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RESEARCH ARTICLE

Oil and natural gas development has mixed effects on the density and reproductive success of grassland songbirds

Sarah M. Ludlow,[1]* R. Mark Brigham,[1] and Stephen K. Davis[1,2]

[1] Department of Biology, University of Regina, Regina, Saskatchewan, Canada
[2] Canadian Wildlife Service, Regina, Saskatchewan, Canada
* Corresponding author: Sarah.Ludlow306@gmail.com

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ABSTRACT

Oil and natural gas development has increased dramatically in native grasslands over the past 25 years. Some grassland songbirds are less abundant in areas with oil and gas development, but the effects vary among species and geographically within a species' range. The reproductive consequences of nesting in areas with oil and gas development are unknown. We assessed how the density and reproductive success of five species of grassland songbird in Alberta, Canada, varied with distance to oil and gas wells, gravel roads, and trails, and cover of crested wheatgrass (*Agropyron cristatum*), an aggressive alien plant that often becomes established following anthropogenic disturbance. Crested wheatgrass cover had the greatest impact on the grassland songbird community. Sprague's Pipit (*Anthus spragueii*) nest survival decreased as the amount of crested wheatgrass increased. As crested wheatgrass cover increased from 0% to 60%, density of Savannah Sparrows (*Passerculus sandwichensis*) declined by 50%, but they fledged 25% more young from successful nests. Density of Savannah Sparrows was twice as high near wells, and fledging success was 40% higher compared with 700 m away. Distance to gravel roads did not influence the density or reproductive success of any species. Sprague's Pipits and Baird's Sparrows (*Ammodramus bairdii*) avoided nesting within 100 m of trails, and both species fledged fewer young from successful nests near trails. In contrast, Vesper Sparrows (*Pooecetes gramineus*) nested close to trails and fledged more young from successful nests near trails. Western Meadowlarks (*Sturnella neglecta)* were not strongly affected by any variable. Brown-headed Cowbird (*Molothrus ater*) abundance was three times higher in study plots with wells, although we detected no associated increase in brood parasitism. Our results indicate that the introduction and spread of crested wheatgrass and the creation of access trails to well pads have negative reproductive consequences for primary endemic species such as Sprague's Pipit and Baird's Sparrow, although these results do not extend to other grassland birds. The spread of crested wheatgrass and the disturbance of access trails could be reduced by directional drilling of multiple wells from a single well pad.

Keywords: energy development, mixed models, distance effects, nest survival, mixed-grass prairie, crested wheatgrass, nest predation, brood parasitism

El desarrollo de petróleo y gas tiene efectos mixtos sobre la densidad y el éxito reproductivo de aves canoras de pradera

RESUMEN

El desarrollo de petróleo y gas ha incrementado enormemente en las praderas de pastos nativos en los últimos 25 años. Algunas aves canoras de praderas son menos abundantes en áreas con desarrollo de petróleo y gas, pero los efectos varían entre especies y entre regiones para una especie. Se desconocen las consecuencias reproductivas de anidar en áreas con desarrollo de petróleo y gas. Evaluamos como la densidad y el éxito reproductivo de cinco especies de aves canoras varían con la distancia a pozos de petróleo y gas, rutas enripiadas, senderos y con la cobertura del pasto *Agropyron cristatum*. La cobertura de *A. cristatum* tuvo el mayor impacto en la comunidad de aves canoras de pradera. La supervivencia del nido de *Anthus spragueii* disminuyó a medida que la cantidad de *A. cristatum* aumentó, mientras que *Passerculus sandwichensis* emplumó un 25% más de jóvenes provenientes de nidos exitosos a medida que la cobertura de *A. cristatum* aumentó de 0 a 60%. Sin embargo, la densidad de *P. sandwichensis* fue el doble de alta en áreas sin *A. cristatum* en comparación con una cobertura de 60%. El éxito de emplumamiento de *P. sandwichensis* fue 40% más alto cerca de los pozos y la densidad de estas aves fue el doble de alta cerca de los pozos que a una distancia de 700 m. La distancia a las rutas enripiadas no influenció la densidad o el éxito reproductivo de ninguna especie. *A. spragueii* y *Ammodramus bairdii* evitaron anidar a menos de 100 m de los senderos y ambas especies emplumaron menos jóvenes provenientes de nidos exitosos cerca de los senderos. En contraste, *Pooecetes gramineus* anidó cerca de los senderos y emplumó más jóvenes provenientes de nidos exitosos cerca de los senderos.

Nuestros resultados indican que la introducción y propagación de *A. cristatum* y la creación de senderos de acceso a las plataformas de perforación tienen consecuencias reproductivas negativas para especies endémicas primarias como *A. spragueii* y *A. bairdii*. El futuro desarrollo de petróleo y gas debería minimizar la creación de senderos por medio de perforación dirigida de múltiples pozos desde una única plataforma de perforación y debería minimizar la propagación de *A. cristatum*.

Palabras clave: Agropyron cristatum; depredación del nido; desarrollo de energía; efectos de la distancia; modelos mixtos; parasitismo de nidada; pradera de pastos mixtos; supervivencia del nido

INTRODUCTION

Human activities have altered natural landscapes worldwide. As human populations expand, resource exploitation is likely to continue to stress natural systems, resulting in additional habitat destruction and loss of species (Tilman et al. 2001). The grassland biome is the most drastically altered biome in North America, and has experienced continent-wide loss and degradation due to agricultural activities, fire suppression, and industrial and urban development (Askins et al. 2007). It is estimated that <25% of original native grassland remains in Canada, with the largest contiguous tracts occurring in southern Alberta (Gauthier and Wiken 2003). The widespread loss and degradation of native grasslands have likely been major contributors to population declines of grassland species (Askins et al. 2007).

