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Effects of Twice-Over Rotational Grazing on Songbird Nesting Success in Years With and Without Flooding

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ABSTRACT

Rotational grazing is sometimes promoted for grassland bird conservation, but the benefits to wildlife have not been comprehensively documented. We examined effects of twice-over rotational grazing on nesting success of grassland songbirds in southwestern Manitoba, Canada in comparison to season-long grazing. We monitored nesting attempts and collected structural vegetation data in 2011 (during a 1/300 flood event), and 2012 (average water levels), for five species of obligate grassland bird species ($n = 110$) and one shrub-nesting species ($n = 41$). Nesting analyses were conducted using logistic exposure models. Nesting success was 2.4 to 4 times lower in twice-over grazed pastures compared with season-long grazed pastures, perhaps because of the increased cattle density during the short grazing periods of the twice-over system. Nests protected by shrubs from grazing activities of cattle did not show this pattern. The grazing system did not have an effect on vegetation structure. This suggests that twice-over rotational grazing does not benefit grassland songbirds in northern mixed-grass prairies, and that caution must be taken before implementing this grazing system in areas intended to promote biodiversity conservation.

Introduction

Grasslands have undergone the highest rate of natural vegetation conversion and degradation of any biome on earth (Hoekstra et al., 2005). Therefore, it is not surprising that grassland bird populations have also declined more than any other guild of terrestrial birds in North America (Askins, 1993; Fuhlendorf and Engle, 2001; Knopf, 1996; With et al., 2008). Natural prairie vegetation loss is primarily caused by conversion for agricultural and urban development, and oil and gas extraction (Askins et al., 2007; Brennan and Kuvlesky, 2005; Samson and Knopf, 1994). Remaining prairies are also being degraded by overgrazing, fire suppression, woody plant encroachment, and exotic species introduction (Brennan and Kuvlesky, 2005; With et al., 2008). In Manitoba, 82% of the area historically covered by the mixed-grass prairie eco-region has been lost (Thorpe, 2011), and the remaining areas of intact mixed-grass prairie are fragmented and primarily grazed by cattle (Small and McCaughey, 1999).

Grassland bird populations have continued to decline over the last 25 years (Samson et al., 2004), suggesting that modern rangeland management practices are insufficient for maintaining prairie biodiversity (Fuhlendorf and Engle, 2001). One explanation is that habitat requirements of different grassland bird species vary greatly, and thus supporting a diverse grassland bird community may depend on having an interspersion of diverse habitat types (Fuhlendorf et al., 2006; Hovick et al., 2014, 2015). In contrast, traditional rangeland management focuses on increasing foraging efficiency and livestock production by managing grazing intensity and livestock distribution over space and time to create a uniform grazing landscape (Fuhlendorf and Engle, 2001; Holechek et al., 1998). Yet, there may be alternative methods of managing rangeland and grazing activities that could improve biodiversity and grassland bird habitat while still maintaining agricultural productivity (Brown and Kothmann, 2009; Derner et al., 2009; Fuhlendorf and Engle, 2001; Johnson and Igl, 2001).

Rotational grazing systems provide pastures with periods of rest from cattle impacts such as vegetation loss and trampling with the assumption that rested paddocks will allow for increased plant density, herbage production, and improved nutrient quality, thereby improving animal performance. It is also thought that the cattle-free, rested paddocks will allow for undisturbed nesting attempts and increased grassland bird production (Knopf, 1996; Sutter, 1997). Rotational grazing systems have been promoted by several rangeland scientists, government, university, and nonprofit conservation agencies in Canada and the United States as being beneficial to both cattle producers and native prairie wildlife (Barker et al., 1990; Krausman et al., 2009; MHHC, 2010; Teague et al., 2013). However, the assumption that rotational grazing is more beneficial than season-long grazing in terms of grassland wildlife habitat quality, diversity, and/or cattle production is still debated (e.g., Briske et al., 2008, 2011), in part because rotational grazing methods

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can vary by stocking rate, grazing period, and grazing duration, which makes comparisons among grazing systems difficult.

Livestock grazing can alter predator communities, available vegetation cover, and Brown-headed Cowbird parasitism rates, and these risks can vary among grazing management regimes (Bleho et al., 2014). The majority of studies on rotational grazing have focused on plant productivity and cattle performance, whereas the few studies that have looked at impacts on grassland bird populations have shown little to no positive effects. For example, neither abundance nor nesting success of grassland birds increased on rotationally grazed pastures (Kerns et al., 2010; Perlut and Strong, 2011; Ranellucci et al., 2012; Temple et al., 1999). Temple et al. (1999) even found that rotationally grazed pastures attract grassland birds in higher densities, but that breeding productivity is low. This suggests that rotationally grazed pastures may be grassland bird ecological traps (e.g., Gates and Gysel, 1978), wherein birds may be attracted to rotationally grazed pastures (likely when cattle are absent and vegetation has partially recovered), only to suffer low nesting success when the cattle return due to either trampling, changes in vegetation structure, or disturbance part way through a nesting cycle.

Nonetheless, there are ongoing efforts to develop alternative rotation systems, such as the twice-over system, that might yield the benefits predicted to result from rotational grazing, while avoiding its disadvantages. The twice-over grazing uses a three-to-six paddock rotation, with each paddock grazed twice per season. The first grazing event occurs when grasses have reached the three-leaf stage and before flowering, and is intended to increase tillering (the production of more shoots and leaves). Secondary growth is then available for a second round of grazing. The twice-over rotation system requires landowners to follow a grazing schedule that optimizes the amount of time for both grazing and recovery, and thus is hypothesized to improve overall pasture and cattle health.

