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RESEARCH ARTICLE

Reproductive success of songbirds and waterfowl in native mixed-grass pasture and planted grasslands used for pasture and hay

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ABSTRACT

Conservation of grassland birds in agricultural landscapes requires an understanding of the demographic consequences of nesting in native and planted grasslands. Much of the native grassland in agricultural regions has been converted to cropland. Subsequently, seeding cropland to perennial grasslands has become a common strategy to restore habitat for grassland birds, but these grasslands also may be used as hay and pasture forage for livestock. Our objectives were to determine (1) if the abundance of grassland songbirds and the reproductive success of songbirds and waterfowl varied between native pasture and planted grassland, and (2) if the amount of grassland in the surrounding landscape influenced the abundance and reproductive success of songbirds or the nest survival of waterfowl in native and planted grasslands. Our results suggest that planted grasslands used for pasture and hay in our region are likely ecological sinks for grassland specialist songbirds. Sprague's Pipit (*Anthus spragueii*) nested only in native pasture, and Chestnut-collared Longspur (*Calcarius ornatus*), Lark Bunting (*Calamospiza melanocorys*), and Baird's Sparrow (*Ammodramus bairdii*) were sometimes more abundant in planted pasture or hayfields, but fledged 1.4–4.5 times as many young per nest in native pasture. The reproductive success of waterfowl and grassland songbird generalists was similar in planted grasslands and native pasture. The abundance of all songbirds varied with the amount of grassland or cropland in the surrounding landscape, but landscape composition only weakly influenced the nest survival rates of 1 of 8 songbirds and 4 of 6 waterfowl species. Our results demonstrate that the preservation of native pasture is critical for the conservation of grassland specialists. Other grassland songbirds and waterfowl likely will benefit from the conservation of native and planted grassland and conversion of cropland to perennial grassland used for pasture and hay.

Keywords: bird abundance, clutch initiation, clutch size, daily survival rates, grassland birds, habitat use, logistic exposure, nest survival

Éxito reproductiva de aves canoras y anseriformes en pastizales nativos de pastos mixtos y en praderas plantadas usadas para pastoreo y producción de heno

RESUMEN

La conservación de las aves de praderas en paisajes agrícolas requiere comprender las consecuencias demográficas de anidar en praderas nativas o plantadas. Muchas de las praderas nativas en regiones agrícolas se han convertido a cultivos. En consecuencia, el sembrado de pastos perennes en tierras de cultivo se ha convertido en una estrategia común para restaurar el hábitat de las aves de pradera, al tiempo que también pueden usarse para la producción de heno y el pastoreo de ganado. Nuestros objetivos fueron determinar si 1) la abundancia de aves canoras de pradera y el éxito reproductivo de aves canoras y anseriformes varía entre pastizales nativos y plantados; y 2) si la cantidad de pastizales en las áreas circundantes afecta la abundancia y el éxito reproductivo de aves canoras y la supervivencia de los nidos de anseriformes en praderas nativas y plantadas. Nuestros resultados sugieren que las praderas plantadas usadas para pastoreo y producción de heno en nuestra región probablemente son sumideros ecológicos para las aves canoras endémicas de praderas. Los individuos de *Anthus spragueii* sólo anidaron en pastizales nativos y los individuos de *Calcarius ornatus, Calamospiza melanocorys* y *Ammodrammus bairdii* a veces fueron más abundantes en los pastizales plantados o los campos de heno, pero emplumaron entre 1.4 y 4.5 veces más jóvenes por nido en los pastizales nativos. El éxito reproductivo de los anseriformes y de las aves canoras de pradera generalistas fue similar en los pastizales plantados que en los nativos. La abundancia de todas las aves canoras varió con la cantidad de praderas o tierras de cultivo en el paisaje circundante pero la composición del paisaje sólo afectó débilmente las tasas de supervivencia de los nidos de 1 de 8 especies de aves canoras y de 4 de 6 especies de anseriformes. Nuestros resultados demuestran que la preservación de los pastizales nativos es crítica para la conservación de las aves especialistas de praderas. Otras aves canoras de pradera y otros anseriformes probablemente se beneficiarán de la conservación de praderas nativas y plantadas y de la conversión de áreas de cultivo en pastizales perennes usadas para pastoreo y producción de heno.

Palabras clave: abundancia de aves, aves de pradera, exposición logística, iniciación de la nidada, supervivencia de los nidos, tamaño de la nidada, tasas diarias de supervivencia, uso de hábitat

INTRODUCTION

Temperate grasslands constitute one of the most endangered and least protected ecosystems on the planet (Henwood 2010). In North America, ~75% of the native mixed-grass prairie has been lost from the Northern Great Plains (Samson and Knopf 1994), primarily through the conversion of grassland to cropland. Consequently, grassland birds are considered to be one of the most at-risk bird assemblages in North America and have exhibited steep continental declines (Askins et al. 2007). Once common on the Canadian prairies, species such as Sprague's Pipit (*Anthus spragueii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Baird's Sparrow (*Ammodramus bairdii*) are now designated species at risk (Government of Canada 2015).

Seeding cropland to perennial grasslands is a common strategy used by wildlife conservation agencies to increase the amount of habitat available to grassland-nesting species (Arnold et al. 2007). Furthermore, agricultural programs in North America have resulted in large amounts of cultivated land being converted to grasslands planted with exotic grass and forb species (Johnson and Schwartz 1993, McMaster and Davis 2001). In Canada, these planted grasslands are typically used for forage as hay or pasture (McMaster and Davis 2001). Most waterfowl and some grassland songbirds occur frequently and in high abundance in planted grasslands, while others, such as Sprague's Pipit, occur rarely or in reduced numbers in planted grasslands compared with native grasslands (McMaster and Davis 2001, Emery et al. 2005, Davis et al. 2013).

Native grasslands are expected to be higher-quality habitat than planted grasslands for songbirds because of increased heterogeneity in plant structure and composition, greater abundance and diversity of invertebrate prey (D'Antonio and Vitousek 1992, Flanders et al. 2006), or better access to prey (Kennedy et al. 2009). Indeed, Lloyd and Martin (2005) and Fisher and Davis (2011) found that Chestnut-collared Longspur and Sprague's Pipit reproductive success was lower in grasslands seeded with exotic grasses than in native grassland. Reproductive success may be lower for songbirds in planted grasslands because of increased predation (Lloyd and Martin 2005) due to a paucity of safe nesting, roosting, or foraging sites, or due to increased density and foraging efficiency of predators. In addition, reduced abundance and accessibility to preferred prey may affect the ability of parents to feed themselves and their offspring, and the ability of juveniles to adequately feed themselves. Consequently, females may delay or abandon nesting, or may lay smaller eggs or clutches, when food resources are limited (Martin 1987, Reynolds et al. 2003). Nestlings may starve and become more susceptible to predation because slow growth rates cause them to stay in the nest longer or beg more loudly and more persistently for food (Christe et al. 1996, Haff and Magrath 2011).

In contrast to songbirds, upland-nesting waterfowl use grasslands primarily for nesting, with the young dispersing to aquatic habitats shortly after hatching. Waterfowl reproductive success in upland grasslands is largely determined by nest survival (the probability that a nest hatches at least 1 egg), which in turn is driven primarily by predation (Sargeant and Raveling 1992, Greenwood et al. 1995, Emery et al. 2005). Although waterfowl nest survival rates vary among habitat types, they are typically as high as or higher in planted grasslands than native grassland (Greenwood et al. 1995, Emery et al. 2005). Thus, planted and native grasslands both may offer relatively high-quality habitat to grassland-nesting waterfowl.

Management also can have a profound impact on the suitability and reproductive potential of grassland habitat. Haying can have catastrophic effects if the timing overlaps the nesting season (Klett et al. 1988, Bollinger et al. 1990, Perlut et al. 2008). Haying also may reduce nesting cover available in the following year (Emery et al. 2005), causing reduced nesting densities (Arnold et al. 2007). Similarly, intensive grazing can reduce nesting cover and, over time, cause increased cover of exotic species and woody vegetation. Such changes may lead to lower songbird and waterfowl densities and reproductive success (Krausman et al. 2009, Bloom et al. 2013). Density and reproductive success within a grassland patch may additionally be influenced by the surrounding landscape. Increased amounts of grassland surrounding native and planted grassland sites may positively influence the abundance of grassland songbirds (Davis et al. 2013) and the nest survival rates of waterfowl (Stephens et al. 2005, Howerter et al. 2014). Therefore, land managers aiming to provide high-quality habitat for grassland songbirds and waterfowl must consider both native and planted grassland parcels, as well as the landscape matrix surrounding the parcels.

Conservation partners within the Prairie Habitat Joint Venture deliver a number of programs aimed at grassland-nesting waterfowl and often assume that nongame birds also benefit from such programs. However, Koper and Schmiegelow (2006) found that waterfowl may not be a good proxy for identifying management regimes that benefit the grassland-nesting community. Our objectives were to determine (1) if the abundance of grassland songbirds and the reproductive success of songbirds and waterfowl varied between native pasture and planted grassland, and (2) how the amount of grassland in the surrounding landscape influenced the abundance and reproductive success of songbirds and waterfowl in native and planted grasslands. We postulated that native pasture would be higher-quality habitat than planted grassland for endemic grassland songbird specialists (i.e. Sprague's Pipit, Chestnut-collared Longspur, Lark Bunting [*Calamospiza melanocorys*], and Baird's Sparrow; Mengel 1970), and therefore that these species should occur in greater abundance and experience greater reproductive success in native pasture compared with planted grassland. Wider-ranging species that are more generalized in their habitat selection (hereafter, grassland generalists), including Clay-colored Sparrow (*Spizella pallida*), Vesper Sparrow (*Pooecetes gramineus*), Savannah Sparrow (*Passerculus sandwichensis*), Grasshopper Sparrow (*Ammodramus savannarum*), and Western Meadowlark (*Sturnella neglecta*; Mengel 1970), should occur in similar abundance in native and planted pasture. We also predicted that grassland generalist species and waterfowl would experience similar reproductive success in native and planted pasture. However, because haying can have catastrophic consequences for all ground-nesting birds, we predicted that reproductive success would be lowest for all species nesting in hayfields.

