



# Cattle Grazing Intensity and Duration Have Varied Effects on Songbird Nest Survival in Mixed-Grass Prairies<sup>☆</sup>



Emily N. Pipher<sup>a,1</sup>, Claire M. Curry<sup>b,\*</sup>, Nicola Koper<sup>c</sup>

<sup>a</sup> MNRM Graduate, Natural Resources Institute, University of Manitoba, Winnipeg, MB, Canada

<sup>b</sup> Postdoctoral Fellow, Natural Resources Institute, University of Manitoba, Winnipeg, MB, Canada

<sup>c</sup> Associate Professor, Natural Resources Institute, University of Manitoba, Winnipeg, MB, Canada

## ARTICLE INFO

### Article history:

Received 12 October 2015

Received in revised form 21 April 2016

Accepted 1 July 2016

### Key words:

chestnut-collared longspur

grasslands

Sprague's pipit

stocking rate

vesper sparrow

## ABSTRACT

Grassland bird species are declining more quickly than birds of any other biome in North America, but effects of the most widespread use of native mixed-grass prairies, livestock grazing, on nest survival of songbirds are not well understood. We used an adaptive management grazing experiment in southwestern Saskatchewan to evaluate effects of cattle grazing intensity and number of years grazed on nest survival of five songbird species in 2009 and 2010. Two 300-m<sup>2</sup> plots were located in each of 12 pastures. Three pastures were ungrazed controls, while the remaining pastures had grazing intensities ranging from 0.23 to 0.83 animal unit months (AUM) · ha<sup>-1</sup> (very low to very high for this region) and were grazed for 2–3 or > 15 yr. Analyses were conducted using logistic exposure regression. We found few effects of grazing on nest survival. Exceptions to this pattern were that the lowest nest survival rates occurred at low-moderate grazing intensities for Sprague's pipits (*Anthus spragueii*) in 2009, at low grazing intensities for chestnut-collared longspurs (*Calcarius ornatus*) in 2009, and at moderate grazing intensities for vesper sparrows (*Poocetes gramineus*) in 2010. Increasing grazing duration lowered nest survival for Sprague's pipits and increased nest survival for chestnut-collared longspurs in 2009. Although low or moderate grazing intensities are generally recommended to promote wildlife conservation, this may not promote productivity of all species. Nonetheless, our results suggest that in the short term, a wide range of grazing intensities is consistent with conservation of grassland songbirds.

© 2016 The Society for Range Management. Published by Elsevier Inc. All rights reserved.

## Introduction

The rapid and alarming decline of grassland bird species has been called a “conservation crisis” (Brennan and Kuvlesky, 2005). This decline has been driven in part by the loss and degradation of their breeding habitat (Knopf, 1992; Herkert, 1994). Grazing by livestock, particularly domestic cattle (*Bos primigenius*), is the most common anthropogenic use of native prairies in North America, affecting about 85% of mixed-grass prairies (Willms and Jefferson, 1993). North American flora and fauna evolved in the presence of grazing by native species such as bison (*Bison bison*; Knapp et al., 1999), but ecological effects of cattle grazing differ from historical effects of bison grazing. Cattle consume more forbs and leave less grass at the start of the

growing season, whereas bison consume more perennial grasses; the two grazers also use the landscape differently on the basis of topography and water sources (Peden et al., 1974; Plumb and Dodd, 1993; Steuter and Hiding, 1999). Thus, their ecological effects may also differ (Lueders et al., 2006). Although using native prairies as rangelands may be among the most sustainable of agricultural practices, as it allows commercial use of the landscape while preserving the floral and faunal species of the prairie ecosystem, cattle grazing may decrease nesting success (Hartway and Mills, 2012) and thus management must be refined to optimize the conservation of wildlife on modern rangelands.

Cattle can influence nest survival directly by trampling nests (Paine et al., 1996; Perlut and Strong, 2011). However, trampling rates in mixed-grass prairies are low, presumably as a result of comparatively low stocking rates (and thus low grazing intensities) in this arid ecoregion (Koper and Schmiegelow, 2007), and thus typically there are few direct impacts of cattle trampling on nests in Canadian prairies (Bleho et al., 2014). However, numerous indirect effects of grazing, such as altering vegetation, predator communities (Ribic et al., 2012), or food availability (Evans et al., 2005), may influence nest survival. Greater vegetation height and density, litter depth, and less bare ground may provide protection from both predators and heat stress (Sutter, 1997) and are consistent with preferences for nest sites (Dieni and Jones, 2003; Lusk et al., 2003; Davis, 2005; Fisher and Davis, 2011). Conversely,

<sup>☆</sup> Research was funded by the Canadian Foundation for Innovation, Natural Sciences and Engineering Research Council, Manitoba Graduate Scholarship, Grasslands National Park of Canada, and the World Wildlife Fund–USA. Funding sources had no involvement in study design, analysis, writing, or publication.

\* Correspondence: Claire M. Curry, Natural Resource Institute, University of Manitoba, 303-70 Dysart Rd, Winnipeg, Manitoba, R3T 2N2, Canada. Tel.: +1 204 293 5745.

E-mail address: [curryc@umanitoba.ca](mailto:curryc@umanitoba.ca) (C.M. Curry).

<sup>1</sup> Current address: Emily N. Pipher, 1709 Roberta Ave, Sebring, FL 33870, USA.

in some ecosystems tall and dense vegetation provides protection for small mammalian predators and thus indirectly results in lower nest survival (Weidinger, 2002). As a result, changes in predator communities can strongly affect patterns of nest survival (With, 1994; Dion et al., 2000; Benson et al., 2010), and because predator communities may differ between grazed and ungrazed areas (Ribic et al., 2012), grazing may influence nest survival.

Grazing intensity influences grassland vegetation by altering seral stage, species composition, invasion by exotic species, and productivity (Ellison, 1960; Willms et al., 1985, 2002; Finnoff et al., 2008). Vegetation structure, which also varies with grazing intensity (Fondell and Ball, 2004; Sliwinski, 2011), strongly influences grassland bird habitat use (Fisher and Davis, 2010). Chestnut-collared longspurs (*Calcarius ornatus*), for example, tend to utilize moderately (Milchunas et al., 1998) or heavily grazed (Bleho, 2009; Sliwinski, 2011) pastures, whereas Sprague's pipits (*Anthus spragueii*) are found more frequently in pastures with low to moderate grazing intensity (Saab et al., 1995).