In the northeastern Great Plains, twice-over grazing typically allows for 30 days of pasture rest during the first rotation (completed by July 15) and up to 60 days rest for the second rotation (completed by October 15), leaving large areas of grassland cattle free over the grazing season. It is thought that the twice-over grazing system could allow for an increase in nesting success of grassland birds by eliminating cattle activity during a long portion of the breeding cycle; conversely, the rotation of cattle onto formerly idle pastures might introduce high densities of livestock to grasslands that had been initially selected by birds as nest sites because they were undisturbed. The twice-over rotation grazing system has been growing in popularity across the Northern Great Plains, in part because it is hypothesized to improve habitat for wildlife. Unfortunately, Christie (1997), and Ranellucci et al. (2012) both found that obligate grassland nesting birds had significantly lower species diversity on twice-over rotational pastures. However, the effects of twice-over grazing on nesting success is unstudied and may be different than its effect on habitat use, as mechanisms that influence habitat selection, such as vegetation preferences, differ from mechanisms that influence nesting success, such as predator communities. Therefore, twice-over grazing may either positively or negatively impact grassland bird nesting success and productivity despite its impacts on diversity, and requires further study to evaluate the potential conservation benefits.

To assess the effects of twice-over rotational grazing on productivity of grassland songbirds in northern mixed-grass prairies, we conducted a 2-year study (2011–2012) to compare nesting success between twice-over grazed and season-long grazed pastures. Additionally, we had the opportunity to evaluate whether effects of grazing system varied with environmental conditions, as our first field season took place during a record flood event. The Assiniboine and Souris rivers experienced a 1-in-300-year flood in our study area in 2011, resulting in water inundating large areas of land for the majority of the breeding season. The following field season (2012) did not experience any flooding, and farming and ranching operations proceeded as normal, thus reflecting average environmental conditions.

We hypothesized that increased disturbance from high cattle densities during grazing periods might outweigh benefits of rest periods, resulting in lower nesting success in twice-over grazed pastures. We hypothesized that if effects on nesting success resulted from disturbance by cattle or grazing of vegetation by cattle, impacts should be detected among ground-nesting species but not shrub-nesting species, as nests in shrubs are protected from cattle (Dion et al., 2000). We also hypothesized that flooding might force songbirds to nest in close proximity on the reduced area of grassland "islands" that remained above flood waters, and this might make it easier for predators or nest-parasites (cowbirds) to find nests, resulting in lower nesting success in the flood year. Our objectives were, thus, to compare nesting success of ground-nesting species and shrub-nesting species between twice-over and season-long grazed pastures, and to compare nesting success in a flood year compared with a climatically typical year.

Methods

Study Sites

Our study was situated in the mixed-grass prairie region of southwestern Manitoba, within the boundaries of the West Souris River Conservation District, and within the Assiniboine and Souris River drainage basins. Nest survey sites were located between the Canada-US border (48°59'59.9"N) to 120 km north (49°55'52.3"N), and between the Saskatchewan-Manitoba border (101°25'08.4"W) to approximately 70 km east (100°37'21.2"W).

Study sites were all grazed with cattle using twice-over rotational grazing or season-long grazing. On season-long sites, cattle grazed continuously between May and October (typically 153 d grazing season), whereas on twice-over sites cattle were grazed rotationally between pastures starting 1 June and ending 15 October (typically 137-d grazing season). In the northeastern Great Plains, landowners divide pastures into three to six paddocks. Cattle enter the first paddock on 1 June, and are rotated through each paddock every 7 to 15 d. The number of days is determined by the number of paddocks in the rotation (e.g., 3 paddocks = 15 d/paddock. 6 paddocks = 7 d/paddock). The first rotation is typically complete by 15 July, or after 45 d of grazing. The second rotation within each paddock is double the number of days of the first rotation, and is typically completed by 15 October. In a three-paddock system, this rotation allows for approximately 30 d of pasture rest during the first rotation, and 60 d rest for the second rotation. The average stocking rates (animal units grazed on an area during a month [AUM] divided by acre) for the study area were slightly but significantly higher ($P < 0.0001$) on season-long pastures (0.878 AUM · acre^{-1}) than on twice-over pastures (0.757 AUM · acre^{-1}; Ranellucci et al., 2012). Fifteen sites were surveyed over 2 years: nine twice-over grazed and six season-long grazed pastures.

Site Selection

In 2011, twice-over sites were selected based on years in the twice-over program (>3 yr) and accessibility. We selected season-long sites based on landowner volunteers who were approached through a contact with Manitoba Habitat Heritage Corporation (MHHC), or by referral from neighbouring landowners already involved in the project. We selected pastures where cattle remained on the pasture from 1 June until mid-October for both treatments. Study sites in 2011 were dispersed throughout the rural municipalities (RMs) of Albert, Edward, Pipestone, and Sifton, and ranged in size from 0.65 to 2 km^2. Thirteen sites were surveyed in the 2011 field season, nine twice-over and four season-long. Flooding restricted access to all but these 13 sites. Each site was surveyed twice throughout the field season. In 2011, within the rural municipalities of the study area, between 60% and 90% of cropland went unseeded due to flood conditions (WSCD, 2014). Grassland pastures also experienced high rates of flooding and water remained on the landscape throughout the grassland songbird-breeding season.

Unfortunately, we were unable to map flood locations to include in our analysis; we could not procure a map layer from provincial or insurance agencies covering the study sites, and we were unable to map the water perimeter in the fields ourselves because water levels varied daily, and thus the perimeter of the flooded areas varied over the season and within each nest exposure period.

