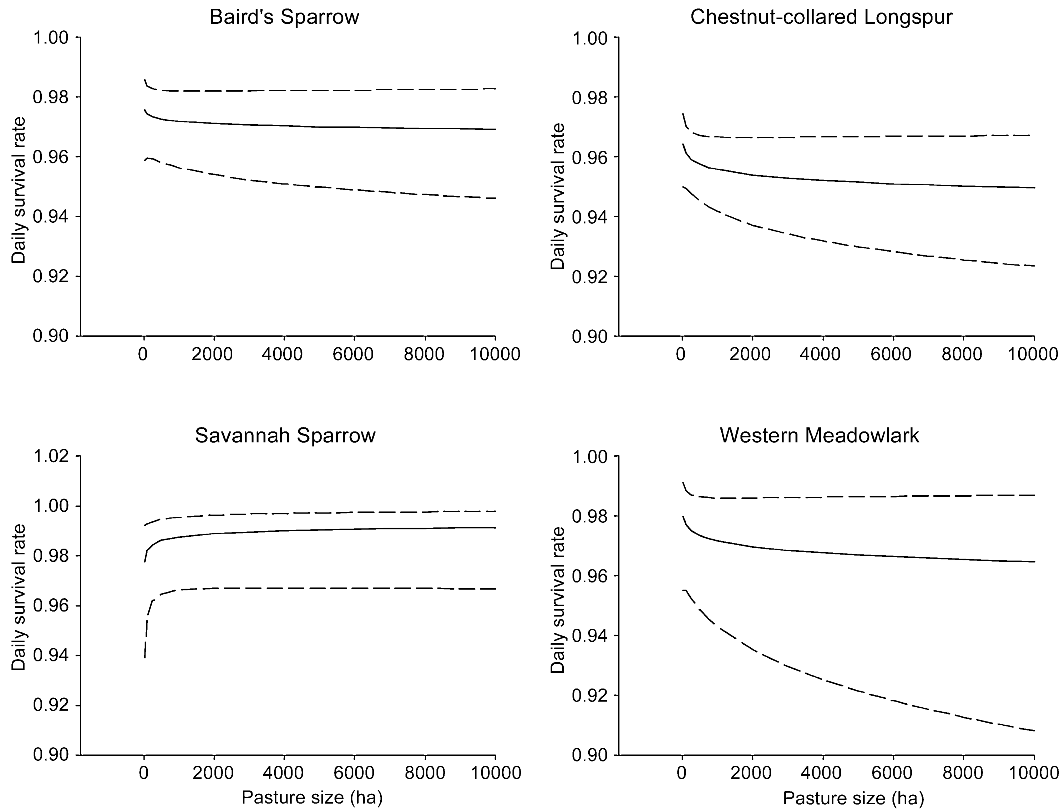
T 3. Selection results for models explaining variation in nest survival as a function of patch size and time-specific variables for six mixed-grass prairie passerines. Models include the best model (lowest AIC_c value), candidate models within two ΔAIC_c units from the best model, the best time-specific model, and null (constant survival) models. Number of parameters (K) and AIC_c weights (W_i) for each model are provided. Models included a linear e ect of size, additive e ect of size and year, interaction between size and year, the best time-specific model with and without pasture size added, and a null and a global model (n = e ective sample size and actual number of nests used in analyses).

