

Title: Direct effects of cattle on grassland birds in Canada

Running head: Effects of cattle bird nests

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Abstract

Effects of grazing on grassland birds are generally thought to be indirect, through alteration of vegetation structure; however, livestock can also affect nest survival directly through trampling and other disturbances (e.g., livestock-induced abandonment). We extracted data on nest fates from 18 grazing studies conducted in Canada. We used these data to assess rates of nest destruction by cattle among 9 ecoregions and between seasonal and rotational grazing systems. Overall, few nests were destroyed by cattle (average 1.5% of 9132 nests). Nest destruction was positively correlated with grazing pressure (i.e., stocking rate or grazing intensity), but nest survival was higher in more heavily grazed areas for some species. Because rates of destruction of grassland bird nests by cattle are low in Canada, management efforts to reduce such destruction may not be of ecological or economic value in Canada.

Introduction

Livestock production is an important part of the global economy; over 3450 million ha of land worldwide are used as pastures or rangelands (Goldewijk 2001). These lands also support grassland birds, many of which are experiencing large population declines, primarily from habitat loss and degradation (Vickery et al. 1999; Donald et al. 2006). Understanding relationships between livestock and cohabitant birds is critical to designing and implementing ecologically sustainable livestock management practices (Derner et al. 2009).

Numerous studies show or suggest that grazing benefits some grassland birds, primarily by modifying vegetation structure (Table 1). Consequently, grazing is sometimes used as a management tool to maintain or improve habitat for birds (e.g., Vickery et al. 2004). Potential negative effects of grazing include degradation of habitat at inappropriate stocking rates, increased risk of predation and parasitism, and direct nest loss to livestock through trampling or other disturbances (hereafter referred to as nest destruction) (Table 1). However, the contexts in which these factors outweigh the benefits of grazing are not clear.

Relatively little information exists in the literature regarding nest destruction by livestock. Most studies have insufficient sample sizes to determine risk factors that might affect rates of nest destruction (e.g., Johnson et al. 2011). Small sample sizes have fostered the belief that rates of nest destruction are low; however, substantial rates have been documented in some studies (e.g., Nack & Ribic 2005; Sutter & Ritchison 2005; full review in Supporting Information). Studies using artificial nests have reported rates as high as 90% (e.g., Paine et al. 1996), though it is uncertain to what extent artificial nest experiments represent natural processes (Faaborg 2010).

Our objective was to provide an assessment of destruction of grassland bird nests by cattle. We evaluated effects of grazing management and geography on rates of nest destruction and situated nest destruction within the broader scope of cattle grazing and its effects on nest survival.

Methods

Data Compilation and Classification

We gathered data from 18 studies in 9 ecoregions in Canada (Supporting Information, Fig. 1). Most data sets were contributed by principal researchers and were either unpublished or published with summarized nest destruction data. We collected data on grazing system (rotational or season-long), grazing pressure (stocking rate or grazing intensity), ecoregion, grassland type (native or seeded), avian species, and nest fate. We defined nest destruction as any nest loss attributed directly to cattle, either through destruction (e.g., trampling, consumption of eggs/young) or abandonment following disturbance.

We used the following nest fate categories: success (≥ 1 fledged young), predation, abandonment (unknown cause), parasitism, cattle, weather, inviable (i.e., eggs did not hatch), unspecified fail (not cattle), and unspecified fate (not cattle). When abandonment was attributed to partial depredation, weather, or cattle, it was categorized as such. We assigned unspecified fail when nests failed for reasons other than cattle, but we were not informed what other causes were. We assigned unspecified fate when nests did not fail due to livestock, but we were not informed if they failed or succeeded. We included 2 nests that were partially destroyed by cattle in all

measures of nest destruction, but these nests were considered successful (≥ 1 fledged young) in nest survival analyses.