Although we attempted to survey each site in 2 years, this was not always possible. Four of the nine twice-over sites surveyed in 2011 could not be surveyed again in 2012 due to changes in grazing management systems between years. Six new sites were added in 2012 (four twice-over, and two season-long) bringing the 2012 site total to nine twice-over sites (five of which were surveyed in both 2011 and 2012), and six season long sites (four of which were surveyed in both 2011 and 2012). Four of the new sites were chosen from the RM of Woodworth, and two sites were chosen from the RM of Albert. Each site was surveyed twice throughout the field season.

Ultimately, we surveyed all available twice-over and season-grazed sites in our study area; there were fewer season-long landowners willing to participate in the study, resulting in more twice-over sites than season-long sites in our study. This resulted in an appropriate study design, as there was greater variability in management within seasons in twice-over grazed pastures (which were both grazed and ungrazed each year) compared with season-long grazed sites (which were only grazed), and we wanted to ensure sufficient samples of nests from twice-over grazed sites that would reflect nesting success both in the presence and absence of cattle.

Field Methods

Nest searching occurred from mid-May through mid-July in 2011 and 2012. We selected one 9-ha plot per site to nest search once every 30 d during the breeding season (minimum 2 visits). In 2011, flooding reduced the amount of dry grassland habitat available on all of the pastures. During the first visit at each site, researchers walked the area to determine the degree of flooding throughout the pasture and selected an area with minimal potential for flooding, generally encompassing all or almost the entire available unflooded upland habitat. Survey plots varied in shape depending on the topography of each site (excluding flooded areas and woodlots). Nest searching occurred between 0700 hours and 1200 hours, and between 1600 hours and 2000 hours when it was not raining or windy (> 20 kph), as vegetation moving in high wind can visually obstruct a nest flush. Nest searching was not conducted between the hours of 1200 hours and 1600 hours when temperatures were highest and when adults are less likely to be attending nests (Winter et al., 2003). We located nests using a rope-drag, consisting of a 20-m rope with rock-filled cans attached every 2 feet, to flush incubating birds. We also located nests incidentally during field travel and nest monitoring. Once a nest was located, we recorded species, nesting stage, and number of eggs and/or young. We marked nests with bamboo stakes and flagging tape 10 m to the north and east, and recorded location coordinates with a GPS unit. We revisited nests every 2 to 4 d to monitor progress and the resulting success or failure (Winter et al., 2003). We classified nests as successful if a minimum of one host young fledged. A successful fledge was characterized by the following cues: adults alarm calling near the empty nest, nestling age at previous visit, nests intact paired with the presence of fecal matter and feather scales in the nest, and/or fledglings observed in the vicinity (Davis, 2003). We visually determined nestling age by observing the developmental timing of feather tracts, eye opening, and behavioral reactions to the observer (e.g., begging for food, remaining motionless and quiet, or looking jumpy; Jongsomjit et al., 2007). Photographs were taken of nestlings each visit to reduce the time spent at the nest and provide a record for later confirmation of nestling ages. Nests of 7 species were monitored. Ground or near-ground nesting species included Chestnut-collared Longspur (*Calcarius ornatus*), Savannah Sparrow (*Passerculus sandwichensis*), Vesper Sparrow (*Pooecetes gramineus*), Western Meadowlark (*Sturnella neglecta*), Le Conte's Sparrow (*Ammodramus lecontii*; only ground nests found), and Bobolink (*Dolichonyx oryzivorus*; only ground nests found). The shrub nesting species was Clay-colored Sparrow (*Spizella pallida*).

Upon completion of a nesting attempt, we measured vegetation structure using methods adapted from Wiens (1969). We measured vegetation at each nest, and at two random locations within 50 m of the nest to represent the potential area available within a territory of our most abundant study species, Savannah Sparrows and Clay-colored Sparrows (Lusk and Koper, 2013; Knapton, 1979; Jones, 2011). The random locations were selected using random number tables for both direction and distance. At each sample location we placed two crossed meter sticks to create quadrats, which were used to visually estimate the percentage cover of live grass, dead grass, forb, shrub, litter, bare ground, and cow excrement. To quantify vegetation density, we dropped a 1-m metal Wien's pole vertically using a stabilizing holder, at the center of the quadrat and at each end of the meter sticks. The Wien's pole was divided into 10-cm segments and live vegetation contacting the pole was counted in two categories, below 10 cm and above 10 cm. We also recorded litter depth and height of tallest vegetation at each Wien's pole location. We defined litter as any horizontal dead vegetation that was not attached to the ground.

Data Analysis

We took a null-hypothesis significance testing approach in our analyses, as we were focussing on testing specific hypotheses represented by individual variables (Mundry, 2011).

To determine effects of twice-over versus season-long grazing on the nesting success of grassland songbirds, we used the logistic exposure method modeled using PROC NLMIXED in SAS 9.3 (SAS Institute, Cary, NC; Dinsmore et al., 2002; Shaffer, 2004). We ran preliminary models to determine whether a polynomial nonlinear model of seasonality (visit date) influenced daily nest survival and whether it should be included in the grazing model. Effect of visit date was not significant, and thus it was not included in subsequent models to avoid overparameterization. Similarly, nesting success did not vary between incubation and nestling nest stages ($P = 0.351$, $t = 0.93$), so this variable was not included in subsequent models. Akaike's Information Criteria (AIC) values indicated that models fit better when the random variable site was excluded from analyses, and parameter estimates for site as a random variable were extremely small (< 0.0001), suggesting that it was not necessary to include site as a random variable; therefore, we excluded it from subsequent models.