Species	Model	K	AIC_c	ΔAIC_c	W_i
Sprague's Pipit	(–)Age, year	5	289.8	0.0	0.65
(n = 793 and 65)	(–)Age, year, (–)size	6	291.6	1.8	0.27
	Null	1	306.3	16.5	0.00
Clay-colored Sparrow	Age * date	4	284.8	0.0	0.61
(n = 543 and 69)	Age * date, (–)size	5	286.6	1.8	0.24
	Null	1	290.9	6.1	0.03
Savannah Sparrow	Year, age^3, (+)date, (+)size	9	287.5	0.0	0.45
(n = 688.5 and 75)	Year, age^3, (+)date	8	288.3	0.8	0.30
	Year, age^3, (+)date, (+)size, size * year	10	288.7	1.2	0.25
	Null	1	303.9	16.4	0.00
Baird's Sparrow	Age^3, year, (–)size	8	686.8	0.0	0.83
(n = 1,576 and 164)	Age^3, year	7	690.3	3.5	0.14
	Null	1	717.2	30.4	0.00
Chestnut-collared	Age^3, year, (–)size	8	1628.7	0.0	0.63
Longspur	Age^3, year	7	1630.6	1.9	0.24
(n = 3,616.5 and 379)	Null	1	1650.6	21.9	0.00
Western Meadowlark	Age^3, (+)date, (–)size	6	336.5	0.0	0.56
(n = 783 and 80)	Age^3, (+)date	5	337.4	0.9	0.36
	Null	1	349.1	12.6	0.0

T 4. Selection results for models explaining variation in productivity (mean number of young fledged per nest) as a function of patch size. Models include the best model (lowest AIC_c value), candidate models within two ΔAIC_c units from the best model, and null (constant survival) models. Number of parameters (K) and AIC_c weights (W_i) for each model are provided. The five models examined include a null model and all combinations of pasture size (size) and year e ects, including a size * year interaction (n = number of pastures). Null models received the most support for Clay-colored and Savannah sparrows and Western Meadowlark.

Species	Model	K	AIC_c	ΔAIC_c	W_i
Sprague's Pipit (n = 24)	(+)Size, year	6	17.4	0.0	0.51
	Size * year	7	19.1	1.7	0.22
	Null	1	19.1	1.7	0.22
Baird's Sparrow (n = 36)	Size * year	7	14.6	0.0	0.57

Longspur, and Western Meadowlark nests exhibited an inverse relationship. However, these relationships were weak, and nest survival was influenced more by time-specific e ects (e.g., age and date) than by patch size or by nest-site vegetation (Davis 2005). The increased support for patch-size e ects was likely a function of the small penalty associated with adding one more parameter (i.e., patch size) to time-specific models.



F . 3. Relationship between daily nest-survival rate and pasture size (ha) for four grassland passerines in southern Saskatchewan. Nest age was held at the mid-incubation period, date was held at the median value, and year was held at 0.25 for each of the four years. Dashed lines are 95% confidence limits.

T 5. Model selection results comparing the best patch-size (size) model with nest survival models incorporating distance-to-edge (edge), patch shape (shape), and proportion of cropland in the landscape for Chestnut-collared Longspur (n = 3,616.5 and 379, with n = e ective sample size and actual number of nests). Proportion of cropland was quantified within circles of 0.8-km (crop8), 1.6-km (crop16), and 3.2-km (crop32) radius from the center of each study plot. Models include the best model (lowest AIC_c value), candidate models within two ΔAIC_c units from the best model, best patch-size model, and null (constant survival) models. Number of parameters (K) and AIC_c weights (W_i) for each model are provided. Global models include cubic e ects of age, year, pasture size and shape, edge distance, landscape, and interactions. Eighteen models were considered. Pasture size e ects were within two ΔAIC_c units of edge, patch, and landscape models for the other five species.

Model	K	AIC_c	ΔAIC_c	W_i
Crop16 * edge, year, age^3	10	1625.9	0.0	0.28
Crop8 * edge, year, age^3	10	1626.4	0.5	0.22
Crop32 * edge, year, age^3	10	1627.3	1.4	0.14
Size, year, age^3	8	1629.9	4.0	0.04
Null	1	1650.6	24.7	0.00

Patch-size e ects were weak in our study likely because agricultural fields and roads were the primary edge habitat bordering our sites. Agricultural edges may not appreciably concentrate predators or influence their foraging behavior. Winter et al. (2000) found that nest success declined with increasing proximity to wooded edges, but not to roads or agricultural fields; they a ributed the increased predation to activity of mid-sized predators along wooded edges. Pasitchniak-Arts and Messier (1995) detected no relationship between survival of artificial nests and proximity to agricultural edges in mixed-grass prairie and aspen parkland, and Howard et al. (2001) failed to detect patch-size or edge e ects in short-grass prairie surrounded by agricultural fields.