Cattle in season-long grazing systems had free access to pasture for the entire growing season (generally May-September). Cattle in rotational systems had restricted access to paddocks within pastures and were moved among paddocks during the growing season. Rotational grazing often included leaving some paddocks ungrazed for some or all of the growing season (rest rotation) or delaying onset of grazing within the growing season (deferred rotation). We did not exclude rested or deferred paddocks from analyses to reflect nest success within entire systems. We used both stocking rate (animal unit months per hectare, AUM/ha) and grazing intensity (percent utilization of available forage) as measures of grazing pressure because of discrepancies in data availability among studies. An animal unit month (AUM) represents the expected amount of forage a 1000 lb (~450 kg) cow with calf will consume in 1 month (Natural Resources Conservation Services 2008). We assigned grazing intensities as light (< 33% utilization), moderate (33-65%), and heavy (> 65%) based on Warren et al. (2008). These categories are consistent with, but not identical to, other sources (e.g., Holechek & Galt 2000).

We used the National Ecological Framework for Canada classification system to delineate ecoregions (Ecological Stratification Working Group 1995). We grouped ecoregions into four ecogroups defined by floristic, climatic, and geographical similarities relevant to vegetative productivity and therefore stocking rates (Fig. 1) to increase sample sizes and reduce overparameterization that might arise from the high number of 2-way categorical comparisons between ecoregions. Parkland Transition represented the Aspen Parkland, Boreal Transition, and

Southwest Manitoba Uplands ecoregions, which receive 400-699 mm of precipitation annually and are characterized by grasslands interspersed with trees. Prairie Grassland represented the Mixed Grassland, Moist Mixed Grassland, Fescue Grassland, and Cypress Upland ecoregions, which receive 250-450 mm of precipitation annually and are dominated by grasses. Cypress Upland was included in this grouping because only mixed-grass and fescue grasslands found at lower elevations were sampled. Palouse Grassland represented the Fraser Plateau ecoregion, which receives 250-300 mm of precipitation annually in the sampled area (around the Chilcotin and Fraser River junction) and is characterized by bunchgrasses. We placed the St. Lawrence Lowlands ecoregion in its own ecogroup because it receives significantly more annual precipitation (800-1000 mm) and is both geographically and floristically distinct from the other ecoregions. Sample sizes for Palouse Grassland and St. Lawrence Lowlands were small, but we included these regions because of their potential to highlight differences in nest destruction among ecosystems.

Data Analyses

Using Proc GENMOD in SAS 9.2 (SAS Institute 2009), we initially allowed for clustering by study by using a generalized linear model with a generalized estimating equation and exchangeable correlation structure to control for variation among studies. However, the working correlation estimate was so small (0.0012, indicating little effect of study) that analyses resulted in a non-positive definite Hessian matrix. It was therefore not necessary (or possible) to allow for clustering.

We conducted analyses at order and species level. We used a generalized linear model to evaluate comparative effects of ecogroup, grassland type, order (ducks, shorebirds, passerines), and nest placement (ground, aboveground) on rates of nest destruction. Thirty-nine species were classified as ground nesters, 8 species as near-ground nesters, and 3 species as both. Grazing system, grazing intensity, and stocking rate were each added separately to the above model ($n = 3$ models) to avoid collinearity among related variables and to maximize sample size for each analysis because each variable was available for only a subset of the data. The quadratic term for stocking rate was not significant ($p > 0.05$), suggesting that the effect of stocking rate was linear, so we removed the quadratic term from final models to reduce collinearity (Quinn & Keough 2002). We used a correlation matrix of parameter estimates to assess degree of collinearity.

We introduced interaction terms between each of the grazing variables, ecoregions, and order to test region- and order-specific effects of grazing. Non-significant ($p > 0.05$) interaction terms were removed from final models to avoid collinearity (Quinn & Keough 2002, p.112). Models containing interaction terms with grazing intensity would not converge; thus, interaction terms were removed from final models. Nonlinear effects of stocking rate were initially modeled using quadratic and cubic polynomial terms. Polynomial terms that were not significant ($p > 0.05$) were removed.

We used a generalized linear model to evaluate effects of grazing system and either grazing intensity, stocking rate, or a quadratic model for stocking rate on 7 species for which we had at minimum 240 nests and at least 4 trampling events because trampling rates lower than this (e.g., 1 or 2 nests) might represent spurious events not driven by grazing pressure. For Chestnut-

collared Longspur (*Calcarius ornatus*), we ran only a grazing intensity model due to insufficient stocking rate data. We ran models separately for stocking rate and grazing intensity to avoid collinearity and to maximize sample sizes.