Native grasslands provide important breeding habitat for many grassland species, but the quantity and quality of remaining habitat may be threatened by oil and gas development. The number of oil and gas wells in Alberta increased from 5,811 to 13,555 between 1998 and 2008 (CAODC 2010), and there is continued economic incentive to increase the number of wells. Wells are typically accompanied by compressor stations, roads, and other linear features (e.g., pipelines and power lines) that lead to habitat loss, increased amounts of edge, increased or altered predator and brood parasite communities, and anthropogenic disturbance to nesting behaviors (Lyon and Anderson 2003, Ingelfinger and Anderson 2004, Klug et al. 2009). Furthermore, such development can increase invasion by exotic plant species, through intentional planting or through establishment and spread due to soil disturbance (Gelbard and Belnap 2003). Although current practices focus on using native seed (Alberta Environment 2010), historically, industrial reclamation practices involved the use of exotic grasses to revegetate impacted sites. These grasses were chosen because they are highly adaptive, inexpensive, and readily available (Richards et al. 1998). As a result, old well sites now serve as point sources for invasion of native grassland by exotic grasses, such as crested wheatgrass (*Agropyron cristatum*). Crested wheatgrass is an aggressive invader of native prairie and often outcompetes native species, resulting in a monoculture that dominates the vegetation community and the seed bank (Christian and Wilson 1999, Henderson and Naeth 2005). This homogenization of habitats with crested wheatgrass reduces habitat suitability for some grassland songbirds (Davis and Duncan 1999, Lloyd and Martin 2005). Fewer birds may occupy areas with oil and gas development that have been planted with, or invaded by, crested wheatgrass.

Oil and gas development has reduced bird abundance in grasslands (Dale et al. 2009, Kalyn Bogard and Davis 2014), boreal forests (Habib et al. 2007, Bayne et al. 2008), and sagebrush-steppe habitat (Walker et al. 2007, Gilbert and Chalfoun 2011). Roads and trails are commonly associated with oil and gas development because wells need to be visited for maintenance. The presence of roads also reduces bird abundance in adjacent habitats (Sutter et al. 2000, Ingelfinger and Anderson 2004), and may reduce reproductive success for those individuals that do occupy these areas (Halfwerk et al. 2011). Bird abundance may be reduced near oil and natural gas wells because of traffic associated with their maintenance, alterations to habitat resulting from construction and maintenance, or noise generated by the structures themselves. The purpose of our study was to assess how density and reproductive success varied with (1) distance to wells, roads, and trails, and (2) the amount of crested wheatgrass (the primary invasive plant species in the area). Previous research on the effects of energy development on avian species abundance has been conducted in native grasslands (Dale et al. 2009, Hamilton et al. 2011, Kalyn Bogard and Davis 2014), but currently there are no published data on the extent to which oil and gas development affects grassland songbird reproductive success. We postulated that primary endemic species (Mengel 1970) typically associated with native grassland (e.g., Sprague's Pipit [*Anthus spragueii*], Baird's Sparrow [*Ammodramus bairdii*]) would experience reduced density and reproductive success near oil and gas infrastructure and in areas with increased cover of crested wheatgrass. In contrast, we hypothesized that species that are more broadly distributed and more general in their habitat requirements (secondary endemic species; Mengel 1970), such as Vesper (*Pooecetes gramineus*) and Savannah sparrows (*Passerculus sandwichensis*), would not be affected, or would be more abundant, or experience greater reproductive success in areas with oil and gas development.

METHODS

Study Site and Data Collection

We conducted our study in the Antelope Creek Habitat Development Area (ACHDA; 50°33′N, 111°53′W) in southeastern Alberta, Canada. The ACHDA is characterized by large tracts of native, dry, mixed-grass prairie. The predominant vegetation consists of needle-and-thread (*Stipa comata*) and blue grama grass (*Bouteloua gracilis*), sage (*Artemisia* spp.), club moss (*Selaginella densa*), and various native forbs. Crested wheatgrass and sweet clover (*Melilotus officinalis*) radiate out from roads, wells, and other energy development infrastructure.

In 2010, we established 12 plots distributed across the ACHDA. We determined plot placement prior to the start of the nesting season, and attempted to maximize coverage of the ACHDA while ensuring plots were not directly adjacent to one another. Plot locations were chosen based on the availability of upland grassland vegetation, the location of energy development infrastructure, and percent cover of crested wheatgrass. Plot placement in 2010 was limited due to large amounts of standing water. In 2011, conditions were drier and we added 4 plots to increase the sample size of nests. Plots were 35–448 m apart (mean $\pm$ SD $= 227 \pm 134$ m) and ranged from 14 to 21 ha (18 ± 2 ha). Over the course of each summer, locations of all oil and gas wells, roads, trails, and patches of crested wheatgrass were determined by ground truthing. We calculated the percent cover of all roads, trails, well sites, and patches of crested wheatgrass in a geographic information system (ArcMap 9.3; ESRI, Redlands, CA, USA), and then summed this value to determine the amount of overall disturbance for each plot. Plots were classified along a disturbance gradient, which ranged from 0% to 60% of the plot area (mean $\pm$ SD $= 16\% \pm 19\%$). Ten of our 16 study plots contained a well site. The aspects of oil and gas development that we measured included distance to oil ($n = 10$) and gas ($n = 35$) wells (grouped as 'wells'), gravel roads and trails, and percent cover of crested wheatgrass. Trails consisted of two tracks through the grass which were mowed each year to reduce the risk of fire. Roads in the ACHDA provided access to the paddocks in the pastures and were not strictly associated with oil and gas development, although the majority of the traffic was by oil and gas company vehicles. In contrast, trails in the ACHDA existed solely to provide employees of the oil and gas industry with access to wells.