Our inability to detect patch-size e ects may also be a ributable to our study not explicitly considering patch sizes within landscapes of varying amounts of grassland habitat or woody cover. Instead, landscape composition surrounding our prairie patches was such that small patches occurred in cropland-dominated landscapes and larger patches occurred in grass-dominated landscapes. However, Winter et al. (2006) found no evidence that patch- or landscape-level factors influenced nest survival of grassland passerines in the northern tallgrass prairie. Furthermore, the authors found no support for any interaction between patch size and amount of woody cover in the landscape, a result a ributed to nest predators not being influenced by patch- or landscape-level features. Although we are unsure of the most appropriate scale for examining landscape e ects, or whether such landscape–patch relationships can be expected in open grasslands, our exploratory analyses suggest that edge e ects for Chestnut-collared Longspurs may be governed by landscape-level factors. Nest survival decreased with distance to edge in landscapes with >50% cropland. Similarly, Grant et al. (2006) found that Clay-colored Sparrow and Vesper Sparrow (*Poocetes gramineus*) nest survival was inversely related to distance from a wooded edge in North Dakota. The authors a ributed these pa erns to thirteen-lined ground squirrels (*Spermophilus tridecemelineatus*) being more abundant in grassland interior habitat than near woodland edges. It is unknown whether thidsc33 tesurepoandr

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bisevend were resulted from nest predators-)]TJ T* 0.8275 Tw(be

shrubland edge distances with the

amount of cropland in the landscape, 600 m)Tj T* 0.3417 Tw radiluscircle6) for Chestnut-collared(Longspus)Tj T* 0.9203 Tw [nesrs i

area; Appendix 17), all years was

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Although speculative, the reasoning is based on the fact that predation was the primary source of nest failure in our study (Davis 2003), and any patterns in nest survival are likely attributable to patterns in predation. This might also account for Chestnut-collared Longspurs fledging fewer young in large pastures, but it does not explain why this pattern would be unique to Chestnut-collared Longspurs, given that grassland nest predators are typically opportunistic (Vickery et al. 1992). Although predation patterns on Chestnut-collared Longspur nests might be expected to differ because their nest sites are much different than the other species, vegetation structure had very little influence on nest predation (Davis 2005).

Conclusion.—Our results indicate that patch size had relatively small and variable influence on the reproductive success of grassland passerines. Nest survival was influenced mostly by time-specific effects, particularly the age of the nest. Nest survival for four of the six species was greatest in early incubation, decreased to approximately 5–7 days post-hatch, and then increased as the young matured. As Grant et al. (2005) suggested for Savannah and Clay-colored sparrows, these patterns are likely related to the development of young and the activity levels of both the young and parents at the nest site.

Our results imply that mixed-grass prairie parcels ≥18 ha (our smallest pasture size) and in fair to excellent range condition play an important role in the conservation of several grassland passerines currently in decline. However, Sprague's Pipit's affinity for native grassland, its steep population decline (Prescott and Davis 1998), and its area-sensitivity (Davis 2004, present study), underscore the urgency in conserving large tracts of native mixed-grass prairie. We recommend that future studies examine more closely the relationships between patch and edge effects and the surrounding landscape in mixed-grass prairie under varying degrees of habitat loss and edge types. In addition, researchers ideally should determine what the primary predators of grassland passerines are—and how they are influenced by nest, patch, and landscape features—to facilitate interpretation of results, because predators will likely continue to be the primary cause of reproductive failure for most grassland birds.

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