METHODS

Study Site and Data Collection

We conducted our study in the Missouri Coteau landscape of southern Saskatchewan, Canada, during 2001–2002. We used Landsat imagery (Agriculture and Agri-Food Canada 2001) to help identify quarter sections (65 ha; McKercher and Wolfe 1986) of native grassland, planted grassland used for pasture (hereafter, planted pasture), and planted grassland used for hay (hereafter, hayfield). We identified all parcels of the 3 habitat types that were within 3.2 km of each other from the satellite imagery and then visited each cluster of sites to confirm the habitat type, land use, and land ownership. We avoided selecting multiple parcels of the same habitat type belonging to the same landowner (i.e. >1 native or planted pasture or hayfield for a given landowner) to ensure that we captured the range of management regimes across our study area. Because our study also had a waterfowl component, we only included parcels that had at least one semipermanent wetland within or adjacent to it. Furthermore, because previous work has indicated that range condition influences the occurrence and abundance of at least some of our target grassland songbird species (Sprague's Pipit and Baird's Sparrow; Davis et al. 2014), we selected native and planted pastures that appeared to be in 'good' or better range condition based on a visual inspection of the pastures in the spring. Range condition assessments (Abouguendia 1990) conducted by range ecologists in both years from July 10 to August 13 confirmed our visual ratings, except for 1 planted pasture rated as being in 'fair' condition by the range ecologist. In 2001, we attempted to select a cluster of 1 planted pasture, 1 hayfield, and 1 native pasture for inclusion in the study. We identified 9 possible clusters in our study area, but only 5 clusters met our site selection criteria and we therefore adjusted our remaining cluster configurations based on what was available. One cluster consisted of a planted pasture and hayfield, the second cluster included a hayfield and a native pasture, the third consisted of a native pasture and a planted pasture, and the fourth cluster comprised 2 planted pastures, 2 hayfields, and 1 native pasture. In total, we sampled 26 parcels (9 hayfields, 9 planted pastures, and 8 native pastures) in 2001. The mean distance between sites within clusters was 3.5 $\pm$ 0.6 (SD) km. In 2002, we relaxed our 3.2-km intersite distance criterion and attempted to select clusters of sites near those used in 2001. We randomly selected parcels in situations in which we had multiple choices of the same habitat for different landowners. The distance between sites averaged 13.1 $\pm$ 8.2 km in 2001 and 9.8 $\pm$ 9.3 km in 2002. Within each parcel, we randomly located a 32-ha plot and focused our nest searching activities and abundance surveys in these areas.

Native pastures were largely dominated by needle and thread (*Hesperostipa comata*), shortbristle needle and thread (*H. curtiseta*), thickspike wheatgrass (*Elymus lanceolatus*), western wheatgrass (*Pascopyrum smithii*), prairie Junegrass (*Koeleria cristata*), blue grama (*Bouteloua gracilis*), lesser spikemoss (*Selaginella densa*), prairie sagewort (*Artemisia frigida*), and a variety of other forbs. Western snowberry (*Symphoricarpos occidentalis*) and silverberry (*Elaeagnus commutata*) were the most common shrubs, and patches of quaking aspen (*Populus tremuloides*) were sparsely distributed in mesic areas. Planted pastures were typically seeded to a mix of alfalfa (*Medicago sativa*) and exotic grasses such as smooth brome (*Bromus inermis*), crested wheatgrass (*Agropyron cristatum*), and Russian wildrye (*Psathyrostachys juncea*). Native and planted pastures were grazed during the study by domestic cattle and stocked at 3.2 $\pm$ 2.2 Animal Unit Months (AUM) per ha (range = 1.2–6.1) and 10.5 $\pm$ 7.1 AUM per ha (range = 3.6–26.3), respectively. Hayfields were a mix of smooth brome and alfalfa and were usually cut in the first week of July in our region (McMaster et al.

2005), with 75%–95% of the hayfields having been cut by early August (T. Bedard personal communication). Hayfields were typically cut once per year because of the relatively short growing season, but some producers may have attempted a second cut toward the end of July if weather conditions and personal schedules were favorable (T. Bedard personal communication). Hayfields in our study were cut between June 26 and July 28 in 2001 (median = July 9) and between July 14 and July 30 (median = July 21) in 2002.

A single observer conducted two 100-m belt-transect surveys that were 800 m long in each plot to estimate the relative abundance of songbirds (Ralph et al. 1993). Surveys were conducted beginning at sunrise and ending 3 hr later on days with no fog or precipitation and with winds <20 km hr^{-1} from May 24 to July 1 in 2001 and May 28 to July 10 in 2002. The surveyor recorded all singing males seen or heard within 100 m of the transect. We used the maximum number of singing males recorded during the 2 visits (typically 3 weeks apart) as our response variable in subsequent analyses.

We located vegetation sampling points by stopping every 50 m along each bird survey transect and walking out a random distance (1–100 m) to the left and right side of each transect. We dropped a 5-mm diameter metal rod vertically in each sampling location and recorded the number of contacts at any point on the rod by vegetation type (standing dead grass, narrow-leaf grass, broad-leaf grass, clumped grass, rhizomatous grass, shrub, and forb). Grass contacts were recorded separately based on both their leaf width (narrow or broad) and growth form (clumped or rhizomatous). For example, a single grass contact from a narrow-leaved clumped species would score a 1 as a narrow-leaf variable and a 1 for a clumped grass variable. We also recorded maximum vegetation height and bare ground and cow dung cover within a 1-m^2 quadrat. We calculated the mean of the vegetation measurements taken along each transect to obtain a single value for each vegetation variable in each plot for subsequent analyses.

We located nests mostly between 07:30 and 14:00 Mountain Standard Time by systematically dragging a 25-m nylon rope, weighted with metal cans, through each study plot to flush incubating birds from nests from May 1 to Aug 10 in 2001 and May 3 to Aug 1 in 2002. Nests also were located opportunistically while conducting other activities in the area. We conducted nest searches in each plot every ~2 weeks throughout the summer in both years. We did not conduct nest searches during cold, wet weather, we took care to avoid creating paths which ended at a nest, and we conducted nest checks as quickly as possible to minimize human-induced nest failure. We candled eggs (Weller 1956, Lokemoen and Koford 1996) to determine clutch initiation dates and to estimate hatching dates to increase the precision of nest survival estimates (Shaffer 2004). We recorded nest locations with a hand-held global positioning system (GPS) unit and placed colored surveyor's flags 5 m north and south of the nest to facilitate relocation. Surveyor's flags were kept just above the height of the vegetation in pastures, but the vegetation in hayfields became higher than the flags as the season progressed. We replaced surveyor's flags with flagging tape close to the ground as the expected date of haying approached. We checked songbird nests every 3–4 days until chicks fledged or the nesting attempt failed, and we checked waterfowl nests every 7 days until the eggs hatched or the nesting attempt failed. We considered a songbird or waterfowl nest successful if it fledged at least 1 host young or hatched at least 1 duckling, respectively. For songbirds, we also used cues such as the presence of fledglings, parent alarm calls, droppings or feather scales in the nest, and age of the chicks at the last visit to indicate successful nests. We used the presence of egg membranes to assist with assigning nest fate for waterfowl nests. For nests with known fate, the midpoint between the last visit when the nest was observed to be active and the subsequent visit was used to determine exposure days. Exposure days for nests with unknown fate were included up to the last visit when the nest was observed to be active (Manolis et al. 2000).

Statistical Analyses

We performed all analyses using SAS 9.4 (SAS Institute 2015). We used generalized linear models (PROC GENMOD) to determine whether songbird abundance varied with habitat type and landscape composition. We modeled abundance with a negative binomial distribution and a log link for all species except Sprague's Pipit and Vesper Sparrow. We used a Poisson distribution for these 2 species because negative binomial habitat models would not converge. We used Akaike's Information Criterion adjusted for small sample size (AIC$_c$) to rank models (Burnham and Anderson 2002), and we considered the model with the lowest AIC$_c$ value to be the best of those considered.

We calculated the proportion of native pasture, planted pasture, planted hay, and cropland surrounding each quarter section. We considered landscape composition at 3 scales: 400-m, 800-m, and 1,600-m radius buffers around each study plot. For each species, we compared each land cover variable at the 3 spatial scales as a linear and quadratic model and retained the linear model at the 400-m scale for subsequent analyses unless it was >2 AIC$_c$ units larger than the quadratic form or larger landscape scale. With the exception of Lark Bunting, we created a model set ($n = 14$ models) that included landscape-type variables along with habitat type as both additive and interactive effects (e.g., habitat, land cover, habitat + land cover, habitat*land cover, and the null model). Because

Lark Bunting was not recorded in hayfields, for this species we restricted our analyses to only native and planted pasture because its absence from hayfields was likely a result of the habitat type itself and not the surrounding landscape. Furthermore, we did not consider habitat*landscape interactions for Lark Bunting because of the small sample size. We used a canonical correspondence analysis (PROC CORRESP) to quantify the relationships between songbird abundance, vegetation structure, and habitat type.

We converted clutch initiation date to an ordinal date by setting January 1 to 0, and used linear mixed models (PROC MIXED) to quantify the effect of habitat type on clutch initiation date. We used the parcel as a random effect to account for the likelihood that the clutch initiation dates of females nesting in the same plot may have been more similar than those of females nesting in other plots. We used repeated measures generalized linear models (PROC GENMOD) to determine the extent to which clutch size and number of songbirds fledged differed among habitat types. We assigned a Poisson distribution and a log link and used the nest as a repeated measure to account for multiple nests within the same plot. We did not use the parcel as a random effect because of model convergence problems. We excluded nests from the clutch size analysis if the original number of host eggs laid could not be estimated. Furthermore, we consider clutch size to reflect an "apparent" clutch size since we did not monitor individual eggs during laying and therefore could not be entirely certain of the true clutch size.

We used logistic exposure analysis (Shaffer 2004) to determine how daily nest survival rates varied with nest age, date, habitat type, and landscape composition. We did not include the egg-laying stage for most songbird analyses because we found few nests during laying (<5%). We did include the laying stage for Lark Bunting because 12% of nests were located during the egg-laying stage. We combined years for all analyses because AIC_c values for our treatment by year interaction models (nest age*year, date*year, habitat*year, landscape*year) were greater than for models with an additive effect of year (nest age + year, date + year, habitat + year, landscape + year) or for models without a year effect included. We identified the best temporal model (nest age and date) by comparing all subsets of our global model (linear effects of age and date, quadratic effects of age and date, cubic effect of age, and the null model) and used this best temporal model as the base model for subsequent analyses. We did not include a cubic effect of age in waterfowl models because we did not consider it to be biologically plausible. We used the same modeling approach described for abundance models, except that we did not consider habitat by landscape interactions for songbird species except Savannah Sparrow and Baird's Sparrow because of small sample sizes in $\geq$1 habitat types. We used 85% confidence intervals to identify uninformative model parameters (Arnold 2010) and based our inferences on model-averaged estimates. Mean values are reported $\pm$ SE.