We converted parameter estimates and confidence intervals to odds ratios for easier interpretation of results. Values > 1 indicated positive relationships between dependent and independent variables; values from 0 to 1 indicated negative relationships.

We used generalized linear models to conduct nest destruction analyses of the raw data (i.e., nest destruction events detected per nests surveyed, or apparent nest destruction levels), which may underestimate rates of nest destruction because nests lost to cattle prior to surveys cannot be found (e.g., Johnson 1979). However, we were unable to account for this in our analyses because exposure periods were unknown for regions other than prairies and rates of nest destruction were so low that precise estimates were highly dependent on individual data sets. Only analyzing nests from prairie ecosystems would decrease our ability to detect many nest destruction events, particularly in lightly grazed pastures. Nonetheless, we recognize we could not account for nests that might have been lost to cattle but not detected and thus urge caution in application of our results.

Nest Survival

Seven data sets included sufficient information (visit interval length and fate) for us to evaluate effects of grazing on nest survival of ducks and passerines (Supporting Information). We followed the logistic exposure method (Shaffer 2004) and used PROC NLMIXED in SAS 9.2.

We used presence of grazing and, when available, grazing intensity (i.e., light, moderate, heavy) as predictors in separate models. Ungrazed habitat was ungrazed at the time of study, but length of time idled and state of vegetation varied among studies. We initially included study as a random variable, but in a few cases this prevented models from converging, and in all remaining cases, the random variable was not significant, so we omitted it from final analyses. We reported both overall and daily nest survival rates. Daily survival rates allowed us to compare survival among species with different nesting periods, whereas overall survival rates better represented the probability that a nest ultimately succeeded or failed. We also assessed whether nests were depredated or not to test if depredation rates drove observed effects of grazing.

Multinomial methods of modeling diverse nest fates represent an alternative approach to analyzing nesting success data (e.g., Etterson et al. 2007). These may give similar results to logistic exposure analyses when the same independent variables are included in models (Etterson et al. 2007); thus, our conclusions regarding effects of grazing on overall nest survival are probably not strongly influenced by our use of the logistic exposure method. One benefit of the logistic exposure method is that it allows for random variables to be included in models, whereas the Markov-chain nest-failure analysis has not yet been generalized to include random variables (Etterson et al. 2007). While random variables proved uninformative in our final analyses, we initially believed that it was important to evaluate whether random variables accounted for variation in nest survival among studies. While our general conclusions should be robust, we recognize that our analytical method was imperfect and that relative risks of nest destruction and predation might be slightly over- or underestimated.

Results

Nest Fates and Nest destruction

Data from 18 studies totaled 9132 nests. Overall, 38% of nests were successful, 53% failed, and 9% had unspecified fates. Most nest failures (87%) were caused by predation. Cattle accounted for 2.8% of nest failures, primarily through trampling. Two nests were abandoned following prolonged cattle grazing near the nests, and 1 failed when cattle defecated on it.

Nest destruction was highest in St. Lawrence Lowlands (33%), lowest in Prairie Grassland (0.85%), and moderate in Parkland Transition (3.1%) and Palouse Grassland (4.6%) (Supporting Information, Table 2); however, these results should be interpreted with caution as sample sizes for Palouse Grassland and St. Lawrence Lowlands were small and possibly confounded by avian order. There was no difference in nest destruction between native and seeded grassland (Table 2). Nest destruction was similar between grazing systems, but lower in lightly and moderately grazed than heavily grazed areas (Table 2). We detected no effect of stocking rate or nest placement on rates of nest destruction for all species combined (Table 2).

Passerines had the highest rate of nest destruction (Table 2). Both passerines and shorebirds were at similar risk of nest destruction at all grazing intensities; however, almost 20 times more duck nests were lost to cattle at heavy than moderate intensity, though no differences were detected between light and heavy grazing (Table 3). The risk of nest destruction for ducks increased with stocking rate, but was independent of stocking rate for passerines (Table 4). The model did not converge for shorebirds.