Traditionally, the goal of rangeland management has been to maximize long-term cattle production through moderate grazing intensity, which tends to homogenize the prairie landscape (Augustine and McNaughton, 1998; Fuhlendorf and Engle, 2001). Homogenous management regimes only benefit a narrow range of species (Morrow et al., 1996; Chapman et al., 2004), and thus heterogeneous grazing regimes at the regional scale have sometimes been recommended for wildlife conservation (Fuhlendorf and Engle, 2001; Toombs et al., 2010). Maintaining a gradient of grazing regimes may maximize the availability of suitable nest sites for diverse species (Madden et al., 2000; Derner et al., 2009), but more research in northern mixed-grass prairies is needed. Surprisingly, given the extent of livestock grazing across North American prairies, little empirical information exists regarding the effects of cattle grazing on songbird nesting success in mixed-grass prairies.

Two studies that evaluated effects of grazing on nest survival of songbirds in native mixed-grass prairies in Alberta (Koper and Schmiegelow, 2007) and Saskatchewan (Lusk and Koper, 2013) found little effect of cattle grazing on nest survival of songbirds, whereas a third study in North Dakota (Kerns et al., 2010) found both positive and negative effects of cattle grazing. As birds are highly selective of the vegetation structure at nest sites (e.g. Sutter, 1997; Davis, 2005; Fisher and Davis, 2011) and vegetation structure affects nest survival (Sugden and Beyersbergen, 1986; DeLong et al., 1995), it would be surprising if nest survival was independent of livestock grazing. Inconsistent effects of grazing among previous studies may be because grazing intensities are generally low to moderate in mixed-grass prairies, probably resulting in high within-pasture heterogeneity (Koper and Schmiegelow, 2007; Lusk and Koper, 2013); higher local grazing intensities might have a greater effect on nest survival (Bleho et al., 2014). In support of this hypothesis, negative effects of grazing on nest survival have been found in ecoregions where grazing intensities are generally higher than in mixed-grass prairies (Rahmig et al., 2008; Harrison et al., 2011; Bleho et al., 2014). Therefore, range managers who aim to contribute to wildlife conservation may be faced with a dilemma: Although having higher grazing intensities in some pastures might increase regional habitat diversity and provide more habitat for species that prefer shorter vegetation, including some species at risk, this more intensive use might also lead to lower nest survival and thus negative population trends for other sensitive species. Understanding the effects of cattle grazing intensities on nest survival for a diversity of grassland species, therefore, has important implications for how we manage mixed-grass prairies for both conservation and economic uses.

We evaluated effects of cattle grazing intensities and duration on nest survival of five grassland songbird species within a large-scale adaptive management grazing experiment (Koper et al., 2008) in southwestern Saskatchewan, Canada. We monitored nests to determine if nest survival of our focal species varied with grazing intensity and duration. We hypothesized that 1) if the predator community is

predominately visual predators, such as raptors, nest survival would decline as grazing intensity increased; 2) if the predator community is predominately small mammals, nest survival would increase as grazing intensity increased; and 3) if the diversity of the predator community was maximized at intermediate grazing intensities, then nest survival would be lowest at intermediate grazing intensities.

## Methods

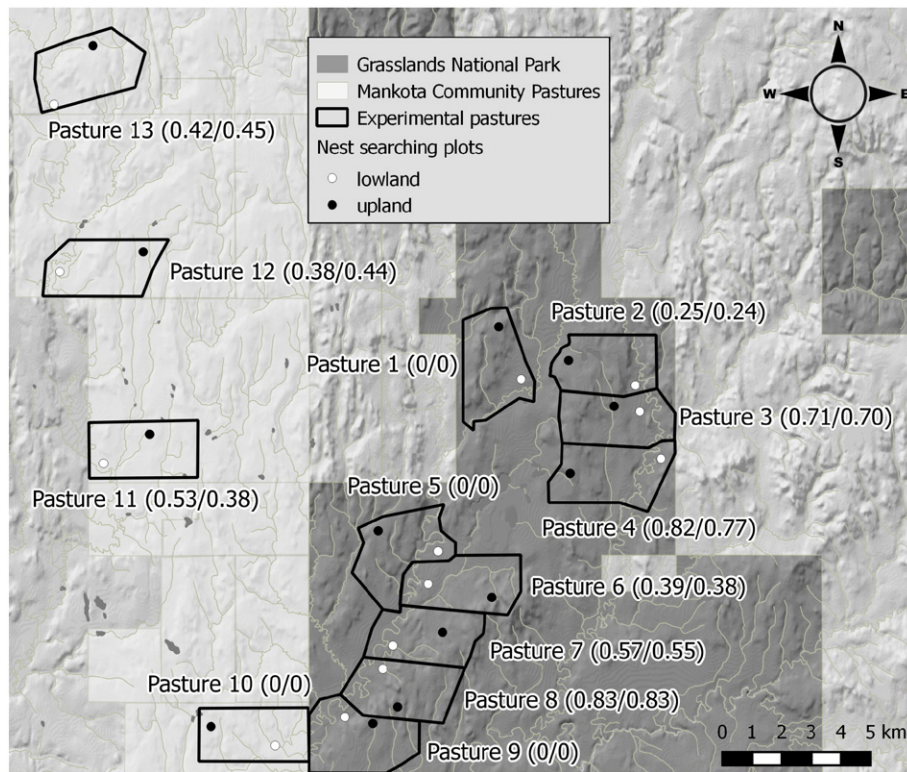
### Study Area

Our study was conducted in the East Block of Grasslands National Park of Canada (GNPC) in southern Saskatchewan, Canada (lat 49°01'00"N, long 106°49'00"W), and in the adjacent Mankota community pastures (Fig. 1). Between homesteading in the early 1900s and its establishment by Parks Canada in 1981, GNPC remained unfragmented by either cultivation or heavy grazing (Henderson, 2006). Upland areas were dominated by blue grama (*Bouteloua gracilis* Kunth), northern wheatgrass (*Elymus lanceolatus* [Scribn. & J.G. Sm.] Gould), needle-and-thread grass (*Hesperostipa comata* Trin. & Rupr.), and June grass (*Koeleria macrantha* Ledeb.). Clubmoss (*Selaginella densa* Rydb.) was widespread, with common forbs including prairie sage (*Artemisia ludoviciana* Nutt.) and scarlet globemallow (*Sphaeralcea coccinea* [Nutt.] Rydb.). Lowland areas were dominated by sagebrush (*Artemisia cana* Pursh), western snowberry (*Symphoricarpos occidentalis* Hook.), and graminoids such as wheatgrasses, saltgrasses (*Distichlis stricta* [Torr.] Rydb.), and bluegrasses (*Poa sandbergii* J. Presl.). Study plots were in an area of relatively low elevation (750–850 m above sea level), with a mean annual precipitation of approximately 350 mm: 2009 had below-average precipitation (Lwiwski et al., 2015). Potential nest predators at our sites included a range of small mammals, mesopredators, and avian predators, including Richardson's ground squirrel (*Urocyon richardsonii*), 13-lined ground squirrel (*Ictidomystris decemlineatus*), long-tailed weasel (*Mustela frenata*), plains garter snake (*Thamnophis radix*), western hognose snake (*Heterodon nasicus*), brown-headed cowbird (*Molothrus ater*; Pietz and Granfors, 2005), American badger (*Taxidea taxus*; With, 1994), coyote (*Canis latrans*; Pietz and Granfors, 2000), and mice and voles. Cattle may also deplete grassland songbird nests (Bernath-Plaisted, 2015).