We divided nests into two groups for analyses: ground-nesting species ($n = 110$), and shrub nesting Clay-colored Sparrows ($n = 41$). We also evaluated effects of twice-over and season-long grazing on three individual species, Savannah Sparrow ($n = 41$), Vesper Sparrow ($n = 32$), and Clay-colored Sparrow ($n = 41$), in which the number of monitored nests with a confirmed outcome was greater than $n = 20$, thus, providing an adequate sample size for analysis. Year was included in all models to account for the flood event in 2011 and other year effects; the other independent variable was grazing treatment. The interaction between grazing treatment and year was also included in the analyses to evaluate whether the effect of grazing treatment differed between the flood year and normal water level year. The interaction was not significant and thus was removed from the final model to avoid collinearity (Quinn and Keough, 2002). Therefore here and below, the independent fixed variables in the final logistic models were Year and Grazing Treatment.

We calculated overall probability of nesting success for each species by exponentiating daily nest survival estimates by the mean number of days between first egg laid and fledgling (included egg laying, incubation, and nestling days). We used 23 d of nest exposure for Clay-colored Sparrows, 26 d for Savannah Sparrows, 25 d for Vesper Sparrows, and 26 d for ground nesters (averaged from the exposure days of all our ground nesting species; Ehrlich et al., 1988). We calculated predicted probabilities of nesting success and associated confidence intervals

Table 1
Number of nests found in twice-over and season-long grazed pastures in southwestern Manitoba, 2011 to 2012.

Grazing System	Clay-colored Sparrow	Total Ground nesters	Savannah Sparrow	Vesper Sparrow	Western Meadowlark	LeConte's Sparrow	Bobolink	Unknown Sparrow
Twice-over	30 (1.1)	65 (2.3)	24 (0.9)	16 (0.6)	18 (0.6)	3	0	4
Season-long	11 (0.6)	45 (2.3)	17 (0.9)	16 (0.8)	7 (0.4)	4	1	0
Total	41	110	41	32	25	7	1	4

Total nests $n = 151$. Average nests found per 9 ha nest drag in parenthesis.

using the "estimate" command in NLMIXED and the additive model linking grazing treatment and year with nesting success. We used a chi-square test to determine whether the number of nests found per unit search effort varied with grazing treatment.

To analyze effects of vegetation on nesting success, we first determined whether similar vegetation variables were correlated to reduce the number of variables, and to avoid collinearity. There was significant correlation between vegetation height and percentage of live grass cover both at the nest ($P < 0.0001$, $r = 0.366$) and at random points ($P < 0.0001$, $r = 0.408$). We chose to use percentage live grass cover because its measurement was more consistent among years and observers. Litter depth and percentage dead grass cover was also significantly correlated at the nest ($P < 0.0001$, $r = 0.421$), and random points ($P < 0.0001$, $r = 0.567$). We chose litter depth as the variable to include in subsequent models because it is a consistent vegetation predictor often used in the analysis of habitat use by grassland birds (Fisher and Davis, 2010). We then used logistic exposure modeling to examine how litter depth, live grass cover, and bare ground cover affected nesting success at the nest and within the available landscape (i.e., at random points) on twice-over and season-long pastures.

We evaluated effects of grazing system on three vegetation structure variables: litter depth, percentage live grass cover, and percentage bare ground cover. Diagnostic graphs and the deviance:df ratio suggested that residuals best fit a negative binomial distribution. We used generalized linear mixed models (PROC GLIMMIX; SAS Institute) with a negative binomial distribution, maximum likelihood estimation, and site as a random variable to determine the effects of grazing treatment on the three vegetation variables. Initially, the model included the independent variables year, grazing treatment, and their interaction. The interaction was not significant ($P > 0.7905$, $t = -0.75$), so we removed this variable from all models to reduce collinearity.

We also assessed whether grazing scheme influenced probability of brood parasitism by Brown-headed Cowbirds. We used a chi-square test with parasitism events as the response variable and grazing regime as the independent variable. We were unable to analyze parasitism rates for each species separately because there were an insufficient number of events (< 5) for individual species to meet the chi-square test requirements (Van Emden, 2008).

For all analyses we used an alpha value of 0.1 to reduce the chance of making a Type II error, a potentially significant problem in conservation biology (Taylor and Gerrodette, 1993).

Results

Nest Monitoring

In 2011 and 2012, 175 nests were located and monitored; 151 of the monitored nests were included in the analysis on effects of grazing treatment (Table 1). Twenty-four nests were removed from the nesting success analyses because the pastures were not grazed according to the twice-over guidelines due to flooding in 2011. Grazing treatment analyses included 60 nests from 2011 and 91 nests from 2012. There were 28 nest searches on twice-over pastures, and 20 nest searches on season-long pastures. Clay-colored Sparrow and Savannah Sparrow nests were the most frequently located (Table 1); Vesper Sparrow, Western Meadowlark, Le Conte's Sparrow, and Bobolink made up the remainder of nests found and monitored (Table 1). Overall, grazing regime did not have a significant effect on the number of nests per unit search effort (X^2 test, $P = 0.367$).

Of 151 nests included in the grazing analysis, 37% successfully fledged at least one young (apparent nesting success; Table 2). Clay-colored Sparrows had the highest apparent nesting success at 59%, whereas Western Meadowlarks were lowest with 28% success. Nest predation was the leading cause of failure; 80% of failed nest attempts were depredated. The other causes of nest failure were trampling by livestock (8%), abandonment (6%), Brown-headed Cowbird parasitism (2%; where parasitism caused failure, e.g., host eggs pecked, nest abandoned after cowbird egg laid, only cowbird chick survived, etc.), and other causes (3%).