Density

We quantified bird density using spot-mapping surveys (Svensson 1979). Each plot was visited 6 times in 2010 and 10 times in 2011. The number of male and female Brown-headed Cowbirds (*Molothrus ater*) observed in each plot was also recorded during spot-mapping surveys to allow determination of mean cowbird abundance. We conducted spot-mapping surveys from 05:00 to 09:00 Mountain Standard Time (MST) on clear days with wind velocities <20 km hr^{-1}. Spot-mapping surveys were performed May 24–July 3 in 2010 and May 23–July 23 in 2011.

We quantified vegetation structure using 50×50 cm quadrats. Quadrats were placed at random distances in each of the four cardinal directions at every second grid point in each plot, resulting in 77 ± 10 quadrats per plot (range $=$ 68–108 quadrats, depending on plot shape). In each quadrat, we visually estimated percent cover of live native grass, dead native grass, forbs, crested wheatgrass, bare ground, and lichen and club moss to the nearest 5%. At the center of each quadrat, we measured both mean vegetation height and litter (unattached, unconsolidated plant material) depth using a 30 cm ruler, and we indexed vegetation density using a Robel pole (Robel et al. 1970). We took 4 visual obstruction readings (VOR) per quadrat (1 in each of the cardinal directions), and averaged these values to obtain a single value for each quadrat. We measured vegetation in each plot once each year, from June 6 to July 9, 2010, and from June 21 to July 9, 2011. To obtain plot-level distance variables, we measured the distance of the nearest well, road, and trail from the center of each plot.

Nest Survival and Reproductive Success

We located nests by systematically dragging a weighted 25 m rope between 2 people across each study plot to flush incubating birds from their nests (Davis 2003). We conducted nest searches 06:00–14:00 MST from early May to late July in each year, and also located nests fortuitously while conducting other activities. We searched each plot for nests 5 times, and took precautions to minimize human-induced nest failure (Martin and Geupel 1993). We checked nests every 3–4 days until completion of the nesting attempt, and candled eggs (Lokemoen and Koford 1996) to determine clutch initiation and hatching dates to increase the precision of our nest survival rate estimates (Shaffer 2004). We aged chicks based on images of known-age young for nests found after hatching. We considered a nest attempt successful if at least one host young fledged, and used cues such as age of nestlings at last nest visit, presence of droppings and feather scales in the nest, and young observed in the area to identify successful nests.

Statistical Analyses

Density. We performed all analyses using SAS Enterprise Guide 4.3 (SAS Institute 2010). We used the GLIMMIX procedure to model the density of singing males as a function of vegetation structure and oil and gas disturbance. We modeled the number of territories using a Poisson distribution, and used the log of plot area as an offset and study plot as a random effect to account for use of the same sites in both years. We first considered models with both the additive and interactive effects of year to determine whether we could combine the data on density from the 2 years. We combined data if models containing no year effect or an additive effect of year performed better than those with an interactive effect of year. Explanatory variables included vegetation features identified as important predictors of grassland songbird habitat use (Fisher and Davis 2010), as well as disturbance features associated with oil and gas development. Grassland bird habitat and nest-site selection are influenced by both vertical and horizontal vegetation cover (Fisher and Davis 2010). Therefore, to avoid overparameterizing models, we divided our vegetation variables into two model categories based on vegetation structure: horizontal (percent cover of bare ground, lichen and club moss, forbs, live grass, and dead grass) and vertical (mean vegetation height and VOR) structure (Table 1). Litter depth was included as a separate model. None of the vegetation variables were highly correlated ($r < 0.70$). We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to rank models (Burnham and Anderson 2002), and considered the model with the lowest AIC_c value to be the best of those considered. We first identified the best horizontal and vertical vegetation model by ranking all subset models in each model set (Table 1), and then used variables from these models along with litter depth to generate a global vegetation model. We compared all subset models along with a null model to identify our best vegetation model for each species. We analyzed development variables (distance to roads, trails, and wells, and percent cover of crested wheatgrass) as a separate model set (Table 1), and included a null model, a global model, and all subsets of the development variables, for a total of 16 models. We compared the top development and vegetation models with a null model and the vegetation and development models combined to determine whether variation in bird density was due mainly to vegetation characteristics or to oil and gas development. We calculated 85% confidence intervals to identify uninformative parameters (Arnold 2010) and to assess the strength of effect for each parameter. We modeled the mean number of Brown-headed Cowbirds per plot as a function of proximity to wells, trails, and roads, percent cover of crested wheatgrass, and presence of a well in a plot using mixed linear models (PROC MIXED; SAS Institute 2010) with plot as a random effect to account for using the same plots each year.

Nest distribution. We used Fisher's exact test ($\alpha = 0.05$) to determine whether nest placement relative to energy development infrastructure differed from random. We tallied the number of nests for each species in each 100 m distance category up to 600 m for wells and roads and up to 500 m for trails. We chose the 500 m and 600 m distance cutoffs because at least 75% of nests of all species were located within these distances. We used ArcGIS (ESRI, Redlands, CA, USA) to place 100 random points within each plot, and summed the number of random points within each 100 m distance category. For both nests and random points we calculated the proportion of nests or random points within each distance interval by dividing the number of nests within each interval by the sum of all nests or random points. We used the proportion of nests and random points within each distance interval as 'observed' and 'expected', respectively, in further analyses.