Fifty-one species were represented in the data. Average rates of nest destruction for 21 species with ≥ 50 nest records ranged from 0 to 3.2% (Supporting Information). Nest destruction increased with both grazing intensity and stocking rate for Blue-winged Teal (*Anas discors*), Northern Shoveler (*Anas clypeata*), and Sprague's Pipit (*Anthus spragueii*); decreased with both grazing intensity and stocking rate for Clay-colored Sparrow (*Spizella pallida*); and remained constant among grazing intensities and stocking rates for Vesper Sparrow (*Pooecetes gramineus*; Tables 3, 4). Nest destruction increased with stocking rate, but remained constant among grazing intensities for Savannah Sparrow (*Passerculus sandwichensis*; Tables 3, 4). Nest destruction increased with grazing intensity for Chestnut-collared Longspur (*Calcarius ornatus*; Table 3). Stocking rate also had a quadratic effect on nest destruction for Sprague's Pipit (Table 4), with the probability of take approaching 0.3 at stocking rates of 0.8-0.9 AUM/ha and approaching 0 at stocking rates of 0.2-0.4 AUM/ha and 1.3 AUM/ha. .

Nest Survival

Data from 7 studies totaled 6443 nests. Ducks had lower nest survival in grazed areas (Table 5). Passerine nest survival was similar between grazed and ungrazed habitat, but lower in lightly grazed than moderately, heavily, and ungrazed habitat. Nest survival was highly species specific. Baird's Sparrow (*Ammodramus bairdii*) and Savannah Sparrow appeared to benefit from grazing, but Blue-winged Teal, Mallard (*Anas platyrhynchos*), Sprague's Pipit, and Vesper Sparrow did not (Table 5). Significant differences in nest survival between grazed and ungrazed areas often existed only among some grazing intensities (e.g., between light and heavy intensity, with moderate intensity similar to both). Results were similar between nest survival and

depredation analyses, except for Mallard, which had lower nest survival in grazed areas, but similar probability of depredation between grazed and ungrazed areas (Table 5).

Discussion

Nest destruction was very low. For every nest lost to cattle, about 31 nests were lost to predators. However, there was substantial variation in nest destruction among ecoregions, reflecting different land use practices, climates, and grazing histories (Shorthouse 2010). Relatively high rates of nest destruction in Palouse Grassland and St. Lawrence Lowlands may have occurred because neither system has been exposed to extensive grazing by ungulates throughout its evolutionary history (Mack & Thompson 1982), so the selective pressure on nest site selection is absent. High primary productivity, which permits high stocking rates, may make the St. Lawrence Lowlands region especially sensitive to grazing pressure, though we caution only ducks were sampled in this region. It is possible our results for Palouse Grassland and St. Lawrence Lowlands may be spurious as a result of small sample sizes from heavily grazed sites; however, relatively high rates of nest destruction have also been observed in grasslands of western Europe (e.g., Beintema & Müskens 1987) and eastern United States (e.g., Perlut & Strong 2011). Grasslands in those regions are mostly anthropogenic in origin, with limited grazing histories, and high primary productivity relative to central North American grasslands (Scholz 1975; Brennan & Kuvlesky 2005). Parallels among these systems suggest that grassland productivity and grazing history may be useful measures that can be used universally to predict the potential risk of nest destruction.

Nest destruction was similar between rotational and seasonal grazing systems, consistent with studies using artificial nests (e.g., Koerth et al. 1983). Because relatively few nests were destroyed by cattle, there are presumably few benefits of removing disturbance by cattle via rotational grazing systems. Further, rotational systems may not adequately create or preserve nesting habitat for some bird species because they promote uniform land use with the goal to maximize cattle forage intake (Derner et al. 2009). Recent studies suggest perceived benefits of rotational grazing have not been realized (Briske et al. 2008), and our results are consistent with their observation that rotational grazing systems have few ecological benefits over continuous systems managed at equivalent stocking rates. Patch-burn grazing, which employs both prescribed burns and cattle grazing to manage grasslands, may be more beneficial to grassland birds because it promotes heterogeneity in the landscape (Fuhlendorf et al. 2006) and may provide nesting habitat for more bird species (Fuhlendorf et al. 2006). However, birds nesting in burned areas in these systems may be vulnerable to higher rates of nest destruction than in continuous or rotational systems because of the concentration of livestock.