Flood conditions negatively affected nesting success. Eight of the total 10 nests trampled and 8 of the 10 nests abandoned occurred in 2011; Table 2). Brown-headed Cowbird parasitism was also higher in 2011; 25% of nests monitored from 2011 were parasitized by cowbirds, compared with 13% in 2012 (X^2 test, $P = 0.0693$; Table S1).

Nesting Success

Success of ground nests was significantly influenced by grazing regime ($P = 0.0186$, $t = -2.36$) and year ($P = 0.0091$, $t = 2.62$; Fig. 1).

Table 2
Fates of songbird nests in southwestern Manitoba in 2011 and 2012.

	Ground nesters[1] $n = 110$		Clay-colored Sparrow $n = 41$		Total $n = 151$		Savannah Sparrow $n = 41$		Vesper Sparrow $n = 32$		Western Meadowlark $n = 25$	
	2011	2012	2011	2012	2011	2012	2011	2012	2011	2012	2011	2012
Success	10	22	8	16	18 (7)	38	5	9	1	9	4	3
Failure	38	40	4	13	42 (17)	53	15	12	9	13	7	11
Depredated	28	35	3	10	31 (8)	45	10	10	7	11	5	11
Abandoned	3	2	1	0	4 (4)	2	0	1	2	0	0	0
Livestock	6	1	0	1	6 (2)	2	4	0	0	1	2	0
Parasitized	0	0	0	2	0 (1)	2	0	0	0	0	0	0
Other[2]	1	2	0	0	1 (2)	2	1	1	0	1	0	0

Sample sizes represent the number of nests with known fates. Parentheses include the 24 nests not included in the statistical analysis due to flooding in 2011.
[1] Ground nesters: Savannah Sparrow, Vesper Sparrow, Western Meadowlark, Le Conte's Sparrow, Bobolink, unidentified sparrow.
[2] Two nests were destroyed unintentionally by humans (landowner vehicle, field assistant), one unknown, two flooded.

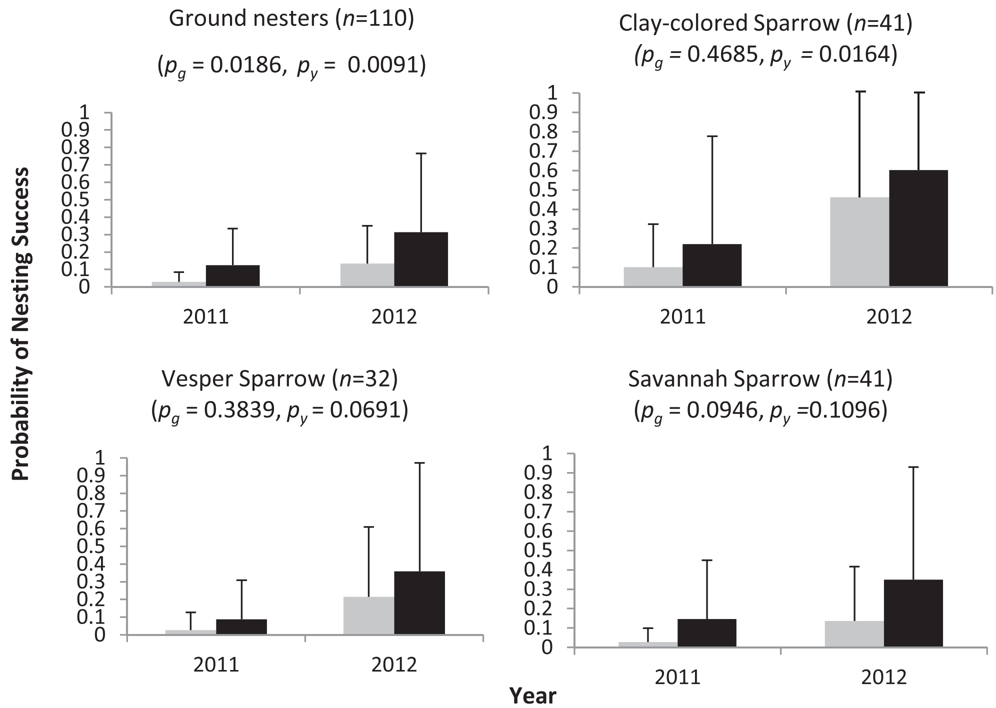

Figure 1. Probability and 90% upper confidence intervals of nesting success of grassland songbirds on twice-over rotationally grazed pastures (gray) versus season-long grazed pastures (black) in southwestern Manitoba, 2011 to 2012. Pg and Py indicate effect of grazing treatment and year, respectively. Probability of nest success calculated by exponentiating daily nest survival estimates over nest period.

Nesting success probability was lower in twice-over rotationally grazed pastures in both 2011 and 2012. The probability of a nest succeeding on twice-over grazed pastures was 4 times lower in 2011 (daily survival rate of 2.8% vs. 12.4%), and 2.4 times lower in 2012 (13.5% vs. 31.4%), compared with nests in season-long grazed pastures. However, there was no significant interaction between year and grazing regime ($P >$ 0.3263, $t = -0.84$).