### Experimental Design

Nest surveys conducted in 2006 and 2007 provided us with 2 yr of pregrazing data from the study area, which had remained free of livestock grazing since its purchase by Parks Canada in 1985 (Henderson, 2006). In 2008, cattle were reintroduced to the East Block of GNPC. Six experimental pastures ( $\approx 300$  ha each) were built, each including riparian, lowland, and upland areas characteristic of this diverse prairie landscape. Each pasture was assigned a different grazing intensity, which ranged from 0.23 AUM  $\cdot$  ha $^{-1}$  (very low) to 0.83 AUM  $\cdot$  ha $^{-1}$  (very high for this region; Table 1; see Fig. 1) dispersed across the experimental study area, following a Beyond-BACI experimental design (Underwood, 1994; Koper et al., 2008), which is a modified before-after, control-impact design that evaluates the effects of any existing environmental impacts before evaluating effects of the treatment manipulations. These pastures contained cattle between late May and mid-September annually, at the same grazing intensity for the duration of the experiment. Three additional 300-ha sites within GNPC were ungrazed by cattle (controls), though they, like the pastures with cattle, were lightly grazed by low densities of native grazers such as mule deer (*Odocoileus hemionus*) and pronghorn antelope (*Antilocapra americana*). Grazed pastures were fenced, whereas ungrazed pastures were unfenced.

Data were also collected between 2006 and 2010 from three sites within the adjacent Mankota pastures, in which moderate grazing (0.34–0.56 AUM  $\cdot$  ha $^{-1}$  for 2008–2010; average = 0.40 AUM  $\cdot$  ha $^{-1}$ , SD = 0.09



**Fig. 1.** Design of Grasslands National Park of Canada's East Block Grazing Experiment, southwestern Saskatchewan, Canada, 2009–2010. Units associated with each numbered pasture are in  $\text{AUM} \cdot \text{ha}^{-1}$  and presented as Pasture # (2009 grazing/2010 grazing). Contains information licensed under the Open Government License—Canada (<http://open.canada.ca/en/open-government-licence-canada>) (elevation, Grasslands National Park administrative boundaries, and water).

$\text{AUM} \cdot \text{ha}^{-1}$ ) typical of local grazing management had occurred for > 15 yr, to represent long-term grazed pastures typical of the region (see Table 1 and Fig. 1; pastures 11–13). Cattle were present in the Mankota pastures between late May and October (Henderson, 2006). Although these long-term grazed pastures were located to the west and northwest of the experimental sites (see Fig. 1), preliminary analyses on vegetation height and density suggested no evidence of any east-west environmental gradients (Koper, unpublished data).

#### Nest Surveys

We sampled two plots (each 9 ha, one in uplands and one in lowlands, to capture heterogeneity within each pasture) in 12 experimental pastures for a total of 24 nest plots. These plots were unfenced

subsamples within the larger pastures, and the same plots were surveyed in each year of the study. All were ungrazed in 2006–2007. Twelve plots were grazed for two (in 2009) and three (in 2010) yr, and six were ungrazed in 2009 and 2010. Six additional long-term grazed plots (> 15 yr) were located in the Mankota pastures. Plot locations were chosen randomly within upland and lowland but avoided water bodies, streams, and steep areas with vegetation transitioning from upland to lowland.

Each plot was searched for nests twice per year between 5 May and 31 July in 2006, 2007, 2009, and 2010. We monitored five species with the highest abundances of nests in our study area: Sprague's pipit, chestnut-collared longspur, vesper sparrow (*Poocetes gramineus*), Savannah sparrow (*Passerculus sandwichensis*), and Baird's sparrow (*Ammodramus bairdii*). We found nests using the rope-drag method (Davis, 2003). Nests found during other research activities were also monitored if they were in an experimental pasture. To avoid heat stress to nestlings during the hottest part of the day, rope-dragging took place between approximately 0730 and 1400 hours. Nests were marked with a flag to the west and a bamboo stake to the south, both set 10 m from the nest to reduce the risk of attracting predators or cattle to the nests (Picozzi, 1975).

We checked nests every 3–4 days (or every 2 days as fledging date approached) (Martin and Geupel, 1993). Nestling age was estimated using feather growth and coverage and extent of begging behavior (Bird Studies Canada, 2001). We determined outcome on the basis of age of nestlings upon last visit, presence (or absence) of eggshells and/or feathers in the nest, obvious disturbance of the nest, and adult activity at or near the nest. A nest was determined to be abandoned if several visits yielded no evidence of parental attentiveness, cold eggs, or no signs of hatching despite nest age. A nest was considered successful if it fledged at least one individual. Up to half of depredated nests show no physical signs of depredation, including those taken by large mammals (Pietz and Granfors, 2000). Therefore, nests where eggs or chicks had disappeared before it was possible for them to fledge were

**Table 1**

Average grazing intensities for study sites in Grasslands National Park of Canada, southwestern Saskatchewan, Canada, 2006–2007 and 2009–2010

| Pasture | Hectares | 2006–2007   |   | 2009–2010   |   |
|---------|----------|-------------|---|-------------|---|
|         |          | Average AUM | Average $\text{AUM} \cdot \text{ha}^{-1}$ | Average AUM | Average $\text{AUM} \cdot \text{ha}^{-1}$ |
| 1       | 301.6    | 0           | 0   | 0           | 0   |
| 2       | 281.6    | 0           | 0   | 69.5        | 0.25                                      |
| 3       | 288.4    | 0           | 0   | 202.4       | 0.7                                       |
| 4       | 313.6    | 0           | 0   | 249.9       | 0.8                                       |
| 5       | 295.2    | 0           | 0   | 0           | 0   |
| 6       | 296.1    | 0           | 0   | 112.9       | 0.38                                      |
| 7       | 280.4    | 0           | 0   | 158.1       | 0.56                                      |
| 8       | 289.6    | 0           | 0   | 241.3       | 0.83                                      |
| 9       | 320.9    | 0           | 0   | 0           | 0   |
| 10      | 2460     | 716.25      | 0.29                                      | 0           | 0   |
| 11      | 1942     | 917.57      | 0.47                                      | 846         | 0.44                                      |
| 12      | 1942     | 991.48      | 0.51                                      | 794.65      | 0.41                                      |
| 13      | 2072     | 1166.64     | 0.56                                      | 898.65      | 0.44                                      |