Nest survival and reproductive success. We calculated daily nest survival rate as a function of distance to the various disturbance features using the logistic exposure method (Shaffer 2004). We considered five a priori models, including a null model (constant survival), distance to wells, roads, and trails, and percent cover of crested wheatgrass, for each species. We determined whether the relationship between daily nest survival rate and distance to the various disturbance features depended upon the year of the study using the same procedure outlined in our density analysis. We used generalized linear models (PROC GENMOD; Burton 2006) with a Poisson distribution and a log link to determine the extent to which the number of young fledged per nest and per successful nest varied with proximity to gravel roads, trails, and wells. We used logistic regression models (PROC LOGISTIC; SAS Institute 2010) to determine the extent to which the probability of cowbird parasitism (parasitized vs. nonparasitized nests) varied with distance to roads and trails and the presence of a well. To maximize available sample size, we combined parasitized nests of all songbird species for analysis ($n = 24$). Unless indicated otherwise, all results are presented as mean $\pm$ standard error (SE). Only results for which 85% confidence intervals did not overlap or include zero are presented and discussed.

RESULTS

We found 332 passerine nests during the 2 years of our study. However, only species for which at least 20 nests were found were included in our analyses (Hensler and Nichols 1981). This resulted in 325 nests of 5 grassland songbird species: Sprague's Pipit ($n = 21$), Vesper Sparrow ($n = 53$), Savannah Sparrow ($n = 190$), Baird's Sparrow ($n = 35$), and Western Meadowlark (*Sternella neglecta*; $n = 26$). For all species, the relationship between disturbance and density did not vary as a function of year; therefore, we combined the data for both years in all analyses. Clutch size, daily survival rate, and fledging success in the AHCDA were similar to rates reported elsewhere (Ludlow et al. 2014).

TABLE 1. List of the models representing horizontal vegetation structure, vertical vegetation structure, and oil and gas development used in the density analyses for five species of grassland songbird in southeastern Alberta, Canada, 2010–2011. The variables in the horizontal vegetation structure model set include percent cover of live grass (live), dead grass (dead), forbs (forb), bare ground (bare), and lichen (lichen). The variables in the vertical vegetation model set include vegetation height (veg_ht) and visual obstruction (robel). The oil and gas development variables include distance to gravel roads (roads), trails (trails), and oil and gas wells (wells), and percent cover of crested wheatgrass (pcwg).

Model set
Horizontal vegetation structure
Global (live + dead + forb + bare + lichen)
Live + dead + forb + bare
Live + dead + forb + lichen
Live + forb + bare + lichen
Live + dead + bare + lichen
Dead + forb + bare + lichen
Live + dead + forb
Live + dead + bare
Live + dead + lichen
Live + forb + bare
Live + forb + lichen
Live + bare + lichen
Dead + forb + bare
Dead + forb + lichen
Dead + bare + lichen
Forb + bare + lichen
Live + dead
Live + forb
Live + bare
Live + lichen
Dead + forb
Dead + bare
Dead + lichen
Forb + bare
Forb + lichen
Bare + lichen
Live
Dead
Forb
Bare
Lichen
Null
Vertical vegetation structure
Global (veg_ht + robel)
Veg_ht
Robel
Null
Development variables
Global (roads + wells + trails + pcwg)
Roads + wells + trails
Roads + wells + pcwg
Roads + trails + pcwg
Wells + trails + pcwg
Roads + wells
Roads + trails
Roads + pcwg
Wells + trails
Wells + pcwg
Trails + pcwg
Roads
Wells
Trails
Pcwg
Null

Density

The top model explaining variation in Savannah Sparrow density included litter depth, percent cover of crested wheatgrass, and distance to roads, wells, and trails (Table 2). Density was most strongly influenced by well proximity and percent cover of crested wheatgrass (Table 3). Savannah Sparrow density was lower near wells and decreased with increasing cover of crested wheatgrass (Figure 1). Baird's Sparrow density was most influenced by Robel VOR (Table 2 and Table 3) and decreased as VOR increased. Variation in Vesper Sparrow density was best explained by percent cover of bare ground (Table 2 and Table 3), with density increasing with greater amounts of bare ground cover. The top model explaining Western Meadowlark density included distance to gravel roads (Table 2), but confidence limits included zero (Table 3). Sprague's Pipit density was best explained by litter depth (Table 2 and Table 3), and was lower in areas with increased depth of litter. Mean cowbird abundance was best explained by the presence of a well in the study plot, and was almost three times higher in plots containing an oil or gas well (2.5 $\pm$ 0.3 birds 18 ha^{-1}) than in plots where wells were absent (0.9 $\pm$ 0.3 birds 18 ha^{-1}).

Nest Distribution

Nest locations relative to wells did not differ from random for Sprague's Pipit, or for Vesper, Savannah, and Baird's sparrows. The proportion of Western Meadowlark nests within 100 m of wells was higher than expected by chance alone ($P < 0.001$), although meadowlarks tended to avoid nesting within 100 m of gravel roads ($P = 0.05$). Baird's Sparrows also tended to avoid nesting within 100 m of roads ($P = 0.03$). Nest locations relative to roads did not differ from random for Savannah and Vesper sparrows and Sprague's Pipits. The proportion of Vesper Sparrow nests within 100 m of trails was higher than expected based on chance ($P < 0.001$), whereas Baird's Sparrows ($P = 0.03$) and Sprague's Pipits ($P < 0.001$) tended to avoid nesting within 100 m of trails. The distribution of Savannah Sparrow and Western Meadowlark nests relative to trails did not differ from random.