All species showed a trend for lower nesting success in the twice-over grazing treatment, although not all trends were significant (Fig. 1). Nesting success of Savannah Sparrows was negatively affected by the twice-over grazing scheme ($P = 0.0946$, $t = -1.68$). Clay-colored Sparrow and Vesper Sparrow nesting success were significantly affected by year ($P = 0.0164$, $t = 2.43$; $P = 0.0691$, $t = 1.84$; Fig. 1) but not by grazing scheme.

Nesting success was significantly higher in the nonflood year, 2012, than during the flood (Fig. 1) for all ground nesters collectively ($P =$ 0.0091, $t = 2.62$), and for Clay-colored Sparrows ($P = 0.0164$, $t =$ 2.43). Nesting success was greater in 2012 on both twice-over and season-long pastures. Two nests were abandoned due to flood water in 2011.

Brown-headed Cowbird parasitism

Brown-headed Cowbirds were present throughout the study sites, on both season-long and twice-over grazed pastures (Table S1). Clay-colored Sparrow nests were the most likely to be parasitized (25%; Table S1). However, there was no significant association between cowbird parasitism and grazing system ($P = 0.1150$, $t = 2.48$) or between cowbird parasitism and nesting success (X^2 test, $P = 0.3046$).

Vegetation Results

Nesting success of ground-nesting birds decreased as litter depth at nests increased ($\beta = -0.104$, SE $= 0.124$, $P = 0.059$); there were no other significant impacts of vegetation structure on nesting success (P > 0.148; Table S2). Grazing treatment did not have a significant effect on any of the vegetation variables analyzed ($P > 0.180$; Table S3). Percentage of live grass cover was higher in 2011 ($\beta = 0.396$, SE $=$ 0.0583, $P < 0.0001$), probably because of increased moisture during the flooding of 2011 (Table S3).

Discussion

Our study suggests that nesting success of ground-nesting songbirds is strongly negatively affected by twice-over grazing in southwestern Manitoba. There are several reasons why depredation, abandonment, and trampling may be affected by twice-over grazing. Twice-over paddocks may attract some species to nest due to limited disturbance and dense vegetation found there early in the nesting season; however, during the rotational system's grazing period, the probability of trampling and abandonment due to disturbance increases due to the high density of cattle in relatively small paddocks (Bleho et al., 2014), and removal of vegetation cover through livestock grazing may increase visibility of nests and thus probability of depredation by visual predators (Dion et al., 2000; Temple et al., 1999). Although trampling typically has a minimal impact on nesting success in the northern mixed-grass prairies (Bleho et al., 2014; Koper and Schmiegelow, 2007), higher cattle densities associated with short, intense grazing periods increase trampling risk (Bleho et al., 2014; Johnson et al., 2012). This may partially explain why trampling rates in this study (8%) were higher than rates found in several other grazing studies with similarly moderate stocking rates (< 3.2%: Johnson et al., 2012; Kerns et al., 2010; Ludlow et al., 2014; Lusk and Koper, 2013). Trampling rates were also increased by the reduced availability of dry land during the flood year, which further concentrated both cattle and bird nests onto the driest patches of grassland. Although rest periods during the rotation are 30 to 60 d, these do not necessarily correspond with start and end dates of each ~26-d songbird nest duration, and thus most nests within twice-over pasture systems will be exposed to disturbance by cattle at some point, perhaps explaining why these rest periods do not result in increased nesting success. As our sample sizes were small, we could not survey all sites in both years, and moisture levels varied greatly between years, further research is recommended.

However, nesting success of the shrub-nesting species, Clay-colored Sparrow, was independent of grazing system. Clay-colored Sparrow nests were located almost exclusively in western snowberry in the study area (Knapton, 1979; Dechant et al., 2002), which is common on both season-long and twice-over pastures in Manitoba. Cattle do not graze on snowberry and generally avoid thick shrub patches; therefore, Clay-colored Sparrow nests are rarely trampled and vegetative nest cover for this species is rarely reduced by cattle (Bleho et al., 2014). That ground nest success was reduced in twice-over pastures, while shrub nests protected from cattle disturbance were not, provides further evidence that decreased nesting success in twice-over pastures is probably caused by the effects of cattle activity on graminoid and forb vegetation and local disturbance by cattle, and not due solely to cattle presence within the pasture.

In mixed-grass prairies, Savannah Sparrows are associated with tall grass cover, high vegetation density, and deep litter (Swanson, 2002), and they may be attracted to the taller vegetation that is found on temporarily rested paddocks. For example, Ranellucci et al. (2012) found that Savannah Sparrows had higher densities in twice-over pastures in this region in some years. The negative impact of twice-over grazing on nesting success of this species suggests that twice-over pastures might function as ecological traps (Gates and Gysel, 1978) or attractive sinks (Delibes et al., 2001), wherein Savannah Sparrows are attracted to rested pastures only to suffer lower nesting success when cattle return. Similarly, Temple et al. (1999) found that nesting success of Savannah Sparrows was lower in rotationally grazed pastures.

We found little effect of vegetation structure on nesting success, with the exception of the negative effect of litter depth. Small mammalian predators use litter cover for protection against aerial predators, and may, therefore, opportunistically encounter and consume more ground nests of those bird species that thoroughly conceal their nests (Dion et al., 2000). Thus, increased litter depth may decrease nesting success by facilitating movement of small mammalian predators.