RESULTS

We located 1,536 nests of 39 species during the 2 yr of the study. We focused on the 9 songbird and 6 waterfowl species that comprised ~95% of songbird ($n = 1{,}003$) and waterfowl ($n = 425$) nests and for which at least 20 nests were found: Gadwall (*Anas strepera*; $n = 107$), American Wigeon (*A. americana*; $n = 24$), Mallard (*A. platyrhynchos*; $n = 115$), Blue-winged Teal (*A. discors*; $n = 69$), Northern Shoveler (*A. clypeata*; $n = 45$), Northern Pintail (*A. acuta*; $n = 55$), Sprague's Pipit ($n = 35$), Chestnut-collared Longspur ($n = 82$), Clay-colored Sparrow ($n = 192$), Vesper Sparrow ($n = 320$), Lark Bunting ($n = 44$), Savannah Sparrow ($n = 109$), Grasshopper Sparrow ($n = 23$), Baird's Sparrow ($n = 78$), and Western Meadowlark ($n = 67$). We could not analyze the effect of habitat type on the reproductive success of Sprague's Pipit because we located nests only in native pastures.

Songbird Abundance

The abundance of grassland songbirds typically was influenced by both habitat type and landscape composition (Table 1). Sprague's Pipit and Clay-colored Sparrow abundance was much greater in native pastures than in planted grasslands (Table 2). Baird's Sparrow and Western Meadowlark abundance was about twice as high in native grasslands compared with planted pastures. The abundance of Chestnut-collared Longspur was comparable in native and planted pastures, and Vesper and Grasshopper sparrows were more abundant in planted grasslands than in native pasture. Lark Bunting was not detected in hayfields, and its abundance in native and planted pastures was not statistically different ($P = 0.43$). Savannah Sparrow was nearly twice as abundant in hayfields compared with planted pastures (Table 2).

Our intermediate analyses to determine which landscape extent (400 m, 800 m, or 1,600 m) best predicted grassland songbird abundance revealed that Sprague's Pipit was most influenced by land cover within 400 m of the study plot (Supplemental Material Table S1). Similarly, the 400 m landscape scale was identified as most relevant for Clay-colored Sparrow, whereas Vesper Sparrow abundance was most influenced by the amount of native pasture within 400 m and hayland within 1,600 m of the study plot (Supplemental Material Table S1). The 1,600 m scale was most relevant for Lark Bunting, particularly the amount of native pasture and cropland (Supplemental Material Table S1). The abundances of the other 4 species were equally influenced by the 3 landscape extents, as ΔAIC_c values

TABLE 1. Rankings of top and competing (within 2 AIC_c units of the best model and with the same or a fewer number of parameters) models relating variation in grassland songbird abundance to habitat and landscape composition surrounding study plots in southern Saskatchewan, Canada, 2001–2002. *K* is the number of parameters in the model, AIC_c is Akaike's Information Criterion adjusted for small sample size, ΔAIC_c is the scaled value of AIC_c, w_i is the Akaike weight, and 2Log(*L*) is the model log-likelihood. Habitat represents the 3 habitat types (native pasture, planted pasture, and hay); Native400, Hay400, Crop400 and P_Pasture400 is the proportion of native pasture, hayland, cropland, and planted pasture within 400 m of the study plot, respectively; Native1,600, Hay1,600, and Crop1,600 represent the proportion of native pasture, hayland, and cropland within 1,600 m of the study plot, respectively; and Null is the intercept-only model (shown for comparison). Plus and minus signs in the model indicate the direction of the relationship for linear continuous variables.

Model	*K*	ΔAIC_c	w_i	2Log(*L*)
Sprague's Pipit (SPPI) [a]				
Habitat (+)Native400	5	0.0 [b]	0.69	−34.5
Habitat (−)Crop400	5	2.3	0.22	−35.6
Null	2	77.4	0.00	−76.7
Chestnut-collared Longspur (CCLO) [a]				
(+)P_Pasture400 (+)Habitat	5	0.0	0.32	−57.9
(−)Hay400	3	2.0	0.12	−61.4
Null	2	4.0	0.04	−63.6
Clay-colored Sparrow (CCSP) [c]				
Habitat	3	0.0	0.30	−90.3
Null	2	22.4	0.00	−103.9
Vesper Sparrow (VESP) [c]				
Habitat (−)Hay1,600	5	0.0	0.64	−62.8
Null	2	12.2	0.00	−72.4
Lark Bunting (LARB) [a]				
(−)Native1,600	3	0.0	0.47	−25.1
(+)Crop1,600	3	1.8	0.19	−26.0
Null	2	5.3	0.03	−29.0
Savannah Sparrow (SAVS) [c]				
Habitat (+)Native400	5	0.0	0.24	−117.5
Habitat (−)Crop400	5	1.3	0.13	−118.1
(−)Crop400	3	1.4	0.12	−120.7
Habitat	4	1.7	0.10	−119.6
(+)Native400	3	1.8	0.10	−120.9
Null	2	2.9	0.05	−122.6
Grasshopper Sparrow (GRSP) [c]				
Habitat*Hay400	7	0.0	0.69	−57.5
Null	2	4.2	0.08	−66.1
Baird's Sparrow (BAIS) [a]				
(+)Native400	3	0.0	0.17	−103.9
Habitat	4	0.1	0.16	−102.8
Null	2	0.6	0.13	−105.4
Western Meadowlark (WEME) [c]				
Crop400	4	0.0	0.65	−67.7
Null	2	8.9	0.01	−74.6

[a] Grassland specialist.
[b] The AIC_c value of the top model for each species was as follows: SPPI = 78.0, CCLO = 127.5, CCSP = 189.7, VESP = 134.8, LARB = 57.1, SAVS = 246.6, GRSP = 132.3, BAIS = 214.5, and WEME = 144.5.
[c] Grassland generalist.

were within 2 units of each other and/or the landscape models were within 2 AIC_c units of the null model. Therefore, we used landscape composition at the 400 m scale for modeling the abundances of these species.

The abundance of Sprague's Pipit ($\beta = 3.183$, 85% CL = 2.113, 4.252), Savannah Sparrow ($\beta = 1.105$, 85% CL = 0.357, 1.853), and Baird's Sparrow ($\beta = 1.118$, 85% CL = 0.187, 2.049) increased with the amount of native grassland within 400 m of study plots (Figure 1). The abundance of both Sprague's Pipit ($\beta = -3.066$, 85% CL = –4.236, –1.896) and Savannah Sparrow ($\beta = -0.654$, 85% CL = –1.184, –0.124) declined with the amount of cropland surrounding grassland parcels (Figure 1). Western Meadowlark abundance was highest at intermediate levels of cropland within 400 m of study plots ($\beta = 7.481x$, 85% CL = 4.321, 10.642; $\beta = -8.329x^2$, 85% CL = –12.113, –5.545). Lark Bunting abundance declined with the amount of native pasture within 1,600 m ($\beta = -9.281$, 85% CL = –15.031, –3.531) and increased with the amount of cropland ($\beta = 6.755$, 85% CL = 2.015, 11.495; Figure 1). Chestnut-collared Longspur abundance increased with the amount of planted pasture in the surrounding landscape ($\beta = 7.806$, 85% CL = 2.457, 13.156), and the abundance of Chestnut-collared Longspur and Vesper Sparrow decreased with increasing amounts of hayland surrounding study plots ($\beta = -5.989$, 85% CL = –9.928, –2.050 and $\beta = -6.239$, 85% CL = –11.054, –1.425, respectively; Figure 1). Grasshopper Sparrow abundance also declined with increasing amounts of hayland in the surrounding landscape, but only in hayfields; abundance increased with the amount of hayland surrounding planted pasture sites (Figure 1). Clay-colored Sparrow was the only species that did not have a landscape variable included in the top or competing models (Table 1).

The first axis (dimension 1) of the canonical correspondence ordination accounted for 34% of the total variation in the data and was characterized primarily by gradients in shrub and bare ground cover (Figure 2). The second axis (dimension 2) explained 16% of the variation and represented a gradient of cow-dung cover (Figure 2). Habitat type was more strongly associated with dimension 1 than dimension 2, with native pastures having high scores and hayfields and planted pasture having low scores. Native pasture parcels were similar in vegetation structure and were characterized by increased amounts of dead vegetation, narrow-leaf and rhizomatous grasses, and shrubs. Planted pasture and hayfield parcels exhibited much more variation in vegetative structure than native pastures, but planted habitats shared similar vegetative characteristics, such as taller vegetation and increased forb and bare ground cover. The abundance of Sprague's Pipit, Clay-colored Sparrow, Baird's Sparrow, and Western Meadowlark was associated with native grassland characterized by increased cover of shrubs, narrow-leafed, rhizomatous grasses, and standing dead vegetation. Lark

TABLE 2. Maximum mean abundance (lower, upper 85% CL; % frequency of occurrence) of grassland songbirds in native and planted pasture and hayfields in the Missouri Coteau of southern Saskatchewan, Canada, 2001–2002.

Species	Native pasture (n [a] = 14)	Planted pasture (n = 15)	Hayfield (n = 14)
Sprague's Pipit	2.8 (1.5, 4.2; 100)	0.1 (−0.1, 0.3; 13)	0.1 (−0.2, 0.4; 7)
Chestnut-collared Longspur	2.2 (0.3, 4.1; 64)	2.3 (−0.3, 4.8; 27)	0.2 (−0.2, 0.5; 14)
Clay-colored Sparrow	8.4 (5.9, 10.9; 100)	1.3 (0.1, 2.4; 53)	1.6 (0.5, 2.8; 57)
Vesper Sparrow	0.8 (0.2, 1.4; 43)	2.3 (1.6, 2.9; 60)	2.0 (1.1, 2.9; 86)
Lark Bunting	0.5 (−0.2, 1.2; 21)	1.3 (−0.6, 3.3; 20)	0.0
Savannah Sparrow	7.8 (4.7, 10.8; 93)	4.7 (2.5, 6.9; 93)	8.4 (5.9, 10.9; 100)
Grasshopper Sparrow	0.6 (0.1, 1.0; 43)	1.5 (0.4, 2.7; 53)	1.7 (0.1, 3.3; 50)
Baird's Sparrow	5.5 (3.3, 7.7; 93)	2.7 (0.7, 3.8; 60)	3.7 (1.7, 5.8; 79)
Western Meadowlark	2.5 (1.4, 3.6; 86)	1.3 (0.6, 2.0; 73)	1.3 (0.2, 2.3; 64)

[a] Number of plots.

Bunting and Savannah Sparrow abundance was associated with taller vegetation and reduced cow-dung cover. Chestnut-collared Longspur had the highest score of any species along dimension 2, indicating a strong association with the cover of cow dung. The abundance of Vesper and Grasshopper sparrows was associated with planted grassland with increased bare-ground cover.

Nest Success

Overall (for all habitats combined), nest success for songbirds ranged from 20% to 67% and for waterfowl ranged from 4% to 32% (Appendix Table 5). Daily nest survival rates during the incubation period were greater than in the nestling period for all songbirds (Appendix Table 5).