TABLE 2. Model selection results for generalized linear mixed models of territory density for five species of grassland songbird in southeastern Alberta, Canada, 2010–2011. Log(*L*) is the value of the maximized log-likelihood function, *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, and w_i is the Akaike weight. Well, road, and trail represent the distance from the center of the plot to any oil and gas well, gravel road, and trail, respectively. Pcwg represents the percent cover of crested wheatgrass, litter is percent cover of unconsolidated plant material, bare ground is the percent cover of bare ground, and robel represents visual obstruction readings measured with a Robel pole.

Model	Log(*L*)	*K*	ΔAIC_c	w_i
Sprague's Pipit				
Litter [a]	83.84	3	0.0	0.71
Road + litter	82.87	4	1.8	0.29
Null	111.76	2	25.4	0.00
Road	704.10	3	620.3	0.00
Vesper Sparrow				
Road + bare ground [b]	80.08	4	0.0	0.63
Bare ground	84.64	3	1.8	0.26
Road	86.91	3	4.1	0.08
Null	91.58	2	6.2	0.03
Savannah Sparrow				
Well + road + trail + pcwg + litter [c]	157.43	7	0.0	0.83
Well + road + trail + pcwg	165.05	6	4.0	0.11
Litter	175.86	3	5.8	0.45
Null	181.21	2	8.7	0.01
Baird's Sparrow				
Robel [d]	88.15	3	0.0	0.70
Robel + pcwg	87.06	4	1.7	0.30
Pcwg	106.14	3	18.0	0.00
Null	112.85	2	22.2	0.00
Western Meadowlark				
Road [e]	86.34	3	0.0	0.28
Null	90.08	2	1.8	0.15
Road + pcwg	85.35	4	4.1	0.12
Road + trail	86.08	4	6.2	0.08

[a] The AIC_c value for the best model for Sprague's Pipit (litter) = 90.84.
[b] The AIC_c value for the top model for Vesper Sparrow (road + bare ground) = 89.82.
[c] The AIC_c value for the best model for Savannah Sparrow (well + road + trail + pcwg + litter) = 177.03.
[d] The AIC_c value for the best model for Baird's Sparrow (Robel) = 95.15.
[e] The AIC_c value for the top model for Western Meadowlark (road) = 93.34.

TABLE 3. Parameter estimates of the best generalized linear mixed models for territory density of five species of grassland songbird in southeastern Alberta, Canada, 2010–2011. See Table 1 for definitions of model parameters.

Parameter	Estimate	Standard error	Lower 85% CL	Upper 85% CL
Sprague's Pipit				
Intercept	−0.8323	0.2931	−1.2544	−0.4102
Litter	−0.2217	0.0509	−0.2950	−0.1484
Vesper Sparrow				
Intercept	−3.4768	0.4871	−4.1782	−2.7754
Road	0.0007	0.0006	−0.0001	0.0015
Bare ground	0.1561	0.0548	0.0771	0.2351
Savannah Sparrow				
Intercept	0.5445	0.1460	0.3343	0.7547
Well	−0.0010	0.0005	−0.0017	−0.0003
Road	−0.0001	0.0002	−0.0004	0.0001
Trail	0.0005	0.0005	−0.0001	0.0012
Pcwg	−0.0103	0.0037	−0.0156	−0.0050
Litter	0.0223	0.0080	0.0109	0.0338
Baird's Sparrow				
Intercept	0.4525	0.8243	−0.7345	1.6395
Robel	−0.3166	0.0773	−0.4280	−0.2052
Western Meadowlark				
Intercept	−2.0623	0.2185	−2.3769	−1.7477
Road	0.0002	0.0004	−0.0003	0.0008

Nest Survival

We found no effect of proximity to wells, roads, or trails on nest survival, as 85% confidence limits included zero in all cases (Table 4). Nest survival varied with percent cover of crested wheatgrass only for Sprague's Pipits (Table 4), with daily nest survival rate decreasing with increased cover of crested wheatgrass (Table 4 and Figure 2). We failed to find any relationship between the frequency of brood parasitism and distance to gravel roads ($\beta \pm SE = 0.000 \pm 0.001$) or trails ($\beta \pm SE = -0.001 \pm 0.001$), well presence ($\beta \pm SE = 0.647 \pm 0.517$), and percent cover of crested wheatgrass ($\beta \pm SE = -0.009 \pm 0.015$).

Fledging Success

Savannah Sparrows fledged more young per nest closer to wells than farther away (Figure 3A). The number of young fledged per nest did not vary with proximity to wells for the other four species (Table 5). The number of young fledged per nest did not vary with percent cover of crested wheatgrass or distance to gravel roads or trails for any species, as confidence limits included zero in all cases (Table 5).

The number of young fledged from successful nests was lower near trails than farther away for Baird's Sparrows (Figure 3B) and Sprague's Pipits, but was higher closer to trails for Vesper Sparrows (Table 5). The number of Savannah Sparrow young fledged per successful nest increased as the percent cover of crested wheatgrass increased from 0% to 60% (Figure 3C). The number of young fledged per successful nest did not vary with distance to wells or gravel roads for any of the five species (Table 5).