AUM indicates animal unit months.

assumed to have been depredated (Ricklefs, 1969). We could also not determine whether nest losses were the result of depredations of parents, but because no apparent abandonments occurred after the laying stage, it was unlikely to be a frequent cause of failure. We did not include the type of failure in the logistic exposure analyses. All failures, regardless of cause, were included.

### Data Analyses

For all analyses, we used  $\alpha = 0.10$  to determine statistical significance, as the risk of Type II error is of particular concern in conservation biology (Taylor and Gerrodette, 1994). We used logistic exposure (Shaffer, 2004; Rotella et al., 2007) in PROC NLMIXED (SAS Institute, Inc., 2008) to analyze nest survival. We made use of pre-livestock-introduction data to determine if pre-existing environmental conditions at sites resulted in spurious relationships between grazing intensity and nest survival. To do this, we developed models with nest survival data collected at our GNPC study sites in 2006 and 2007, before the introduction of cattle, with average future grazing intensities in a given pasture as the independent variable. A significant effect of future grazing intensity would suggest that inherent site characteristics, not the actual grazing intensity (which had not yet occurred in 2006–2007), were driving nesting success. If we did not find an effect of future grazing intensity, it would suggest that any trends we find relating grazing intensity and nest survival were not due to pre-existing environmental conditions. We first tested for nonlinear effects of average future grazing intensity (A) using a second-order polynomial term (Nest survival =  $A + A^2$ ). If the quadratic term was not significant, then we used the main effects model (Nest survival = A) to increase parsimony and decrease likelihood of problems with collinearity (similarly, we dropped insignificant interaction terms; Quinn and Keough, 2002). A few models (SPPI in 2006 and 2007, CCLO in 2007, and BAIS in 2007) would not converge in PROC NLMIXED, so in those few cases we used PROC GENMOD (Shaffer, 2004).

To determine effects of grazing intensity and grazing duration on nest survival, using data after livestock had been present for 2 (2009), 3 (2010), and > 15 (Mankota pastures) yrs, we evaluated nest survival of the five study species: Sprague's pipits, chestnut-collared longspurs, vesper sparrows, Savannah sparrows, and Baird's sparrows. We used a frequentist approach (Mundry, 2011) to nest survival analysis, with grazing intensity (i.e., stocking rate in  $\text{AUM} \cdot \text{ha}^{-1}$ , I) and years grazed (i.e., grazing duration in years, D) as predictor variables. We first tested for nonlinear effects of grazing intensity using a second-order polynomial term (Nest survival =  $D + I + I^2$ ). If the quadratic term was not significant, then we tested for interactions between grazing intensity and years grazed (Nest survival =  $D + I + D \cdot I$ ). If the interaction was not significant, we used the main effects model (Nest survival =  $D + I$ ). If the quadratic term was significant, we tested for the interaction between the quadratic grazing intensity term and years grazed (dropping this quadratic interaction if not significant) (Nest survival =  $D + I + I^2 + D \cdot I^2$ ). Parameters for all models are given as  $\beta \pm$  Standard Error (SE).

To estimate cumulative nest survival (over the duration of the nesting period) for models with significant coefficients, we used an estimate of the nesting period length (incubation and nestling periods combined) for each species: 28 days for Sprague's pipit, 26 days for vesper sparrow, and 25 days for chestnut-collared longspur (Baichich and Harrison, 1997).

## Results

### Pregrazing Nest Survival

In 2006 and 2007, when no grazing occurred in GNPC, we found 232 nests (Sprague's pipit:  $n_{2006} = 19$ ,  $n_{2007} = 15$ ; chestnut-collared longspur:  $n_{2006} = 49$ ,  $n_{2007} = 44$ ; vesper sparrow:  $n_{2006} = 17$ ,  $n_{2007} = 27$ ; Savannah sparrow:  $n_{2006} = 14$ ,  $n_{2007} = 4$ ; Baird's sparrow:  $n_{2006} =$

$21$ ,  $n_{2007} = 22$ ). We found no relationship between average future grazing intensity and nest survival of chestnut-collared longspurs or vesper sparrows in either 2006 or 2007, or of Savannah sparrows in 2006 (too few observations in 2007,  $n = 8$ ), as we would expect in the absence of spurious trends. Baird's sparrow nest survival was nonlinearly related to future grazing intensity in both 2006 ( $\beta_{\text{averagestockingrate}} = 8.84 \pm 4.57$ ,  $p = 0.056$ ;  $\beta_{\text{averagestockingrate} \cdot \text{averagestockingrate}} = -12.46 \pm 5.89$ ,  $p = 0.037$ ) and 2007 ( $\beta_{\text{averagestockingrate}} = 3.82 \pm 2.71$ ,  $p = 0.158$ ;  $\beta_{\text{averagestockingrate} \cdot \text{averagestockingrate}} = -6.13 \pm 3.15$ ,  $p = 0.052$ ) despite showing no response to grazing intensity in 2010 (insufficient data in 2009), indicating pre-existing environmental trends at these sites for Baird's sparrow. Postgrazing data (next section) suggested that Baird's sparrows respond to neither years grazed nor grazing intensity where we had sufficient data, so it seems unlikely that patterns we detected were caused by pre-existing trends. Sprague's pipit nest survival was not related to future grazing intensity in 2006. In 2007 we had very few failures relative to the number of observations (4/77); as this skewed sampling can cause biased estimates (Peduzzi et al., 1996), we did not analyze those data. Overall, these data suggest that the majority of our results were not driven by pre-existing environmental conditions relevant to each species in experimental pastures.