We found that nest survival rates varied as a function of age or date for all songbird species except Lark Bunting and Grasshopper Sparrow (Supplemental Material Table S2). Although date was included in the top model for Sprague's Pipit, the model was within 2 AIC_c units of the null model (Supplemental Material Table S2). Daily survival rates (DSRs) of Chestnut-collared Longspur and Vesper, Savannah, and Clay-colored sparrows typically increased during incubation until day 5–7, then declined to approximately day 4–6 of the nestling period, after which they increased again (Appendix Figure 5). Baird's Sparrow DSR was lowest near the second day of the nestling period (Appendix Figure 5). Vesper Sparrow and Western Meadowlark DSRs were lowest in the second and third week of June (Appendix Figure 5). Nest age and date were included in the top models for Gadwall, American Wigeon, Mallard, and Northern Pintail (Supplemental Material Table S2). The DSR for 5 waterfowl species increased with nest age (Appendix Figure 6). American Wigeon DSR was highest in mid-June, and Gadwall, Mallard, and Northern Pintail DSR decreased as the season progressed (Appendix Figure 6). Date was included in the top model for Blue-winged Teal nest survival, but the 85% confidence interval included 0.

Our intermediate analyses revealed that the 3 landscape extents equally influenced the DSRs of most songbirds and waterfowl, as land cover models at the 400 m, 800 m, and 1,600 m spatial scales were typically within 2.5 AIC_c units of each other or the null model (Supplemental Material Tables S3 and S4). Therefore, we used the 400 m landscape extent for all species except Sprague's Pipit, Vesper Sparrow, and Western Meadowlark, because nest survival was more influenced by landscape composition at the larger spatial scales for at least 1 landscape variable for these 3 species (Supplemental Material Table S3).

Chestnut-collared Longspur and Western Meadowlark nest survival was most influenced by the amount of planted pasture in the surrounding landscape, whereas cropland cover was the best predictor of Clay-colored and Vesper sparrow nest survival (Table 3). However, relationships were highly variable for Western Meadowlark (85% CL = –79.374, –0.182) and Clay-colored Sparrow (85% CL = –2.024, –0.005), and the addition of the planted pasture variable to the temporal model did little to improve the fit of the model for Chestnut-collared Longspur (Table 3). Vesper Sparrow DSR was lowest where 40%–50% of the landscape within 1,600 m of the study plot was composed of cropland ($\beta = -4.008x$, 85% CL = –6.512, –1.503; $\beta = 4.484x^2$, 85% CL = 1.690, 7.277; Figure 3). Lark Bunting nest survival was most influenced by native pasture cover (Table 3), but the 85% CI included 0.

Habitat type influenced the nest survival of only Lark Bunting and Baird's Sparrow (Table 3). The daily survival rate of Lark Bunting nests was greater in native (0.970, 85% CL = 0.886, 0.992) than in planted (0.843, 85% CL = 0.777, 0.891) pasture, and Baird's Sparrow DSR was lower in hayfields (0.780, 85% CL = 0.603, 0.892) than in native (0.920, 85% CL = 0.887, 0.944) and planted (0.891, 85% CL = 0.812, 0.939) pasture. The nest survival of Sprague's Pipit and Savannah Sparrow was influenced primarily by temporal factors, whereas temporal, habitat, and landscape factors had little influence on Grasshopper Sparrow nest

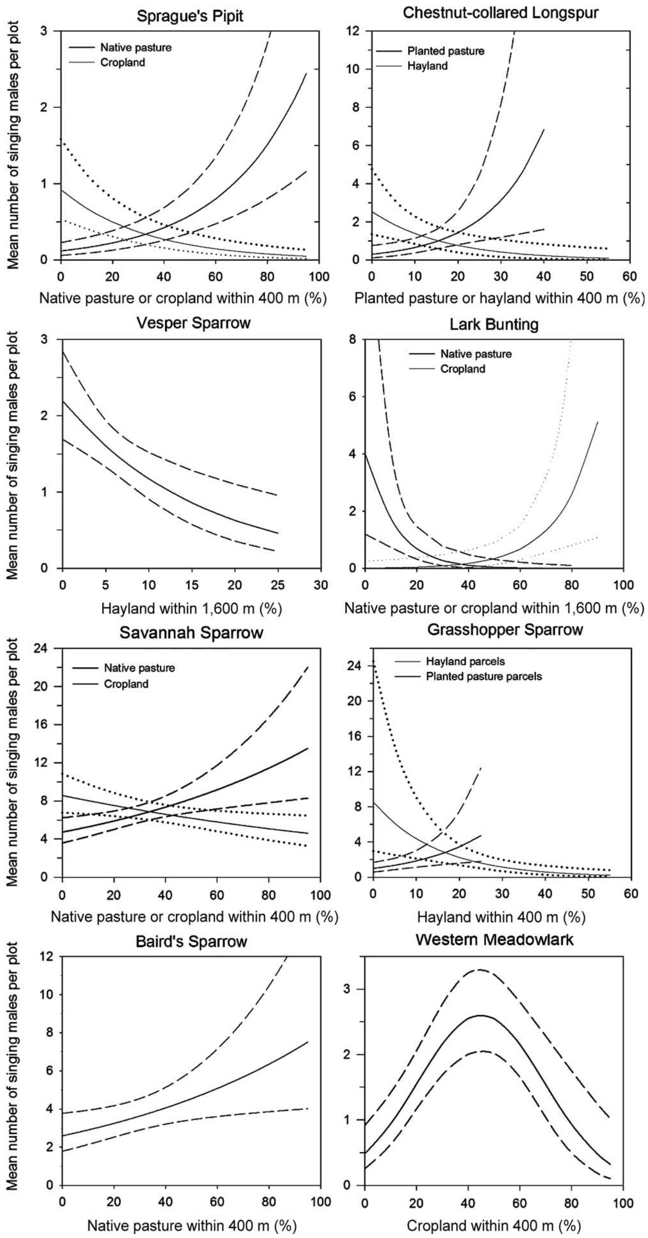

FIGURE 1. Grassland songbird abundance varied with the amount of native and planted pasture, hayland, and cropland surrounding study plots in southern Saskatchewan, Canada, 2001–2002. Dotted and dashed lines represent upper and lower 85% confidence limits.

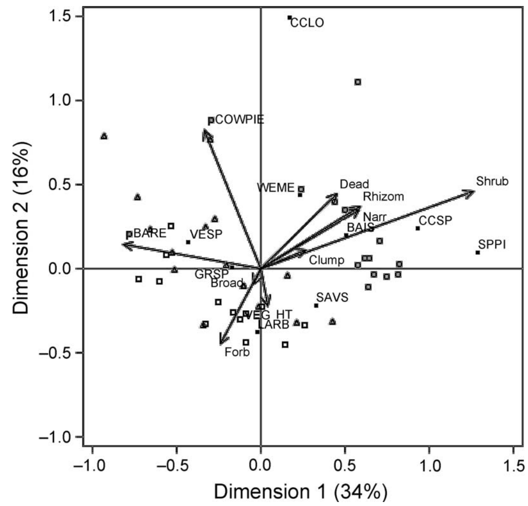

FIGURE 2. Ordination plot of a canonical correspondence analysis relating habitat type, vegetation structure, and species abundance for grassland songbirds in the Missouri Coteau of southern Saskatchewan, Canada, 2001–2002. Hayland, native pasture, and planted pasture are represented by squares, circles, and triangles, respectively. Broad, Forb, Clump, Dead, Rhizom, Narr, and Shrub represent contacts by broad-leaf grasses, forbs, clumped grasses, standing dead vegetation, rhizomatous grasses, narrow-leaf grasses and shrubs, respectively; pCOWPIE and pBARE represent the cover of cow dung and bare ground, respectively; and VEG HT represents vegetation height. See Table 1 for the meanings of bird name acronyms.

survival as the null model was the top model (Table 3, Supplemental Material Table S5).

Waterfowl nest survival was not strongly influenced by habitat type as it was not present in the top or competing models for any species (Table 3). Instead, DSRs were most influenced by the amount of hayland (American Wigeon and Northern Pintail), cropland (Northern Shoveler), and native pasture (Gadwall) in the surrounding landscape (Table 3). Northern Pintail nest survival was greatest when 25%–35% of the surrounding landscape was composed of hayland ($\beta = 7.842x$, 85% CL = 2.976, 12.708; $\beta = -13.858x^2$, 85% CL = –23.036, –4.679), and American Wigeon DSR was lowest when hayland comprised 20% of the surrounding landscape ($\beta = -35.388x$, 85% CL = –57.303, –13.473; $\beta = 71.092x^2$, 85% CL = 35.649, 106.534; Figure 3). Northern Shoveler DSR decreased with the amount of cropland in the surrounding landscape ($\beta = -3.330$, 85% CL = –5.534, –1.126), and Gadwall DSR was lowest when the surrounding landscape was composed of 40% native pasture ($\beta = -3.451x$, 85% CL = –5.545, –1.357; $\beta = 4.653x^2$, 85% CL = 1.980, 7.325; Figure 3).

Clutch Initiation, Apparent Clutch Size, and Fledging Success

Mean clutch initiation dates varied among habitat types for Clay-colored Sparrow ($F_{2,168} = 3.05$, $P = 0.05$), Lark Bunting ($F_{1,38} = 14.90$, $P < 0.001$), and American Wigeon ($F_{2,13} = 5.95$, $P = 0.01$). Both songbird species initiated more nests in native pasture later in the season, and American Wigeon initiated more nests in planted pasture later in the season (Figure 4; see Supplemental Material Figures S1, S2, and S3 for clutch initiation dates for all species in all habitats).

Apparent clutch size was not statistically different among habitats for any species ($P > 0.05$), although

TABLE 3. Model selection results of the best and competing models (within 2 AIC_c units of the top model and with the same or a fewer number of parameters) explaining variation in daily nest survival rate as a function of habitat type, surrounding land cover composition, nest age (Age), and date (Date) for grassland-nesting waterfowl and songbirds in the Missouri Coteau of southern Saskatchewan, Canada, 2001–2002. The null model and best temporal-only model are provided for comparison. Blue-winged Teal, Sprague's Pipit, and Savannah and Grasshopper sparrows are not included because the temporal-only or null model was the top model for these species. *K* is the number of parameters in the model, AIC_c is Akaike's Information Criterion adjusted for small sample size, ΔAIC_c is the scaled value of AIC_c, w_i is the Akaike weight, and Log(*L*) is the model log-likelihood. Variables Hay400, Native400, Crop400, and P_pasture400 are the amount of hayland, native pasture, cropland, and planted pasture, respectively, within 400 m of the study parcel; Crop1,600 and P_pasture800 is the amount of cropland and planted pasture within 1,600 m and 800 m, respectively, of the study parcel. Plus and minus signs in the model indicate the direction of the relationship for linear continuous variables.