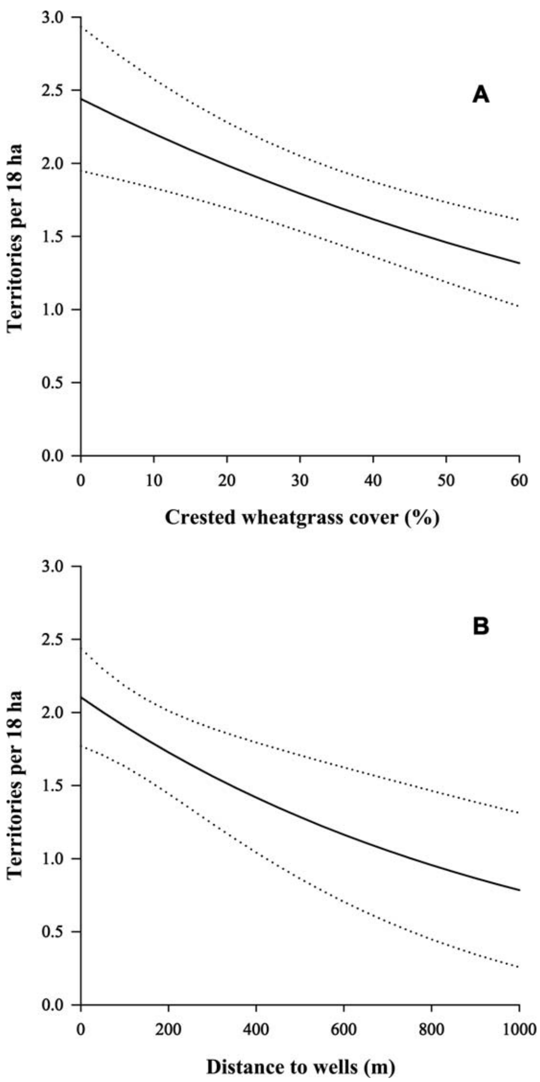

FIGURE 1. Density of Savannah Sparrows (mean and 85% CI) in southeastern Alberta, Canada, 2010–2011, as a function of (**A**) the amount of crested wheatgrass, and (**B**) distance to oil and gas wells.

DISCUSSION

The effect of oil and gas development on grassland songbird density and reproductive success varied by species, despite these species establishing territories in the same plots and nesting in similar habitats. Furthermore, many of the species share similar life history traits, such as diet, parental care, and foraging and nesting behavior (Ehrlich et al. 1988). Differences in responses among species may reflect differences in sensitivity to habitat alteration or intensity of disturbance. If nest placement is adaptive, birds would be expected to place their nests in areas that maximize reproductive success (Martin 1998). Indeed, some species in the ACHDA tended to locate their nests in areas where they were more

TABLE 4. Effects of distance to gravel roads, trails, and oil and gas wells, along with percent cover of crested wheatgrass (% CWG), on the daily nest survival rates of five species of grassland songbird in southeastern Alberta, Canada, 2010–2011. Data presented are mean estimates followed by upper and lower 85% confidence limits.

	Distance			
Species	Roads	Trails	Wells	% CWG
Sprague's Pipit	−0.0012 (−0.0032, 0.0008)	0.0006 (−0.0027, 0.0039)	0.0027 (−0.0010, 0.0064)	−0.0423 (−0.0779, −0.0067)
Vesper Sparrow	−0.0001 (−0.0010, 0.0008)	0.0004 (−0.0005, 0.0013)	−0.0001 (−0.0014, 0.0012)	−0.0008 (−0.0194, 0.0178)
Savannah Sparrow	0.0001 (−0.0005, 0.0007)	−0.0004 (−0.0010, 0.0002)	−0.0003 (−0.0007, 0.0001)	0.0041 (−0.0073, 0.0155)
Baird's Sparrow	0.0017 (−0.0003, 0.0031)	0.0005 (−0.0015, 0.0025)	0.0000 (−0.0009, 0.0009)	0.0144 (−0.0135, 0.0423)
Western Meadowlark	−0.0020 (−0.0040, 0.0000)	−0.0009 (−0.0021, 0.0003)	−0.0008 (−0.0017, 0.0001)	0.0173 (−0.0151, 0.0497)

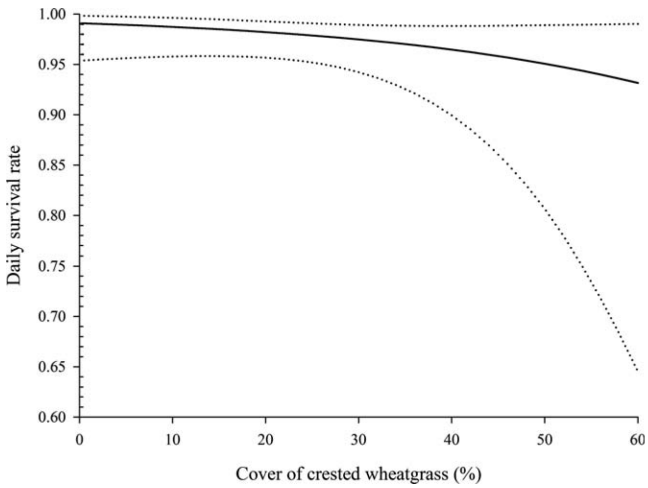

FIGURE 2. Daily survival rate (mean and 85% CI) of Sprague's Pipit nests as a function of percent cover of crested wheatgrass in southeastern Alberta, Canada, 2010–2011.

successful. For example, Sprague's Pipits and Baird's Sparrows tended to avoid nesting within 100 m of trails, and both of these species fledged fewer young from successful nests near trails. In contrast, Vesper Sparrows nested closer to trails than expected by chance and fledged more young from successful nests near trails.