### Postgrazing Nest Survival

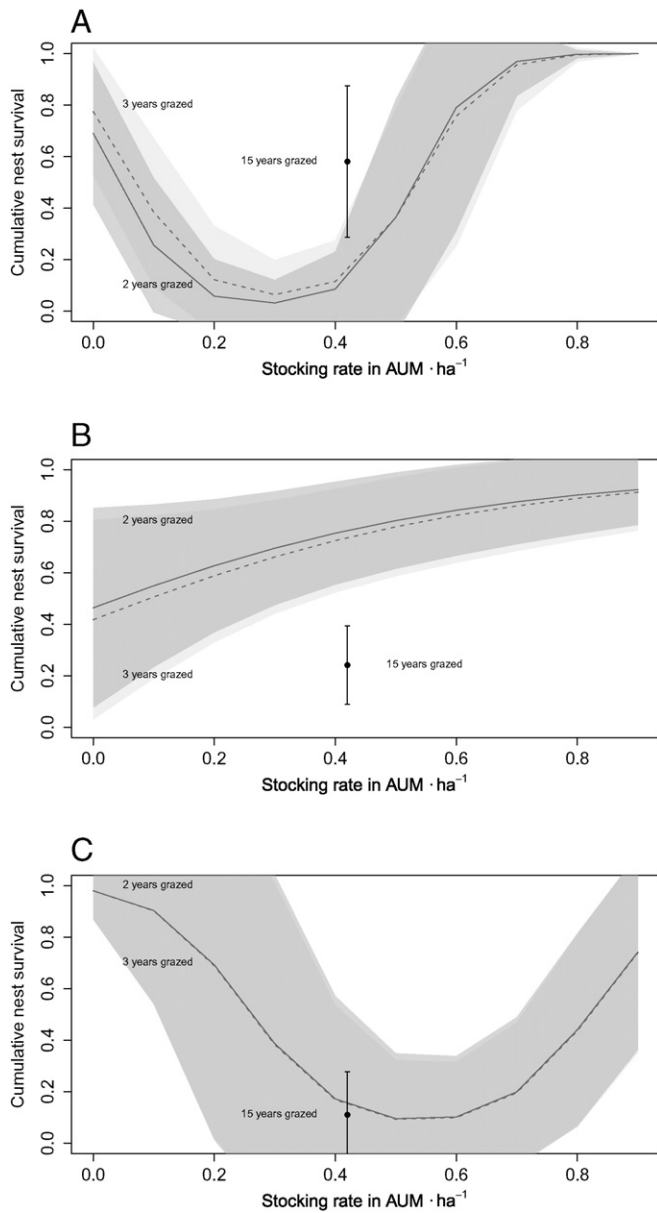
In 2009 and 2010, after grazing had been initiated at GNPC, we found 267 nests (Sprague's pipit:  $n_{2009} = 28$ ,  $n_{2010} = 31$ ; chestnut-collared longspur:  $n_{2009} = 47$ ,  $n_{2010} = 66$ ; vesper sparrow:  $n_{2009} = 13$ ,  $n_{2010} = 23$ ; Savannah sparrow:  $n_{2009} = 11$ ,  $n_{2010} = 21$ ; Baird's sparrow:  $n_{2009} = 4$ ,  $n_{2010} = 24$ ). Among the monitored nests, apparent nest survival was 49%, whereas 44% were apparently depredated. Predation was the leading cause of nest failure. Baird's sparrows had the highest apparent nest survival and lowest depredation rates (75% and 19%, respectively). Chestnut-collared longspurs had the lowest apparent nest survival and highest depredation rates (41% and 50%, respectively).

We detected some effects of grazing on nest survival, though not for every species and not in both years. Logistic exposure models indicated a nonlinear effect of grazing intensity and years grazed on nest survival of Sprague's pipits in 2009 (Fig. 2A;  $\beta_{\text{yearsgrazed}} = 0.38 \pm 0.17$ ,  $p_{\text{yearsgrazed}} = 0.03$ ;  $\beta_{\text{aum}} = -16.00 \pm 6.91$ ,  $p_{\text{aum}} = 0.02$ ;  $\beta_{\text{aum} \cdot \text{aum}} = 30.97 \pm 15.27$ ,  $p_{\text{aum} \cdot \text{aum}} = 0.04$ ;  $\beta_{\text{yearsgrazed} \cdot \text{aum} \cdot \text{aum}} = -1.52 \pm 0.84$ ,  $p_{\text{yearsgrazed} \cdot \text{aum} \cdot \text{aum}} = 0.07$ ). Years grazed and grazing intensity interacted such that nests in pastures grazed for several years had lowest survival rates at low to intermediate grazing intensities ( $0.2 - 0.4 \text{ AUM} \cdot \text{ha}^{-1}$ ). Nests in pastures grazed long term (> 15 yr) had a lower survival rate than those at similar grazing intensities. We found no effect of grazing intensity on nesting success of pipits in 2010.

Nest survival of chestnut-collared longspurs in 2009 was highest in pastures with high grazing intensities and with fewer years grazed (Fig. 2B;  $\beta_{\text{yearsgrazed}} = -0.13 \pm 0.05$ ,  $p_{\text{yearsgrazed}} = 0.01$ ;  $\beta_{\text{aum}} = 2.52 \pm 1.54$ ,  $p_{\text{aum}} = 0.10$ ). We found no effect of nesting success on chestnut-collared longspurs in 2010. There was a nonlinear effect of grazing intensity on vesper sparrows in 2010 (but not in 2009), with highest nesting success at low or high grazing intensities regardless of years grazed (Fig. 2C;  $\beta_{\text{yearsgrazed}} = -0.01 \pm 0.07$ ,  $p_{\text{yearsgrazed}} = 0.87$ ;  $\beta_{\text{aum}} = -17.88 \pm 11.66$ ,  $p_{\text{aum}} = 0.13$ ;  $\beta_{\text{aum} \cdot \text{aum}} = 16.53 \pm 9.88$ ,  $p_{\text{aum} \cdot \text{aum}} = 0.10$ ). There were no effects of either grazing intensity or years grazed on nest survival of either Baird's or Savannah sparrows in 2010. Sample sizes were insufficient ( $n = 4$  and  $n = 11$ , respectively) to analyze these species' nests in 2009.