Model	*K*	ΔAIC_c	w_i	Log(*L*)
Gadwall (*n* =105, 1,043) [a]				
(+)Age (−)Date Native400^2	5	0.0 [b]	0.56	−192.4
(+)Age (−)Date	3	3.5	0.10	−196.1
Null	1	12.8	0.00	−202.8
American Wigeon (*n* = 22, 192)				
(+)Age Date^2 Hay400^2	6	0.0	0.85	−33.2
(+)Age (+)Date^2	4	10.0	0.01	−40.4
Null	1	14.6	0.00	−45.8
Mallard (*n* = 106, 1,020)				
(+)Age (+)Date Hay400*Year	6	0.0	0.47	−181.9
(+)Age (+)Date	3	2.0	0.17	−186.0
Null	1	26.2	0.00	−200.1
Northern Shoveler (*n* = 43, 539)				
(+)Age (−)Crop400	3	0.0	0.37	−74.9
(+)Age	2	5.2	0.03	−78.5
Null	1	8.1	0.01	−80.9
Northern Pintail (*n* = 51, 516)				
(+)Age (+)Date Hay400^2	4	0.0	0.41	−71.9
(+)Age (+)Date	2	2.0	0.15	−74.9
Null	1	20.1	0.00	−86.0
Chestnut-collared Longspur (*n* = 81, 802)				
Age^3 P_pasture400^2	6	0.0	0.27	−122.9
Age^3	4	0.8	0.18	−125.3
Age^3 (+)Crop400	5	1.9	0.10	−124.9
Null	1	11.7	0.00	−133.8
Clay-colored Sparrow (*n* = 177, 1,626)				
Age^3 (−)Crop400	5	0.0	0.28	−336.9
Age^3 (+)P_pasture400	5	0.8	0.19	−337.3
Age^3	4	2.9	0.06	−339.4
Null	1	4.0	0.04	−342.9
Vesper Sparrow (*n* = 304, 3,154)				
Age^3 Date^2 Crop1,600^2	8	0.0	0.59	−522.0
Age^3 Date^2	6	5.9	0.05	−527.0
Null	1	44.9	0.00	−551.5
Lark Bunting (*n* = 39, 401)				
(+)Age (+)Native400	3	0.0	0.35	−78.0
(+)Age Habitat	3	0.1	0.33	−78.0
(+)Age	2	5.8	0.06	−81.9
Null	1	7.3	0.01	−83.7
Baird's Sparrow (*n* = 73, 693)				
Age^2 Habitat	5	0.0	0.27	−131.4
Age^2	3	4.8	0.02	−135.8
Null	1	10.1	0.00	−140.5
Western Meadowlark (*n* = 66, 651)				
Date^2 P_pasture800^2	5	0.0	0.50	−142.0
Date^2	3	4.2	0.06	−146.2
Null	1	7.6	0.02	−149.9

[a] The sample sizes given in parenthese are the number of nests, and effective sample size.
[b] The AIC_c value of the top model for each species was as follows: Gadwall = 394.8, American Wigeon = 78.5, Mallard = 375.9, Northern Shoveler = 155.7, Northern Pintail = 153.8, Chestnut-collared Longspur = 257.8, Clay-colored Sparrow = 683.9, Vesper Sparrow = 1,060.0, Lark Bunting = 165.6, Baird's Sparrow = 272.8, and Western Meadowlark = 294.1.

TABLE 4. Mean ± SE number of songbird young fledged per nest (1st row) and per successful nest (2nd row) in 3 grassland habitats in the Missouri Coteau of southern Saskatchewan, Canada, 2001–2002. Sample sizes (number of nests) are provided in parentheses. A dash indicates that no nests were located in this habitat.

Species	Native pasture	Planted pasture	Hayfield	Test statistics
Sprague's Pipit	2.5 ± 0.4 (33)	—	—	—
	4.0 ± 0.2 (21)	—	—	—
Chestnut-collared Longspur	2.1 ± 0.2 (45)	1.5 ± 0.2 (29)	1.7 ± 0.7 (3)	$\chi^2_2 = 3.17$, $P = 0.18$
	3.6 ± 0.2 (26)	3.1 ± 0.2 (14)	2.5 ± 0.3 (2)	$\chi^2_2 = 3.23$, $P = 0.20$
Clay-colored Sparrow	1.1 ± 0.2 (152)	1.0 ± 0.3 (16)	1.1 ± 0.4 (18)	$\chi^2_2 = 0.09$, $P = 0.95$
	3.0 ± 0.2 (56)	2.4 ± 0.5 (8)	3.9 ± 0.3 (6)	$\chi^2_2 = 3.81$, $P = 0.15$
Vesper Sparrow	1.5 ± 0.2 (29)	1.1 ± 0.1 (128)	1.5 ± 0.2 (152)	$\chi^2_2 = 3.19$, $P = 0.20$
	2.8 ± 0.3 (16)	2.6 ± 0.2 (55)	3.1 ± 0.2 (74)	$\chi^2_2 = 2.89$, $P = 0.24$
Lark Bunting	3.1 ± 0.3 (9)	1.2 ± 0.0 (35)	—	$\chi^2_1 = 4.04$, $P = 0.04$
	4.0 ± 0.1 (7)	3.7 ± 0.0 (11)	—	$\chi^2_1 = 2.57$, $P = 0.11$
Savannah Sparrow	1.3 ± 0.2 (61)	0.6 ± 0.2 (20)	1.0 ± 0.3 (24)	$\chi^2_2 = 4.18$, $P = 0.12$
	2.7 ± 0.0 (28)	2.4 ± 0.5 (5)	3.1 ± 0.4 (8)	$\chi^2_2 = 1.39$, $P = 0.50$
Grasshopper Sparrow	—	1.5 ± 0.3 (15)	2.5 ± 0.6 (7)	$\chi^2_1 = 1.05$, $P = 0.30$
	—	4.3 ± 0.0 (6)	4.0 ± 0.0 (4)	$\chi^2_1 = 2.56$, $P = 0.11$
Baird's Sparrow	1.8 ± 0.3 (54)	0.9 ± 0.4 (11)	0.4 ± 0.3 (11)	$\chi^2_2 = 5.95$, $P = 0.05$
	3.6 ± 0.2 (28)	3.3 ± 0.5 (3)	4.0 ± 0.0 (1)	$\chi^2_2 = 1.06$, $P = 0.59$
Western Meadowlark	1.0 ± 0.2 (40)	1.2 ± 0.5 (21)	0.3 ± 0.1 (5)	$\chi^2_2 = 3.26$, $P = 0.19$
	3.5 ± 0.3 (8)	2.6 ± 0.1 (5)	0.3 ± 0.0 (1)	$\chi^2_2 = 1.82$, $P = 0.40$

Clay-colored Sparrows tended to lay larger clutches in hayfields ($P = 0.07$; Appendix Table 6). The number of fledged songbird young differed between habitats for Lark Bunting ($\chi^2_1 = 4.04$, $P = 0.04$) and Baird's Sparrow ($\chi^2_2 = 5.95$, $P = 0.05$). Lark Buntings fledged 1.9 more young per nest in native than in planted pastures and Baird's Sparrow fledging success was 2.0–4.5 times greater in native pasture than in planted pasture and hayland (Table 4). The number of young fledged from successful nests was similar among habitats for all species ($P > 0.11$; Table 4). Only 3 nests were located in hayfields for Chestnut-collared Longspur, so we restricted their analysis to only native and planted pasture. Chestnut-collared Longspur nests in native pasture fledged 0.6 more young per nest

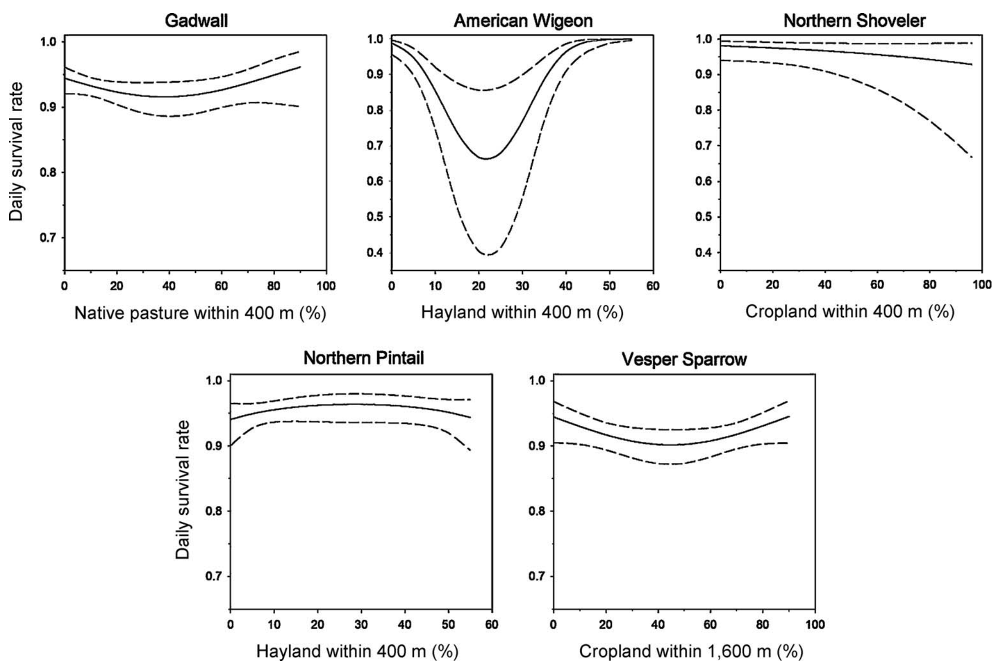

FIGURE 3. Daily nest survival rates of waterfowl and grassland passerines varied with the amount of native and planted pasture, hayland, and cropland surrounding study plots in southern Saskatchewan, Canada, 2001–2002. Dotted and dashed lines represent upper and lower 85% confidence limits.