Several parameters varied between years, probably at least in part due to the record flood events in 2011. Although only two nests were destroyed directly by flooding, we observed numerous indirect impacts. Nesting success was lower during the flood, while trampling, abandonment, and cowbird parasitism rates were higher. Flooding fragmented the landscape and reduced available land for both nesting and foraging cattle, which may have concentrated the locations of both taxa, and thus increased direct interactions between livestock and songbird nests (Nack and Ribic, 2005). Similarly, it seems likely that flooding concentrated search areas for both brood parasites and nest predators, also contributing to decreased nesting success. Higher abandonment rates may have resulted from both prolonged heavy rain events, and increased cattle disturbance around nests. However, flooding did not alter our conclusions about the impacts of twice-over grazing on songbirds; nesting success was 2.4 times lower in average conditions and 4 times lower in the flood year in this grazing system.

Our study adds to the growing body of literature that demonstrates few benefits of rotational grazing on vegetation productivity (Briske et al., 2011) or wildlife conservation (e.g., Temple et al., 1999; Ranellucci et al., 2012). The twice-over grazing method does not provide an exception to this rule; indeed, we documented dramatically lower nesting success in twice-over compared with season-long pastures. It seems likely that maximum cattle density, rather than seasonal cattle stocking rates, mediates the potential impact of cattle grazing on nesting success, and higher cattle densities increase risks to nesting songbirds (see also Bleho et al., 2014). Regardless, we suggest that twice-over grazing should not be promoted as a management method for conservation of grassland songbirds.

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References

Askins, R.A., Chavez-Ramirez, F., Dale, B.C., Haas, C.A., Herkert, J.R., Knopf, F.L., Vickery, P. D., 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. Report of the AOU Committee on Conservation. Ornithological Monographs No. 64.

Askins, R.A., 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. Current Ornithology. Springer, Boston, MA, USA, pp. 1–34.

Barker, W.T., Sedivec, K.K., Messmer, T.A., Higgins, K.F., Hertel, D.R., 1990. Effects of specialized grazing systems on waterfowl production in southcentral North Dakota. Transactions of the North American Wildlife and Natural Resources Conference 55, pp. 462–474.

Bleho, B.I., Koper, N., Machtans, C.S., 2014. Direct effects of cattle on grassland birds in Canada. Conservation Biology 28, 724–734.

Brennan, L., Kuvlesky, W., 2005. Grassland birds: an unfolding North American conservation crisis. Journal of Wildlife Management 69, 1–13.

Briske, D.D., Derner, J.D., Brown, J.R., Fuhlendorf, S.D., Teague, W.R., Havstad, K.M., Gillen, R. L., Ash, A.J., Williams, W.D., 2008. Rotational grazing on rangelands: reconciliation of perception and experimental evidence. Rangeland Ecology & Management 61, 3–17.

Briske, D.D., Sayre, N.F., Huntsinger, L., Fernandez-Gimenez, M., Budd, B., Derner, J.D., 2011. Origin, persistence, and resolution of the rotational grazing debate: integrating human dimensions into rangeland research. Rangeland Ecology & Management 64, 325–334.

Brown, J., Kothmann, M., 2009. Rotational grazing on rangelands: synthesis and recommendations. Society for Range Management 31, 37–38.

Christie, K.R., 1997. Assessment of managed grazing systems for productivity and abundance in non-game birds. MNRM Thesis. Natural Resources Institute, University of Manitoba, Winnipeg, Manitoba, Canada.

Davis, S., 2003. Nesting ecology of mixed-grass prairie songbirds in southern Saskatchewan. Wilson Bulletin 115, 119–130.

Dechant, J.A., Sondreal, M.L., Johnson, D.H., Igl, L.D., Goldade, C.M., Nenneman, M.P., Euliss, B.R., 2002. Effects of management practices on grassland birds: Clay-colored Sparrow. Northern Prairie Wildlife Research Center, Jamestown, ND, USA 22 p.

Delibes, M., Gaona, P., Ferreras, P., 2001. Effects of an attractive sink leading into maladaptive habitat selection. The American Naturalist 158, 277–285.

Derner, J.D., Lauenroth, W.K., Stapp, P., Augustine, D.J., 2009. Livestock as ecosystem engineers for grassland bird habitat in the western great plains of North America. Rangeland Ecology & Management 62, 111–118.

Dinsmore, S.J., White, G.C., Knopf, F.L., 2002. Advanced techniques for modeling avian nest survival. Ecology 83, 3476–3488.

Dion, N., Hobson, K.A., Lariviere, S., 2000. Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. The Condor 102, 629–634.

Ehrlich, P.R., Dobkin, D.S., Wheye, D., 1988. The birder's handbook: a field guide to the natural history of North American birds. Simon and Schuster Inc, New York, NY, USA.

Fisher, R.J., Davis, S.K., 2010. From Wiens to Robel: a review of grassland-bird habitat selection. Journal of Wildlife Management 72, 265–273.

Fuhlendorf, S.D., Engle, D.M., 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience 51, 625–632.

Fuhlendorf, S.D., Harrel, W.D., Engle, S.M., Hamilton, R.G., Davis, C.A., Leslie Jr., D.M., 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16, 1706–1716.

Gates, J.E., Gysel, L.W., 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59, 871–883.

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: global disparities of habitat loss. Ecology Letters 8, 23–29.

Holechek, J.L., Pieper, R.D., Herbel, C.H., 1998. Range Management: Principles and Practices. Prentice-Hall, Upper Saddle River, NJ, p. 542.

Hovick, T.J., Elmore, R.D., Fuhlendorf, S.D., 2014. Structural heterogeneity increases diversity of non-breeding grassland birds. Ecosphere 5, 1–13.

Hovick, T.J., Elmore, R.D., Fuhlendorf, S.D., Engle, D.M., Hamilton, R.G., 2015. Spatial heterogeneity increases diversity and stability in grassland bird communities. Ecological Applications 25, 662–672.