## Discussion

We found little evidence that grazing intensity at the scale of the pasture consistently affected nest survival of grassland songbirds. Similarly, previous work in this system found little effect of vegetation structure, or the presence or absence of grazing, on nest survival of



**Fig. 2.** Effects of grazing on nest survival of songbirds in southwestern Saskatchewan, Canada, 2009–2010. Solid lines indicate 2 yr grazed; dashed lines indicate 3 yr grazed. Shaded areas represent 90% confidence intervals (2 yr in dark gray and 3 yr in light gray). The single points are the estimates and 90% confidence intervals for a typical grazing intensity in the 15-yr grazed pastures, which had a narrower range of grazing intensities. **A.** Effects of grazing intensity and years grazed on Sprague's pipits (2009). **B.** Effects of grazing intensity and years grazed on chestnut-collared longspurs (2009). **C.** Effects of grazing intensity on vesper sparrows (2010).

grassland songbirds in southern Saskatchewan (Lusk and Koper, 2013). This seems surprising, as vegetation structure (including vegetation height, litter depth, forb cover, and % bare ground) changed significantly with grazing intensity and with number of years grazed in this study area (Lwiwski et al., 2015). One possible explanation is that in large pastures, cattle do not graze uniformly, and thus grazed landscapes can support a diverse mosaic of varying vegetation structures (Plumb and Dodd, 1993). Heterogeneous landscapes might be difficult for predators to search (Dalkvist et al., 2011); in addition, they are likely to support a diverse avian community by providing a wide range of microhabitats (Martin, 1993).

The impacts of nest cover on the survival of ground-nesting bird nests vary depending upon the type of predators present. Nests within dense vegetation tend to have higher probabilities of survival when

the primary nest predators are birds (Stokes and Boersma, 1998; Dion et al., 2000), but lower probabilities of survival when the primary predators are small mammals (Schieck and Hannon, 1993), perhaps because small mammals use vegetative cover as shelter against their own aerial predators (With, 1994; Dion et al., 2000). As a result, high predator diversity may lower the overall nest survival of songbirds (Dion et al., 2000). In prairies with a diverse predator community, risks of predation by visual and olfactory predators might be negatively correlated with risks of predation by small mammals, thus minimizing apparent effects of habitat structure, or livestock management, on nest survival. Further, opposite effects of grazing intensity on ground squirrels and American badgers have been observed in this study area (Bylo et al., 2014), both of which are potential ground nest predators, suggesting that effects of grazing on predator communities might be compensatory. We speculate that the similarly low rates of nest survival we detected at low to moderate grazing intensities for Sprague's pipits and vesper sparrows in some years might result from an overlap in the types of predators able to find and depredate nests, consistent with Hypothesis 3 that a diverse predator community will result in lower nesting success at intermediate grazing intensity. If small mammals, mesopredators, and avian predators are all successful at finding nests in moderate vegetation structures, whereas relatively tall or short vegetation both support a more limited diversity of specialist predators, then predation overall might be higher at moderate grazing intensities. Further research on the predator community present at each grazing intensity is required to test this hypothesis.

Effects of grazing intensity and years grazed were not consistent. In our study, weather conditions may have mediated effects of grazing in one year but not others. In 2010, rainfall in southern Saskatchewan was three times greater than in 2009 (Environment Canada, 2011), causing 10 nests to fail directly due to weather in 2010. Although 2009 rainfall was below average, 2010 precipitation was more extreme over the months of the breeding season (high rainfall in May followed by lower rainfall in June and July; Lwiwski et al., 2015). Although we cannot be sure if the differences among years that we observed were due to cumulative effects of grazing or the different environmental conditions among years, we suspect that the heavier rainfall may have reduced effects of grazing through the rapid recovery of grazed vegetation. One indication of this is that the one significant result from 2010 (nest survival of Vesper Sparrows was highest at low or high grazing rates) shows no effect of grazing duration, whereas in 2009, both Sprague's Pipit and Chestnut-collared Longspurs showed effects of both grazing intensity and duration. This is consistent with patterns one would expect if the vegetation rapidly recovered with increased precipitation in 2010. Thus, our results from 2010 may be conservative or only indicative of effects of grazing in wet years.

The negative relationship we detected between years grazed and nest survival of chestnut-collared longspurs and vesper sparrows may have been caused by a time lag in the effects of grazing on vegetation structure. For example, shrubs, which are often used by vesper sparrows for nest protection (Jones and Cornely, 2002), take several years to respond to grazing, and thus effects of grazing might not be detected until several years of grazing have accumulated. Additionally, vesper sparrows have reduced nesting success in other regions with higher grazing intensities (Harrison et al., 2011), so their success may vary with both grazing intensity and the vegetation community present. If sites that have been grazed for many years are ecological traps (Gates and Gysel, 1978), this may be of some concern to the conservation of chestnut-collared longspurs and other species that prefer relatively short vegetation. However, as the effect of years grazed was detected in only 1 yr, this suggests that effects of grazing might be overwhelmed by effects of environmental variability.

## Implications

Understanding how livestock grazing affects nesting success of species in different types of grassland is important for making sound

management decisions throughout grassland ecosystems (Klute et al., 1997; Askins et al., 2007). We detected few effects of grazing on nest survival of mixed-grass prairie songbirds, and those effects we did detect were not consistent among years. Nonetheless, because low to moderate grazing intensities are frequently recommended to promote the conservation of prairie ecosystems, more research should be conducted to determine whether the low nesting success that we detected occasionally at low to moderate grazing intensities occurs regularly. If this pattern occurs elsewhere or regularly, significant changes to livestock management recommendations for conserving grassland songbirds may be necessary. At this point, however, our results suggest that cattle grazing at a range of grazing intensities, at least over a short period of time, is compatible with both the conservation of many species of mixed-grass prairie songbirds and the varying grazing intensities suggested for maintaining economically viable rangelands (Torell et al., 1991; Ritten et al., 2010).

## Acknowledgments

We thank Tonya Lwiwski, Maggi Sliwinski, Josh Smith, Chris Street, Sheilla Taillon, Adrienne Tastad, Jesse Watkins, and Amy Wheeler for invaluable assistance in the field; Spencer Sealy (University of Manitoba) and Kevin Ellison (Wildlife Conservation Society) for support and guidance; two anonymous reviewers and Daniel Twedt for comments that improved earlier drafts of this manuscript; and Jennifer Lusk for providing 2006–2007 data.