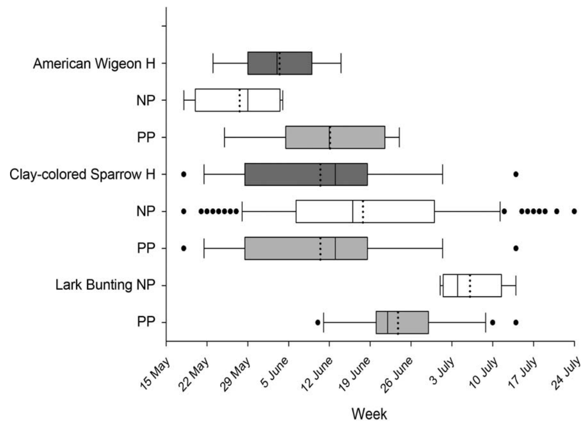

FIGURE 4. Clutch initiation dates differed among hayfields (H), native pastures (NP), and planted pastures (PP) for American Wigeon, Lark Bunting, and Clay-colored Sparrow, in southern Saskatchewan, Canada, 2001–2002. Box plots represent 25th, 50th, and 75th percentiles, whiskers indicate 10th and 90th percentiles, dotted lines represent the mean, and dots are outliers.

than those in planted pasture (2.1 $\pm$ 0.2 vs. 1.5 $\pm$ 0.2; $\chi^2_1 = 3.40$, $P = 0.06$), but the mean number of young fledged from successful nests was not statistically different ($\chi^2_1 = 0.69$, $P = 0.40$).

Haying Impact

The date of haying was later in 2002 (median = July 21) than in 2001 (median = July 9). We located 415 nests of our focal species in hayfields and could determine the nest fate of 411 nests (191 waterfowl and 220 songbird). Most nests in hayfields either failed (54%; 123 waterfowl and 97 songbird) or successfully fledged young from the nest (26%; 43 waterfowl and 65 songbird) prior to haying. Only 52 nests (13%; 25 waterfowl and 27 songbirds) were active during haying, with Gadwall ($n = 12$) and Vesper Sparrow ($n = 18$) being the most common. Nine nests (7 waterfowl and 2 songbird) were destroyed by machinery, 7 waterfowl nests hatched, and 9 songbird nests fledged young. The remaining nests were either depredated (10 waterfowl and 9 songbird) or deserted (1 waterfowl and 7 songbird) after haying. Thirty-one nests (7%) were initiated in hayfields after haying (29 Vesper Sparrow and 1 each of Baird's and Clay-colored sparrow), with 24 nests successfully fledging young and 7 nests being depredated.

DISCUSSION

Habitat Quality

Identifying grassland habitats that contribute to the conservation of nesting songbirds and waterfowl is crucial for stabilizing and maintaining populations. Our results indicate that the conservation of native mixed-grass rangeland is an important step toward stabilizing the decline of grassland specialist songbirds of the Northern Great Plains. Sprague's Pipit and Baird's Sparrow were most abundant in native pasture, their abundance increased with the amount of native pasture in the surrounding landscape, and both species experienced greater reproductive success in native pasture than in planted grassland. Chestnut-colored Longspur and Lark Bunting reproductive success also was greatest in native pasture. Such results are consistent with our hypothesis that native grassland is higher-quality habitat than planted grassland for grassland specialist songbirds.

Greater abundance of Sprague's Pipit in native pasture than in nonnative grassland (Madden et al. 2000, Davis et al. 2013), or the absence of pipits in planted grassland (Johnson and Schwartz 1993, McMaster and Davis 2001), has been well documented. However, few studies have examined Sprague's Pipit reproductive success in planted grassland. In south-central Saskatchewan, where Sprague's Pipit nested in native and planted grassland, female pipits renested after failure only in native pastures (S. Davis personal observation), and juvenile survival was lower in planted grassland than native pasture (Fisher and Davis 2011). These results suggest that planted grassland is not high-quality habitat for this species, and underscore the importance of examining survival and reproductive rates rather than abundance or occurrence alone.

In contrast to Sprague's Pipit, Baird's Sparrow was relatively common in planted grassland and was confirmed to nest in this habitat. Although Baird's Sparrow commonly occurs in planted grassland (Sutter and Brigham 1998, Davis et al. 1999, 2013, McMaster and Davis 2001), the demographic consequences of nesting in this habitat is cause for concern. Nests in planted grassland experienced lower survival rates than nests in native pasture and fledged 0.9 and 1.4 fewer young per nest in planted pasture and hayfield, respectively, than in native pasture. Similarly, Lark Bunting was more abundant in planted pasture, but nest survival was lower than in native pasture, where they fledged >2 more young per nest. For both Baird's Sparrow and Lark Bunting, the number of young fledged per successful nest was similar in native pasture and planted grassland, indicating that the lower reproductive success in planted grassland was not due to more partial clutch losses (e.g., from starvation of weaker nestlings). Rather, lower reproductive success in planted grassland likely was a result of predation: >84% of nest failures were attributed to predators. Planted pasture had greater cattle stocking rates and was characterized by more bare ground and less cover of grasses, residual vegetation, and shrubs than native pasture. Such conditions may have resulted in reduced cover available to nesting females and facilitated nest location by predators. Pleszczynska (1978) found that nestling survival was greater in nests with more overhead concealment. However, the effect of concealment on nest survival is equivocal and likely depends on the predator community (Davis 2005, Jones and Dieni 2007, Ludlow et al. 2014). Nest predator communities typically are diverse and opportunistic in mixed-grass prairie and planted grassland (Pietz et al. 2012), but the types and densities of nest predators in our study were unknown.

Chestnut-collared Longspur abundance and nest survival were similar in native and planted grassland. These results do not appear to support our hypothesis that native grassland is higher-quality habitat than planted grassland for this specialist songbird. However, our results, along with others, show that Chestnut-collared Longspur rarely occupies hayfields (Davis et al. 1999, McMaster and Davis 2001). Chestnut-collared Longspur is typically associated with pastures with moderate to heavy grazing pressure (Bleho et al. 2015). Indeed, this species' abundance was strongly correlated with cow-dung numbers, suggesting that the number of birds increased with grazing intensity (Stumpp et al. 2005, Manthey and Peper 2010), likely up to some point at which the habitat became unsuitable. Chestnut-collared Longspur may have nested in planted pasture in our study because pastures were seeded with crested wheatgrass, which is structurally similar to a number of native grasses (Sutter and Brigham 1998, Davis and Duncan 1999). Lloyd and Martin (2005) also found that Chestnut-collared Longspur was equally likely to nest in native or crested wheatgrass fields, but longspurs in their study experienced lower nest survival, fledged fewer young per nest, and nestlings grew more slowly and fledged at a lower mass compared with those in native fields. Although nest survival was nearly identical in native and planted pasture in our study, Chestnut-collared Longspur fledged 0.6 more young per nest in native habitat in both our study and in the study by Lloyd and Martin (2005), suggesting that crested wheatgrass fields and pastures may indeed be lower-quality habitat than native pasture for this species.

As predicted, we failed to find any strong relationships between abundance, clutch size, nest survival, or fledging success and habitat type for grassland generalist songbirds, except Clay-colored Sparrow. Clay-colored Sparrow was at least 5 times more abundant in native pasture than in planted grassland, but experienced similar reproductive success in each habitat. The greater abundance of Clay-colored Sparrow in native pasture likely was a result of the species' association with shrubs (Grant et al. 2004, Winter et al. 2006), which were lacking in planted grassland. Grassland generalist songbirds are not only more generalized in their habitat preferences than grassland specialist songbirds (Owens and Myres 1973, McMaster and Davis 2001, Wellicome et al. 2014), but they often experience similar levels of reproductive success in native habitats as those that are invaded by exotic grasses (Kennedy et al. 2009) and in nonnative grassland (Rohrbaugh et al. 1999). However, there are too few studies examining reproductive success in planted and native grassland to make strong generalizations as nearly all comparative studies to date have examined only abundance, occurrence, or density (Johnson et al. 2004).

Waterfowl nest survival also was similar in native pasture and planted grassland used for hay and pasture. Waterfowl commonly nest in planted grassland (Klett et al. 1988, Reynolds et al. 2001, Arnold et al. 2007) and typically have nest survival rates as high as, or higher, in planted grasslands than in native pasture (Greenwood et al. 1995, Emery et al. 2005, Howerter et al. 2014). Although our sample of nests was relatively small for each species, our nest success estimates in native and planted pasture were similar to those found by Klett et al. (1988), and our hayfield estimates were similar to those found by Prairie Habitat Joint Venture (PHJV) researchers (PHJV 2014). In contrast to Klett et al. (1988), our nest success estimates in hayfields were greater for Northern Shoveler (19% vs. 2%–6%) and Northern Pintail (27% vs. 2%–4%), and similar to the estimates of McMaster et al. (2005), possibly because most females in our study completed nesting before haying began (see below).

Haying Impact

Hayfields are typically regarded as population sinks (Pulliam 1988), where reproduction and survival rates are not high enough to offset mortality rates (Cowardin et al. 1985, Bollinger et al. 1990, Perlut et al. 2008). As a result, we incorrectly predicted that all individuals nesting in hayland would experience lower reproductive success than those nesting in native or planted pasture. Baird's Sparrow was the only species that experienced lower nest survival and fledged fewer young in hayfields, but the low reproductive success was a result of nest predation, not mowing.

Whether hayfields are sinks or not depends largely on moisture conditions (Greenwood et al. 1995) and the timing, frequency, and extent of haying (i.e. from mowing to baling) relative to the nesting cycle. Unlike the northeastern or midwestern U.S. (Bollinger et al. 1990, Frawley and Best 1991, Perlut et al. 2006), most producers in our region cut their hay later and only once during the growing season (Ducks Unlimited Canada and Saskatchewan Ministry of Agriculture personal communication). Consequently, most waterfowl and songbird nests were initiated well before haying commenced. If producers had cut their hayfields on July 7 in both years of our study (the long-term average in our region; McMaster et al. 2005), then at least 46% of songbird nests (assuming a 28-day nesting period) and 59% of waterfowl nests (assuming a 43-day nesting period) in hayfields would have been exposed to haying operations. Those percentages would have increased to 77% and 69% for waterfowl and songbirds, respectively, if all sites had been mowed on our earliest haying date (June 26). However, because most nests failed or fledged young before haying could affect nests (74% of songbird and 87% of waterfowl nests), the percentage of active nests exposed to haying operations was substantially reduced (12% of songbird and 13% of waterfowl nests).

The primary cause of nest failure for both waterfowl and songbirds in hayfields was predation; >80% of failed waterfowl and songbird nests were depredated. Farm machinery was a minor cause of nest failure for both waterfowl (5% of failed nests) and songbirds (2% of failed nests) in our study. Klett et al. (1988) also found predation to be the primary cause of nest failure for waterfowl nesting in hayfields, but 27% of nest failures were attributed to farm machinery in their study. Although few nests were destroyed directly by equipment in our study, mowing may have increased the chances of nest failure by causing females to abandon nests or may have made nests more susceptible to predation (Bollinger et al. 1990, Perlut et al. 2006). Indeed, 69% of nests that were active during haying were either depredated or deserted. Vesper Sparrow appeared to increase reproductive output in hayfields by renesting after the fields were mowed. Of the 29 Vesper Sparrow nests initiated after haying, 24 successfully fledged young. However, the benefits of successfully nesting late in the season may be modest if late-fledged young are less likely to be recruited into the breeding population the following year (Shutler et al. 2006, Tarof et al. 2011).