Krausman, P.R., Naugle, D.E., Frisina, M.R., Northrup, N., Bleich, V.C., Block, W.M., Wallace, M.C., Wright, J.D., 2009. Livestock Grazing, Wildlife Habitat, and Rangeland Values. Rangelands 3, 15–19.

Johnson, D.H., Igl, L.D., 2001. Area requirements of grassland birds: a regional perspective. The Auk 118, 24–34.

Johnson, T.N., Kennedy, P.L., Etterson, M.A., 2012. Nest success and cause-specific nest failure of grassland passerines breeding in prairie grazed by livestock. Journal of Wildlife Management 76, 1607–1616.

Jones, S.L., 2011. Territory size in mixed-grass prairie songbirds. Canadian Field-Naturalist 125, 12–15.
Jongsomjit, D., Jones, S.L., Gardali, T., Geupel, G.R., Gouse, P.J., 2007. A guide to nestling development and aging in altricial passerines. Biological Technical Publication of the U. S. Fish & Wildlife Service BTP-R6008-2007.
Kerns, C.K., Ryan, M.R., Murphy, R.K., Thompson III, F.R., Rubin, C.S., 2010. Factors affecting songbird nest survival in northern mixed-grass prairie. Journal of Wildlife Management 4, 257–264.
Knapton, R.W., 1979. Optimal size territory in the Clay-colored Sparrow, *Spizella pallida*. Canadian Journal of Zoology 57, 1358–1370.
Knopf, F.L., 1996. Prairie legacies—birds. In: Samson, F.B., Knopf, F.L. (Eds.), Prairie conservation: preserving North America's most endangered ecosystem. Island Press, Washington, DC, USA, pp. 135–148.
Koper, N., Schmiegelow, F.K.A., 2007. Does habitat management for duck productivity affect songbird nesting success? Journal of Wildlife Management 71, 2249–2257.
Ludlow, S.M., Brigham, R.M., Davis, S.K., 2014. Nesting ecology of grassland songbirds: effects of predation, parasitism, and weather. The Wilson Journal of Ornithology 126, 686–699.
Lusk, J., Koper, N., 2013. Grazing and songbird nest survival in southwestern Saskatchewan. Rangeland Ecology & Management 66, 401–409.
Manitoba Habitat Heritage Corporation [MHHC], 2010. Annual report 2009/2010. The Manitoba Habitat Heritage Corporation, Winnipeg, Manitoba, Canada.
Mundry, R., 2011. Issues in information theory-based statistical inference-a commentary from a frequentists perspective. Behavioral Ecology and Sociobiology 65, 57–68.
Nack, J.L., Ribic, C.A., 2005. Apparent predation by cattle at grassland bird nests. Wilson Bulletin 117, 56–62.
Perlut, N.G., Strong, A.M., 2011. Grassland birds and rotational-grazing in the northeast: breeding ecology, survival and management opportunities. Journal of Wildlife Management 75, 715–720.
Quinn, G.P., Keough, M.J., 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK 537 p.
Ranellucci, C.L., Koper, N., Henderson, D.C., 2012. Twice-over rotational grazing and its impacts on grassland songbird abundance and habitat structure. Rangeland Ecology & Management 65, 109–118.
Samson, F.B., Knopf, F.L., 1994. Prairie conservation in North America. BioScience 44, 418–421.
Samson, F.B., Knopf, F.L., Ostlie, W.R., 2004. Great plains ecosystems: past, present, and future. Wildlife Society Bulletin 32, 6–15.
Shaffer, T., 2004. A unified approach to analyzing nest success. Auk 121, 526–540.
Small, J.A., McCaughey, W.P., 1999. Beef cattle management in Manitoba. Canadian Journal of Animal Science 79, 539–544.
Sutter, G.C., 1997. Nest-site selection and nest-entrance orientation in Sprague's Pipit. Wilson Bulletin 109, 462–469.
Swanson, D.A., 2002. Effects of management practices on grassland birds: Savannah Sparrow. Northern Prairie Wildlife Research Center, Jamestown, ND, USA 30 p.
Taylor, B.L., Gerrodette, T., 1993. The uses of statistical power in conservation biology: the Vaquita and northern spotted owl. Society for Conservation Biology 3, 489–500.
Teague, W.R., Provenza, F., Kreuter, U., Steffens, T., Barnes, M., 2013. Multi-paddock grazing on rangelands: why the perceptual dichotomy between research results and rancher experience. Journal of Environmental Management 128, 699–717.
Temple, S.A., Fevold, B.M., Paine, L.K., Undersander, D.J., Sample, D.W., 1999. Nesting birds and grazing cattle: accommodating both on Midwestern pastures. Studies in Avian Biology 19, 196–202.
Thorpe, J., 2011. Vulnerability of grasslands in Southern Manitoba to climate change. Saskatchewan Research Council. SRC Publication No. 12855-1E11. Saskatoon, SK.
Van Emden, H.F., 2008. Statistics for terrified biologists. Blackwell Publishing, USA 360 p.
Wiens, J.A., 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs 8, 1–93.
Winter, M., Hawks, S.E., Shaffer, J.A., Johnson, D.H., 2003. Guidelines for finding nests of passerine birds in tallgrass prairie. USGS Northern Prairie Wildlife Research Center, p. 160.
With, K., King, A., Jensen, W., 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. Biological Conservation 141, 3152–3167.
WSCD, 2014. West Souris Conservation District. Available at:. http://wsrcd.com/news/, Accessed date: 15 May 2014.