Of the variables that we investigated that were related to oil and gas development, the amount of crested wheatgrass had the most wide-ranging effects on the density and reproductive success of grassland songbirds. Savannah Sparrow density was nearly two times lower in areas with 60% cover of crested wheatgrass compared with areas without this exotic grass. Grasslands dominated by exotic grasses are typically poor-quality habitat for songbirds compared with native prairie (Lloyd and Martin 2005, Fisher and Davis 2011). However, increased fledging success of Savannah Sparrows in areas with higher amounts of crested wheatgrass suggests that a density-dependent relationship may exist, whereby a lower density of breeding pairs in a patch of crested wheatgrass may provide increased opportunities to acquire food resources. Population density has been shown to influence fledging success and other reproductive parameters in Song

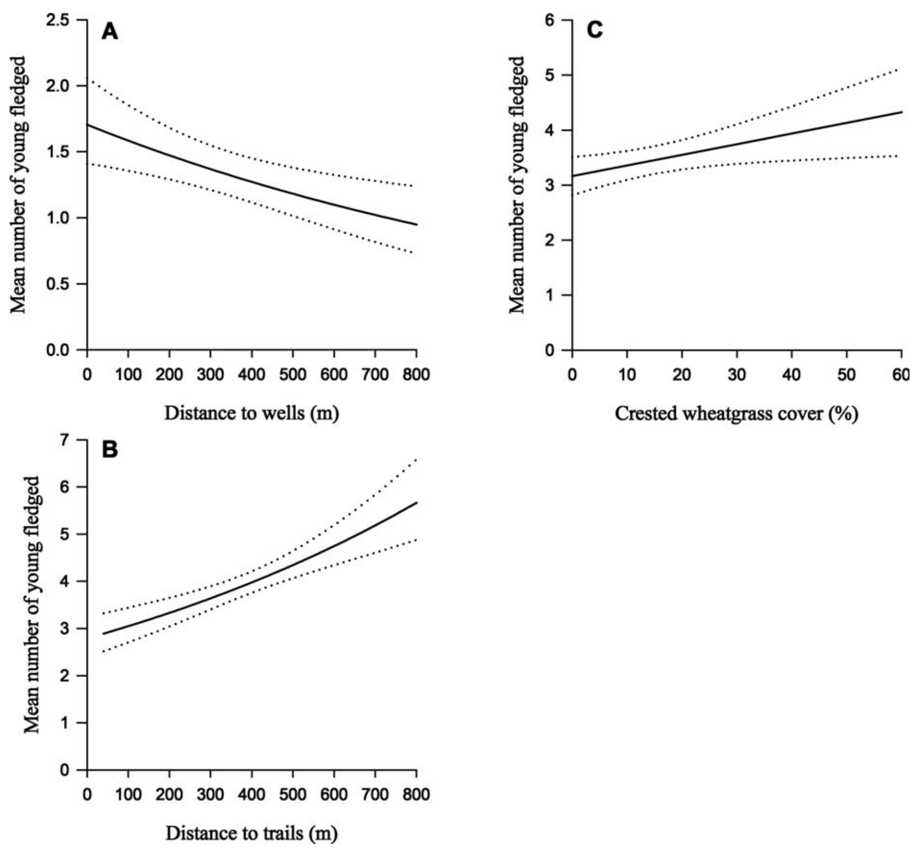

FIGURE 3. The mean number of young fledged from (**A**) Savannah Sparrow nests as a function of oil and gas well proximity, (**B**) successful Baird's Sparrow nests as a function of proximity to trails, and (**C**) successful Savannah Sparrow nests as a function of percent cover of crested wheatgrass in southeastern Alberta, Canada, 2010–2011. Dashed lines show 95% CI.

TABLE 5. Parameter estimates for the number of young fledged from all nests and successful nests as a function of distance to gravel roads, trails, and oil and gas wells, and percent cover of crested wheatgrass (% CWG) for five species of grassland songbird in southeastern Alberta, Canada, 2010–2011. Data presented are mean estimate (EST), standard error (SE), and upper and lower 85% confidence limits (UCL and LCL, respectively).

	All nests				Successful nests			
	Distance				Distance			
Species	Roads	Trails	Wells	% CWG	Roads	Trails	Wells	% CWG
Sprague's Pipit								
EST	−0.0003	0.0006	−0.0003	0.0725	−0.0002	0.0006	−0.0002	0.0182
SE	0.0009	0.0014	0.0008	0.0508	0.0004	0.0002	0.0002	0.0283
LCL	−0.0022	−0.0022	−0.0013	−0.0270	−0.0010	0.0001	−0.0007	−0.0373
UCL	0.0015	0.0033	0.0018	0.1720	0.0007	0.0011	0.0003	0.0737
Vesper Sparrow								
EST	0.0007	−0.0001	−0.0008	0.0066	0.0004	−0.0005	−0.0001	−0.0083
SE	0.0006	0.0005	0.0012	0.0074	0.0003	0.0002	0.0004	0.0177
LCL	−0.0005	−0.0011	−0.0031	−0.0078	−0.0002	−0.0008	−0.0010	−0.0430
UCL	0.0018	0.0010	0.0014	0.0211	0.0011	−0.0001	0.0008	0.0264
Savannah Sparrow								
EST	−0.0006	−0.0002	−0.0007	0.0154	−0.0002	0.0001	−0.0001	0.0194
SE	0.0004	0.0004	0.0002	0.0084	0.0002	0.0001	0.0002	0.0085
LCL	−0.0013	−0.0009	−0.0012	−0.0011	−0.0005	−0.0002	−0.0005	0.0028
UCL	0.0002	0.0006	−0.0003	0.0318	0.0002	0.0004	0.0003	0.0359
Baird's Sparrow								
EST	0.0015	0.0012	0.0002	−0.0064	−0.0002	0.0009	0.0002	0.0558
SE	0.0009	0.0014	0.0007	0.0379	0.0002	0.0002	0.0001	0.0353
LCL	−0.0003	−0.0015	−0.0012	−0.0806	−0.0007	0.0004	−0.0001	−0.0134
UCL	0.0033	0.0040	0.0016	0.0679	0.0002	0.0013	0.0004	0.1250
Western Meadowlark								
EST	−0.0017	−0.0011	0.0000	−0.0380	0.0003	0.0003	0.0001	−0.0290
SE	0.0013	0.0011	0.0000	0.0459	0.0005	0.0002	0.0001	0.0283
LCL	−0.0042	−0.0033	0.0000	−0.1279	−0.0007	−0.0001	−0.0001	−0.0844
UCL	0.0008	0.0011	0.0000	0.0520	0.0013	0.0006	0.0003	0.0265