Landscape Influences

The composition of the surrounding landscape influenced the abundance of all species but Clay-colored Sparrow. Abundance of Sprague's Pipit, Chestnut-collared Longspur, and Baird's and Savannah sparrows increased with the amount of native or planted pasture in the surrounding landscape. These results are consistent with those of Davis et al. (2013) and with findings that the occurrence of these species increases with patch size in some parts of their range (Ribic et al. 2009). Lark Bunting and Western Meadowlark abundances were influenced by the amount of cropland in the surrounding landscape, but in different ways. Western Meadowlark was most abundant in grassland parcels around which the surrounding landscape matrix was composed of 40%–50% cropland, and Lark Bunting abundance increased substantially when landscape matrices were composed of 60%–80% cropland, and decreased when the surrounding landscape was <20% native pasture. Greater abundance of Western Meadowlark in landscapes with intermediate amounts of cropland may result from meadowlarks being better able to supplement resources in grassland habitats embedded in heterogeneous landscapes than in those consisting primarily of cropland or grassland (Dunning et al. 1992). Results for Lark Bunting are difficult to explain, but may be related to the amount of competing habitat surrounding planted and native pasture. Pastures surrounded mostly by cropland may cause males to nest at greater densities within those parcels, whereas pastures surrounded mostly by native grassland may provide more opportunities for males to establish territories within the surrounding landscape (Fretwell and Lucas 1969). A similar explanation may account for Vesper Sparrow density decreasing in grassland parcels surrounded by increased amounts of hayland, given their attraction to hayfields in the region (McMaster et al. 2005).

The effect that the surrounding landscape had on nest survival varied within and among songbird and waterfowl species and was highly variable or weak in most cases. Our results are similar to those of Winter et al. (2006), who found inconsistent and weak landscape effects involving the amount of grassland on nest success of mixed-grass prairie passerines. Although Northern Shoveler nest survival rates tended to decline with increasing cropland cover, we found little support for waterfowl nest survival being positively related to the amount of grassland in the landscape, as has been found by others (Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005). Such differences may be a result of fewer nests or smaller landscape extents in our study, or due to previous studies combining all types of grassland into a single category.

Most of the relatively strong relationships that we found between nest survival and landscape composition were not linear. Nest survival was lowest at intermediate cover values of hayland, native pasture, and cropland for American Wigeon, Gadwall, and Vesper Sparrow, respectively, but greatest at intermediate hayland values for Northern Pintail. Both Stephens et al. (2005) and Horn et al. (2006) found waterfowl nest success to be lowest at intermediate values of grassland edge and grassland patch size. Given that predation was the primary cause of nest failure in these studies (and ours), such patterns may be due in part to more diverse and abundant predator communities in landscapes that have experienced intermediate degrees of habitat loss (Clark and Nudds 1991). It is unclear why the relationship between nest survival and landscape composition would differ so greatly among species in the same area and years when nest predators are purportedly opportunistic (Vickery et al. 1992, Cooper et al. 1999) and diverse (Pietz et al. 2012), however differences in life history traits such as nest-site selection and parental care may expose different species to different suites of predators and risk of predation.

Conclusion

Conservation of native pasture is critical for the conservation of grassland specialists; the species in our study either occurred only in native pasture or had greater reproductive success in native pasture than in planted pasture and hayfields. Other more widely distributed songbirds and waterfowl that are more generalized in their habitat requirements will likely continue to benefit from the conservation of native and planted grassland and the conversion of cropland to perennial grassland used for pasture and hay. Furthermore, our study supports previous research demonstrating that hayfields may be a viable option for generalist songbirds and waterfowl if mowing is delayed until the end, or latter part, of the breeding season (McMaster et al. 2005). The current recommendation of mowing after July 15 (Williams et al. 1999) seems appropriate for our study region given the breeding phenology of birds in this study and the time of year that most producers in the area initiate haying. However, further work is required to quantify the survival and recruitment rates of young that fledge after the haying season. Our results also indicate that the composition of the surrounding landscape influences the nest survival of waterfowl more than songbirds. Although we lack consistent results on which to base any firm recommendations, programs converting cropland to perennial cover will generally be most effective if converted cropland parcels are not situated within cropland-dominated landscapes. We found that the daily survival rates of 11 of 15 species tended to decrease with increasing cropland cover in the surrounding landscape. We recommend that researchers consider treating native and planted pasture and hayland as separate habitats in study designs because they typically possess distinct plant communities and vegetative structure. Such differences might yield different prey and predator communities, which in turn may influence relationships between reproductive success and landscape composition.

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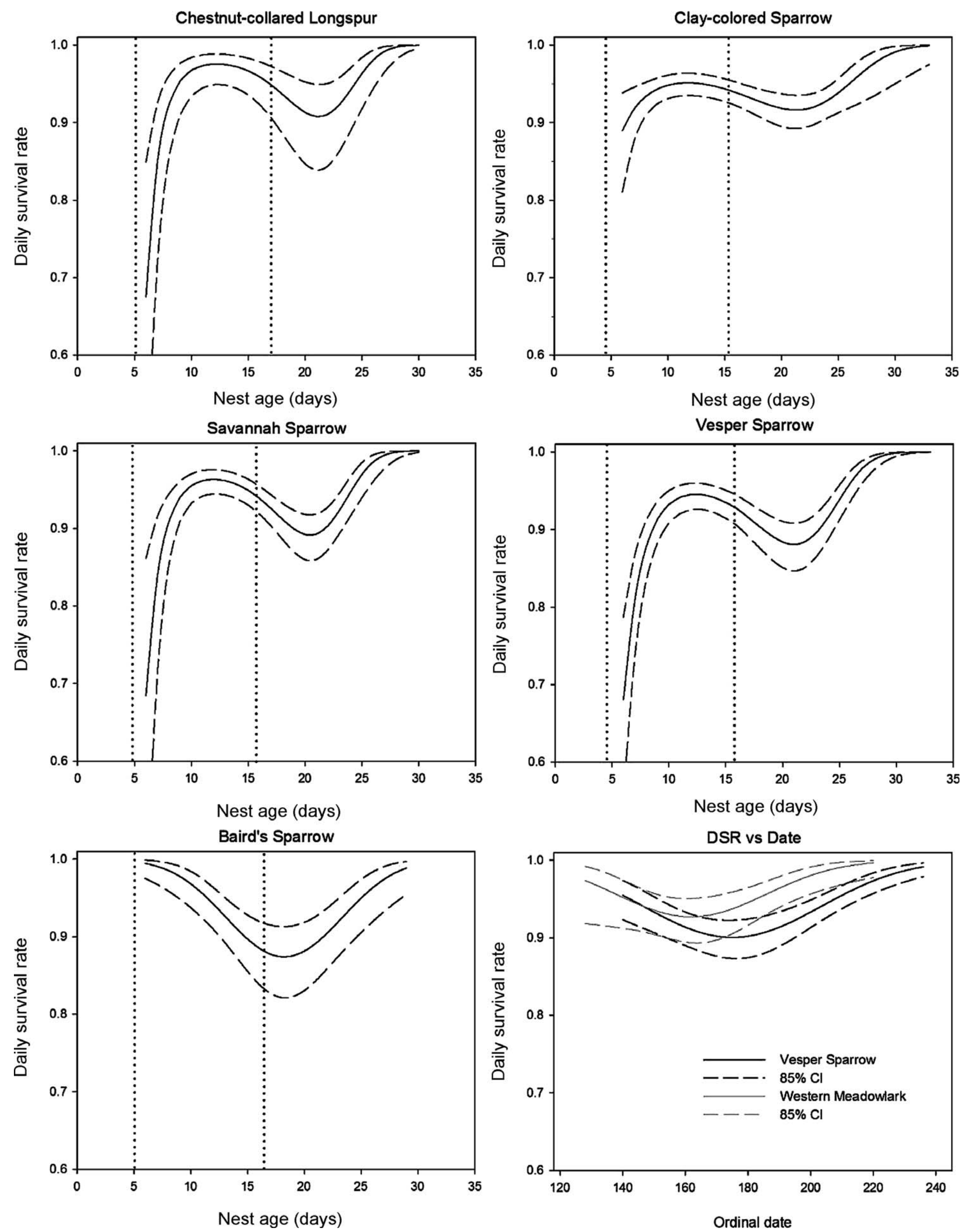


APPENDIX FIGURE 5. Daily nest survival rates (DSR) of grassland songbirds varied with nest age and date in southern Saskatchewan, Canada, 2001–2002. Predicted relationships are bounded by 85% confidence limits, and the vertical dotted lines indicate the transitions between the egg-laying to incubation and incubation to nestling stages. Nest day 1 corresponds to the first day of egg laying, and ordinal dates 120, 140, 160, 180, 200, 220, and 240 correspond to May 1, May 21, June 10, June 30, July 20, August 9, and August 29, respectively.

APPENDIX TABLE 5. Model-averaged daily nest survival rates (85% confidence interval) and associated nest success estimates for 15 grassland-nesting bird species in hayland (Hay), native pasture (N_pasture), and planted pasture (P_pasture) in the Missouri Coteau of southern Saskatchewan, Canada, 2001–2002. Nest success for waterfowl was calculated by raising the daily nest survival rate to the power of the laying and incubation period, and songbird nest success was calculated as the product of the daily survival rate of the incubation period raised to the power of the length of the incubation period and the daily survival rate of the nestling period raised to the power of the length of the nestling period.