## References

- Askins, RA, Chávez-Ramírez, F, Dale, BC, Haas, CA, Herkert, JR, Knopf, FL, Vickery, PD, 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. *Ornithological Monographs* 64, 1–46.
- Augustine, DJ, McNaughton, SJ, 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62, 1165–1183.
- Baicich, PJ, Harrison, CJO, 1997. A guide to the nests, eggs, and nestlings of North American birds. second ed. Academic Press, San Diego, CA, USA, pp. 263–310.
- Benson, TJ, Brown, JD, Bednarz, JC, 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. *Journal of Animal Ecology* 79, 225–234.
- Bernath-Plaisted, J, 2015. The effects of oil and gas development on songbirds of the mixed-grass prairie: nesting success and identification of nest predators [thesis]. University of Manitoba, Winnipeg, MB, Canada.
- Bird Studies Canada, 2001. Ontario nest records scheme coding system. Royal Ontario Museum, Canadian Wildlife Service, Ontario, Canada.
- Bleho, B, 2009. Passerine relationships with habitat heterogeneity and grazing at multiple scales in northern mixed-grass prairie [thesis]. University of Manitoba, Winnipeg, MB, Canada.
- Bleho, B, Koper, N, Machtans, C, 2014. Direct effects of cattle on grassland birds in Canada. *Conservation Biology* 28, 724–734.
- Brennan, LA, Kuvlesky, WP, 2005. North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* 69, 1–13.
- Bylo, LN, Koper, N, Molloy, K, 2014. Grazing intensity influences ground squirrel and American badger habitat use in mixed-grass prairies. *Rangeland Ecology & Management* 67, 247–254.
- Chapman, RN, Engle, DM, Masters, RE, Leslie Jr., DM, 2004. Grassland vegetation and bird communities in the southern Great Plains of North America. *Agriculture, Ecosystems & Environment* 104, 577–585.
- Dalkvist, T, Sibley, RM, Topping, CJ, 2011. How predation and landscape fragmentation affect vole population dynamics. *PLoS One* 6, 1–8.
- Davis, SK, 2003. Nesting ecology of mixed-grass prairie songbirds in southern Saskatchewan. *Wilson Bulletin* 115, 119–130.
- Davis, SK, 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *Condor* 107, 605–616.
- DeLong, AK, Crawford, JA, DeLong Jr., DC, 1995. Relationships between vegetational structure and predation of artificial sage grouse nests. *Journal of Wildlife Management* 59, 88–92.
- Derner, JD, Lauenroth, WK, Stapp, P, Augustine, DJ, 2009. Livestock as ecosystem engineers for grassland bird habitat in the western Great Plains of North America. *Rangeland Ecology & Management* 62, 111–118.
- Dieni, JS, Jones, SL, 2003. Grassland songbird nest site selection patterns in northcentral Montana. *Wilson Bulletin* 115, 388–396.
- Dion, N, Hobson, KA, Larivière, S, 2000. Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. *Condor* 102, 629–634.
- Ellison, L, 1960. Influence of grazing on plant succession of rangelands. *Botanical Review* 26, 1–75.
- Environment Canada, 2011. National Climate Data and Information Archive. Available at: <http://www.climate.weatheroffice.gc.ca> Accessed 7 September 2011.
- Evans, DM, Redpath, SM, Evans, SA, Elston, DA, Dennis, P, 2005. Livestock grazing affects the egg size of an insectivorous passerine. *Biology Letters* 1, 322–325.
- Finnoff, D, Strong, A, Tschirhart, J, 2008. A bioeconomic model of cattle stocking on rangeland threatened by invasive plants and nitrogen deposition. *American Journal of Agricultural Economics* 90, 1074–1090.
- Fisher, RJ, Davis, SK, 2010. From Wiens to Robel: a review of grassland-bird habitat selection. *Journal of Wildlife Management* 74, 265–273.
- Fisher, RJ, Davis, SK, 2011. Habitat use by Sprague's pipits (*Anthus spragueii*) in native pastures and planted, non-native hay fields. *The Auk: Ornithological Advances* 128, 273–282.
- Fondell, TF, Ball, IJ, 2004. Density and success of bird nests relative to grazing on western Montana grasslands. *Biology Conservation* 117, 203–213.
- Fuhlendorf, SD, Engle, DM, 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* 51, 625–632.
- Gates, JE, Gysel, LW, 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59, 871–883.
- Harrison, ML, Mahony, NA, Robinson, P, Newbury, A, Green, DJ, 2011. Nest-site selection and productivity of Vesper sparrows breeding in grazed habitats. *Journal of Field Ornithology* 82, 140–149.
- Hartway, C, Mills, LS, 2012. A meta-analysis of the effects of common management actions on the nest success of North American birds. *Conservation Biology* 26, 657–666.
- Henderson, DC, 2006. Restoring grazing-induced heterogeneity in Grasslands National Park of Canada: landscape-scale experiment and long-term monitoring plan, 9 March 2006. Parks Canada Agency, Western & Northern Service Center, Winnipeg, MB, Canada.
- Herkert, JR, 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications* 4, 461–471.
- Jones, SL, Cornely, JE, 2002. Vesper Sparrow (*Pooecetes gramineus*). In: Poole, A. (Ed.), *The birds of North America*, no. 624. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Kerns, CK, Ryan, MR, Murphy, RK, Thompson III, FR, Rubin, CS, 2010. Factors affecting songbird nest survival in northern mixed-grass prairie. *Journal of Wildlife Management* 4, 257–264.
- Klute, DS, Robel, RJ, Kemp, KE, 1997. Will conversion of Conservation Reserve Program (CRP) lands to pasture be detrimental for grassland birds in Kansas? *American Midland Naturalist* 137, 206–212.
- Knapp, AK, Blair, JM, Collins, SL, Hartnett, DC, Johnson, LC, Towne, EG, 1999. The keystone role of bison in North American tallgrass prairie. *BioScience* 49, 39–50.
- Knopf, FL, 1992. Faunal mixing, faunal integrity, and the biopolitical template for diversity conservation. *Transactions of North American Wildlife and Natural Resources Conference* 57, 330–342.
- Koper, N, Schmiegelow, FKA, 2007. Does management for duck productivity affect songbird nesting success? *Journal of Wildlife Management* 71, 2249–2257.
- Koper, N, Henderson, DC, Wilmhurst, JF, Fargye, PJ, Sissons, RA, 2008. Design and analysis of rangeland experiments along continuous gradients. *Rangeland Ecology & Management* 61, 605–613.
- Lueders, AS, Kennedy, PL, Johnson, DH, 2006. Influences of management regimes on breeding bird densities and habitat in mixed-grass prairie: an example from North Dakota. *Journal of Wildlife Management* 70, 600–606.
- Lusk, J, Koper, N, 2013. Grazing and songbird nest survival in southwestern Saskatchewan. *Rangeland Ecology & Management* 66, 401–409.
- Lusk, JJ, Wells, KS, Guthery, FS, Fuhlendorf, SD, 2003. Lark sparrow (*Chondestes grammacus*) nest-site selection and success in a mixed-grass prairie. *The Auk: Ornithological Advances* 120, 120–129.
- Lwiwski, TC, Koper, N, Henderson, DC, 2015. Stocking rates and vegetation structure, heterogeneity, and community in a northern mixed-grass prairie. *Rangeland Ecology & Management* 68, 322–331.
- Madden, E.M., Murphy, R.K., Hansen, A.J., Murray, L., 2000. Models for guiding management of prairie bird habitat in northwestern North Dakota. *American Midland Naturalist* 144, 377–392.
- Martin, TE, 1993a. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141, 897–913.
- Martin, TE, Geupel, GR, 1993b. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64, 507–519.
- Milchunas, DG, Lauenroth, WK, Burke, IC, 1998. Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. *Oikos* 83, 65–74.
- Morrow, ME, Adamcik, RS, Friday, JD, McKinney, LB, 1996. Factors affecting Attwater's prairie-chicken decline on the Attwater Prairie Chicken National Wildlife Refuge. *Wildlife Society Bulletin* 24, 593–601.
- Mundry, R., 2011. Issues in information theory-based statistical inference—a commentary from a frequentist's perspective. *Behavioral Ecology and Sociobiology* 65, 57–68.
- Paine, L, Undersander, DK, Sample, DW, Bartelt, GA, Schattman, TA, 1996. Cattle trampling of simulated ground nests in rotationally grazed pastures. *Journal of Range Management* 49, 294–300.
- Peden, DG, Van Dyne, GM, Rice, RW, Hansen, RM, 1974. The trophic ecology of *Bison bison* L. on shortgrass plains. *Journal of Applied Ecology* 11, 489–498.
- Peduzzi, P, Concato, J, Kemper, E, Holford, TR, Feinstein, AR, 1996. A simulation study of the number of events per variable. *Journal of Clinical Epidemiology* 49, 1373–1379.
- Perlut, NG, Strong, AM, 2011. Grassland birds and rotational-grazing in the northeast: breeding ecology, survival and management opportunities. *Journal of Wildlife Management* 75, 715–720.
- Picozzi, N, 1975. Crow predation on marked nests. *Journal of Wildlife Management* 39, 151–155.