Sparrows (*Melospiza melodia*; Arcese and Smith 1988). In contrast, Sprague's Pipit nest survival was lower in areas with increased cover of crested wheatgrass. Similarly, Lloyd and Martin (2005) found that Chestnut-collared Longspurs (*Calcarius ornatus*) had reduced reproductive success in crested wheatgrass compared with native grassland. Grasslands composed of exotic vegetation typically have lower plant diversity and reduced arthropod biomass (Hickman et al. 2006) than native grasslands. Sprague's Pipit nest survival may be lower in areas with large amounts of crested wheatgrass if these areas are deficient in the bird's preferred prey. Like the Chestnut-collared Longspur, Sprague's Pipit is a primary endemic grassland specialist (Hill and Gould 1997, Robbins and Dale 1999), and is more sensitive to habitat alteration or degradation than the Savannah Sparrow (Sutter et al. 2000, Davis 2004, Hamilton et al. 2011).

Although proximity to roads did not influence the density or nest success of any species, Baird's Sparrows and Western Meadowlarks avoided placing nests within 100 m of gravel roads. Such avoidance may be a result of unsuitable vegetation structure along roadsides (Gelbard and Belnap 2003), increased predation risk (Knight and Kawashima 1993, Meunier et al. 2000, Dinkins et al. 2014), or disturbance by vehicles (Reijnen and Foppen 2006).

Proximity to wells had several positive effects on grassland songbird density and reproductive success in the ACHDA. The proportion of Western Meadowlark nests located within 100 m of wells was higher than expected by chance. Western Meadowlarks may locate nests near wells due to these structures providing perch sites for territorial males (Davis and Lanyon 2008). Savannah Sparrows had higher fledging success closer to wells, and this may be related to increased rates of parental provisioning. In many socially monogamous species, nestling provisioning by both parents is necessary to successfully raise young, and any adjustments to the level of provisioning by either parent may alter the total number of young fledged (Whittingham et al. 1994). Provisioning rates and nest attentiveness of male Savannah Sparrows may be higher near wells due to elevated levels of corticosterone (Crino et al. 2011), a stress-induced hormone known to influence avian foraging behavior (Lõhmus et al. 2006, Angelier et al. 2008). Higher fledging success near wells may also be the result of increased density of Savannah Sparrows in these areas. However, the fledging success of Savannah Sparrows in southern Saskatchewan, Canada, was not influenced by proximity to natural gas wells (Gaudet 2013). Regional variation in Savannah Sparrow fledging success in response to well proximity highlights the influence of site-level variation on species' responses to development, and suggests that extrapolation of results from a single site across a species' range may be tenuous. This may be especially true for a species like the Savannah Sparrow, which shows variation in habitat preferences across its broad range (e.g., Peterson et al. 2014). More studies across a range of sites are needed to gain a better perspective of the influence of oil and gas wells on grassland songbird reproductive success. It would also be useful to make comparisons among various energy-related activities in grasslands, particularly including indirect effects (Devereaux et al. 2008, Robertson et al. 2012, Stevens et al. 2013, Hale et al. 2014).

Variation in Brown-headed Cowbird abundance was best explained by the presence of a well. The mean abundance of cowbirds in plots containing an oil or gas well was almost three times that in plots where wells were absent. Oil and gas wells provide perch sites for cowbirds to use for displaying and locating host nests (Thompson and Gottfried 1976), and therefore may increase the frequency of cowbird parasitism (Saunders et al. 2003, Patten et al. 2011). However, the frequency of brood parasitism by cowbirds in the ACHDA was not higher in plots containing wells. The lack of a relationship between brood parasitism frequency and well presence may be due to the presence of, or proximity to, other similar perches (e.g., fences, power lines, shrubs) across the landscape; alternatively, the small sample of parasitized nests may have precluded us from finding an effect.

Overall, our results indicated that the effect of oil and natural gas development on grassland songbird density and reproductive success varied with species and type of disturbance. Furthermore, our results supported our initial prediction that primary endemic species would suffer adverse effects of oil and gas development while generalist species would either be positively or not affected. The percent cover of crested wheatgrass had the widest-ranging effects of the disturbance variables that we investigated. Although all species of grassland songbird that we studied had nests located in crested wheatgrass, Sprague's Pipits experienced reduced nest survival in these areas compared with native grassland. Our results are consistent with those of other studies, which have found reduced reproductive rates for grassland songbirds nesting in crested wheatgrass (Lloyd and Martin 2005) and other exotic grasses (Guiliano and Daves 2002, Fisher and Davis 2011). The Savannah Sparrow was the sole species whose reproductive success was positively influenced by crested wheatgrass cover, although its density declined with increased cover of this exotic grass. Our results indicate that the creation of access trails to well pads and the introduction and spread of crested wheatgrass can have negative reproductive consequences for primary endemic species such as Sprague's Pipits and Baird's Sparrows. We encourage future oil and gas developments to minimize trail creation through directional drilling of multiple wells from one lease site, and to continue to minimize the spread of crested wheatgrass in native grasslands.

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