Species	Habitat	No. of nests	Incubation DSR [a]	Nestling DSR	Nest success (%)
Gadwall (35) [b]	Hay	59	0.920 (0.898–0.937)		5
	N_pasture	25	0.917 (0.887–0.939)		5
	P_pasture	21	0.926 (0.897–0.947)		7
	Combined	105	0.921 (0.900–0.938)		6
American Wigeon (34)	Hay	9	0.738 (0.489–0.892)		0
	N_pasture	5	0.747 (0.527–0.887)		0
	P_pasture	9	0.754 (0.533–0.892)		0
	Combined	23	0.746 (0.528–0.886)		4
Mallard (35)	Hay	48	0.923 (0.905–0.937)		6
	N_pasture	33	0.923 (0.906–0.938)		6
	P_pasture	21	0.922 (0.903–0.938)		6
	Combined	102	0.923 (0.907–0.936)		6
Blue-winged Teal (34)	Hay	19	0.956 (0.940–0.968)		22
	N_pasture	22	0.951 (0.935–0.963)		18
	P_pasture	21	0.953 (0.937–0.965)		19
	Combined	62	0.953 (0.941–0.963)		20
Northern Shoveler (34)	Hay	17	0.952 (0.896–0.978)		19
	N_pasture	11	0.962 (0.917–0.982)		26
	P_pasture	16	0.981 (0.790–0.999)		53
	Combined	44	0.967 (0.912–0.988)		32
Northern Pintail (32)	Hay	23	0.960 (0.938–0.974)		27
	N_pasture	11	0.961 (0.935–0.977)		28
	P_pasture	16	0.955 (0.927–0.973)		23
	Combined	50	0.959 (0.938–0.973)		26
Sprague's Pipit (12, 12) [c]	N_pasture	33	0.984 (0.972–0.991)	0.982 (0.970–0.989)	67
Chestnut-collared Longspur (12, 11)	Hay	3	0.975 (0.944–0.989)	0.954 (0.906–0.978)	44
	N_pasture	46	0.970 (0.951–0.982)	0.944 (0.922–0.960)	37
	P_pasture	30	0.968 (0.947–0.981)	0.941 (0.916–0.959)	35
	Combined	79	0.970 (0.952–0.981)	0.943 (0.923–0.959)	36
Clay-colored Sparrow (11, 11)	Hay	19	0.944 (0.914–0.964)	0.905 (0.859–0.937)	18
	N_pasture	143	0.954 (0.942–0.963)	0.921 (0.904–0.936)	24
	P_pasture	16	0.964 (0.938–0.979)	0.938 (0.897–0.963)	33
	Combined	178	0.954 (0.942–0.963)	0.921 (0.905–0.935)	24
Vesper Sparrow (12, 11)	Hay	145	0.960 (0.950–0.967)	0.948 (0.937–0.957)	34
	N_pasture	29	0.960 (0.948–0.969)	0.948 (0.935–0.959)	34
	P_pasture	130	0.958 (0.949–0.966)	0.946 (0.935–0.955)	33
	Combined	304	0.959 (0.950–0.967)	0.947 (0.937–0.956)	33
Lark Bunting (12, 11)	N_pasture	9	0.984 (0.954–0.994)	0.984 (0.954–0.994)	69
	P_pasture	31	0.922 (0.894–0.943)	0.921 (0.890–0.944)	15
	Combined	40	0.964 (0.939–0.979)	0.964 (0.937–0.979)	32
Savannah Sparrow (12, 11)	Hay	23	0.945 (0.923–0.961)	0.922 (0.893–0.944)	21
	N_pasture	58	0.948 (0.927–0.963)	0.926 (0.901–0.945)	22
	P_pasture	19	0.941 (0.914–0.959)	0.916 (0.878–0.943)	18
	Combined	100	0.945 (0.926–0.959)	0.924 (0.900–0.942)	21
Grasshopper Sparrow (12, 11)	Hay	7	0.972 (0.926–0.989)	0.945 (0.893–0.973)	38
	P_pasture	16	0.969 (0.931–0.987)	0.941 (0.897–0.967)	35
	Combined	23	0.969 (0.931–0.987)	0.942 (0.901–0.967)	33
Baird's Sparrow (12, 11)	Hay	11	0.901 (0.830–0.944)	0.814 (0.678–0.900)	3
	N_pasture	55	0.971 (0.951–0.982)	0.940 (0.916–0.958)	36
	P_pasture	10	0.949 (0.907–0.973)	0.900 (0.827–0.944)	17
	Combined	76	0.955 (0.934–0.970)	0.931 (0.906–0.950)	26

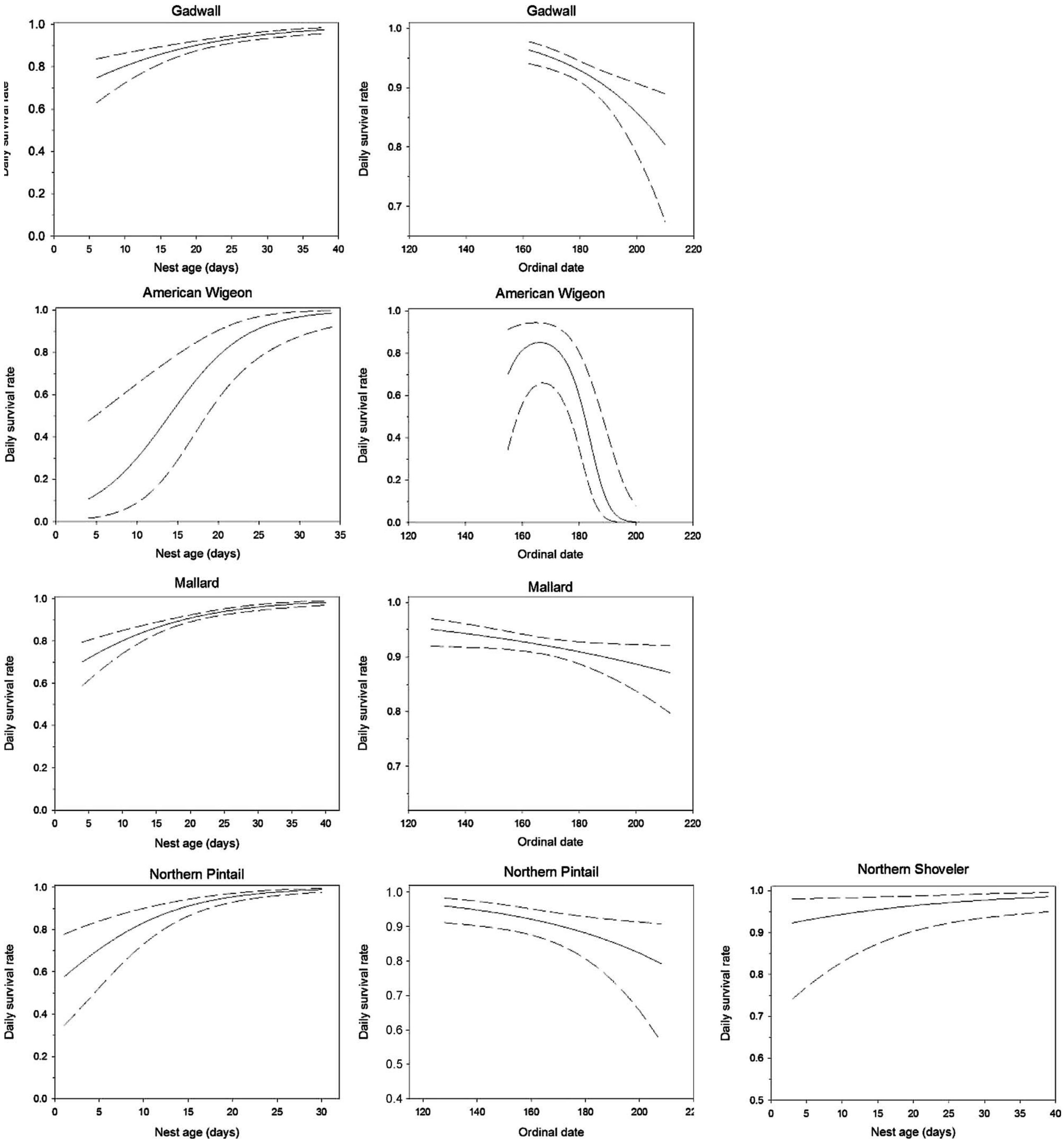
APPENDIX TABLE 5. Continued.

Species	Habitat	No. of nests	Incubation DSR [a]	Nestling DSR	Nest success (%)
Western Meadowlark (12, 12)	Hay	5	0.940 (0.916–0.958)	0.934 (0.905–0.954)	21
	N_pasture	41	0.937 (0.919–0.952)	0.930 (0.908–0.947)	19
	P_pasture	19	0.938 (0.918–0.953)	0.931 (0.907–0.949)	20
	Combined	65	0.938 (0.920–0.952)	0.931 (0.909–0.948)	20

[a] Also includes the laying period for waterfowl.
[b] Exposure days used to calculate nest success for waterfowl.
[c] Exposure days used to calculate nest success for songbirds (incubation period, nestling period).

APPENDIX TABLE 6. Mean apparent clutch size ± SE (*n*) of grassland-nesting waterfowl and songbirds in 3 grassland habitats in the Missouri Coteau of southern Saskatchewan, Canada, 2001–2002. A dash indicates that no nests were located in this habitat.

Species	Native pasture	Planted pasture	Hayfield	*P*
Gadwall	9.6 ± 0.3 (24)	8.8 ± 0.4 (18)	9.7 ± 0.3 (53)	0.42
American Wigeon	10.0 ± 1.6 (4)	8.4 ± 1.0 (9)	9.3 ± 1.2 (6)	0.22
Mallard	8.4 ± 0.5 (32)	8.0 ± 0.4 (18)	9.0 ± 0.2 (36)	0.14
Blue-winged Teal	9.8 ± 0.3 (20)	10.4 ± 0.3 (22)	10.6 ± 0.4 (19)	0.40
Northern Shoveler	10.5 ± 0.3 (10)	9.9 ± 0.3 (12)	8.9 ± 0.0 (18)	0.15
Northern Pintail	9.1 ± 1.0 (10)	7.4 ± 0.2 (12)	8.1 ± 0.2 (19)	0.11
Sprague’s Pipit	4.8 ± 0.3 (35)	—	—	—
Chestnut-collared Longspur	4.2 ± 0.3 (44)	4.5 ± 0.4 (29)	5.0 ± 1.6 (2)	0.24
Clay-colored Sparrow	3.6 ± 0.1 (111)	3.7 ± 0.1 (14)	4.2 ± 0.2 (16)	0.07
Vesper Sparrow	4.0 ± 0.1 (24)	4.0 ± 0.1 (106)	4.2 ± 0.0 (124)	0.22
Lark Bunting	4.2 ± 0.1 (9)	4.9 ± 0.0 (30)	—	0.15
Savannah Sparrow	4.3 ± 0.1 (45)	4.1 ± 0.2 (16)	4.4 ± 0.2 (20)	0.54
Grasshopper Sparrow	—	4.9 ± 0.1 (16)	4.7 ± 0.2 (7)	0.42
Baird’s Sparrow	4.5 ± 0.1 (53)	4.6 ± 0.2 (11)	4.9 ± 0.2 (10)	0.39
Western Meadowlark	4.6 ± 0.2 (37)	5.1 ± 0.2 (15)	4.7 ± 0.6 (4)	0.27



APPENDIX FIGURE 6. Daily nest survival rates of grassland-nesting waterfowl varied with nest age and date in southern Saskatchewan, Canada, 2001–2002. Dashed lines represent upper and lower 85% confidence limits. Nest day 1 corresponds to the first day of egg laying, and ordinal dates 120, 140, 160, 180, 200, and 220 correspond to May 1, May 21, June 10, June 30, July 20, and August 9, respectively.