- Pietz, PL, Granfors, DA, 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management* 64, 71–87.
- Pietz, PL, Granfors, DA, 2005. Parental nest defense on videotape: more reality than "myth". *The Auk: Ornithological Advances* 122, 701–705.
- Plumb, GE, Dodd, JL, 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. *Ecological Applications* 3, 631–643.
- Quinn, GP, Keough, MJ, 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, England.
- Rahmig, CJ, Jensen, WE, With, KA, 2008. Grassland bird responses to land management in the largest remaining tallgrass prairie. *Conservation Biology* 23, 420–432.
- Ribic, CA, Guzy, MJ, Anderson, TJ, Sample, DW, Nack, JL, 2012. Bird productivity and nest predation in agricultural grasslands. *Studies in Avian Biology* 43, 119–134.
- Ricklefs, RE, 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9, 1–48.
- Ritten, JP, Bastian, CT, Frasier, WM, 2010. Economically optimal stocking rates: a bioeconomic grazing model source. *Rangeland Ecology & Management* 63, 407–414.
- Rotella, JJ, Taper, ML, Stephens, SE, Lindberg, MS, 2007. Extending methods for modeling heterogeneity in nest-survival data using generalized mixed models. *Studies in Avian Biology* 34, 34–44.
- Saab, VA, Bock, CE, Rich, TD, Dobkin, DS, 1995. Livestock grazing effects in western North America. In: Martin, T.E., Finch, D.M. (Eds.), *Ecology and management of neotropical migratory birds: a synthesis and review of critical issues*. Oxford University Press, New York, NY, USA, pp. 311–353.
- SAS Institute, Inc, 2008. Version 9.2. SAS Institute, Inc., Cary, NC, USA.
- Schieck, JO, Hannon, SJ, 1993. Clutch predation, cover, and the overdispersion of nests of the willow ptarmigan. *Ecology* 74, 743–750.
- Shaffer, T.L., 2004. A unified approach to analyzing nest success. *Auk* 121, 526–540.
- Sliwinski, MS, 2011. Changes in grassland songbird abundance and diversity in response to grazing by bison and cattle in the northern mixed-grass prairie [thesis]. University of Manitoba, Winnipeg, MB, Canada.
- Steuter, AA, Hidinger, L, 1999. Comparative ecology of bison and cattle on mixed-grass prairie. *Great Plains Research* 9, 329–342.
- Stokes, DL, Boersma, PD, 1998. Nest-site characteristics and reproductive success in Magellanic penguins (*Spheniscus magellanicus*). *The Auk: Ornithological Advances* 115, 34–49.
- Sugden, LG, Beyersbergen, GW, 1986. Effect of density and concealment on American crow predation of simulated duck nests. *Journal of Wildlife Management* 50, 9–14.
- Sutter, GC, 1997. Nest-site selection and nest-entrance orientation in Sprague's pipit. *Wilson Bulletin* 109, 462–469.
- Taylor, BL, Gerrodette, T, 1994. The uses of statistical power in conservation biology: the vaquita and the northern spotted owl. *Conservation Biology* 7, 489–500.
- Toombs, TP, Derner, JD, Augustine, DJ, Krueger, B, Gallagher, S, 2010. Managing for biodiversity and livestock. *Rangelands* 32, 10–15.
- Torell, LA, Lyon, KS, Godfrey, EB, 1991. Long-run versus short-run planning horizons and the rangeland stocking rate decision. *American Journal of Agricultural Economics* 73, 795–807.
- Underwood, AJ, 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological Applications* 4, 3–15.
- Weidinger, K, 2002. Interactive effects of concealment, parental behaviour, and predators on the survival of open passerine nests. *Journal of Animal Ecology* 71, 424–437.
- Willms, WD, Jefferson, PG, 1993. Production characteristics of the mixed prairie: constraints and potential. *Canadian Journal of Animal Science* 73, 765–778.
- Willms, WD, Dormaar, JK, Adams, BW, Douwes, HE, 2002. Response of the mixed prairie to protection from grazing. *Journal of Range Management* 55, 210–216.
- Willms, WD, Smoliak, S, Dormaar, JF, 1985. Effects of stocking rate on a rough fescue grassland vegetation. *Journal of Range Management* 38, 220–225.
- With, KA, 1994. The hazards of nesting near shrubs for a grassland bird, the McCown's longspur. *Condor* 96, 1009–1019.