Nest destruction generally increased with grazing pressure (see also Koerth et al. 1983; Fondell & Ball 2004). However, effects of grazing intensity exceeded effects of stocking rate for some analyses. Climatic variation among regions results in different levels of primary productivity and, therefore, grazing capacity, so a given stocking rate will result in different levels of utilization in different regions (Smart et al. 2010). This suggests that rates of nest destruction vary regionally as a result of livestock carrying capacity.

It has been suggested that nest placement may influence susceptibility to nest destruction (Paine et al. 1996, Rohrbaugh et al. 1999, but see Churchwell et al. 2005); however, we did not detect any differences in susceptibility between ground and near-ground nests.

Passerines were more susceptible to nest destruction than ducks and shorebirds. Ducks are larger than passerines and more conspicuous when flushed, typically flying straight from the nest instead of first running away (Forbes et al. 1994). We speculate cattle may more easily notice and avoid nesting ducks or may be startled from the nest vicinity when a hen flushes. Shorebird nest defenses (e.g., aggressive attacks and broken-wing displays) may divert livestock away from nests (Allen 1980). Ducks were more susceptible to nest destruction at heavier grazing pressure. Duck nest densities are positively correlated with wetland abundance (Koper & Schmiegelow 2007), and cattle spend a disproportionate amount of time near water (Vallentine 2001). Heavier traffic of cattle around water in pastures with higher stocking rates and grazing intensities may have increased the risk of nest destruction for ducks.

Among species, nest destruction generally increased with grazing pressure (see also Fondell & Ball 2004). Most species generally prefer heavier cover and avoid heavily grazed areas, with the exception of Chestnut-collared Longspur (Owens & Myres 1973; Klett et al. 1988; Davis et al. 1999); however, higher nest densities and productivity in grazed habitat may offset direct losses to livestock for this species (Owens & Myres 1973). Although nest destruction is thought to be mostly coincidental, cattle will investigate nests when encountered (Paine et al. 1997), so nest concealment may affect nesting outcome. Clay-colored Sparrow, a shrub-nester, was the only species that responded positively to grazing pressure. Cattle may avoid large patches of shrubs,

which thereby offer protection for nests. Sprague's Pipit was the only species that had a non-linear response to stocking rates; nest destruction was highest at moderate stocking rates, perhaps because this species avoids heavily grazed habitat.

Species-specific variation in nest survival between grazed and ungrazed habitat may explain the lack of effects of grazing on passerines as a group. Low nest survival for Sprague's Pipit and Vesper Sparrow in lightly grazed areas may reflect unknown factors related to the single study from which the data came. Further, the large representation (95%) of these 2 species within lightly grazed areas likely influenced results for passerines overall in lightly grazed areas. Ducks had lower nest survival in grazed areas, which may have been influenced by the large representation (>30%) of Blue-winged Teal. A recent meta-analysis shows livestock exclusion results in species-specific effects on nest survival, though species of concern as a group benefit from removal of livestock (Hartway & Mills 2012). However, the authors of this study did not compare nest survival among grazing intensities. Our results indicate that grouping grazing intensities together can mask effects of grazing on nest survival. Prescott et al. (1998) found higher nest survival in grazed areas despite direct negative effects of cattle. If nest survival is higher in grazed areas or at heavier intensities, indirect benefits of grazing may outweigh the increased risk of nest destruction. Because we could not account for nest densities, net productivity gains per unit of land were unknown. Some studies have documented lower nest densities but higher nest survival and productivity in grazed sites (Barker et al. 1990; Warren et al. 2008). Our nest survival analyses were confined to prairie ecoregions, so we caution against extrapolating these results to other areas. In the central Great Plains, where bison were a major evolutionary driver, grazing by cattle may benefit grassland-obligate birds more than no grazing

at all (Hartnett et al. 1997), but annual heavy grazing can be detrimental to grassland ecosystems and their avifaunas (reviewed in Saab et al. 1995). Further, ungrazed areas support sustainable populations of some species (Klett et al. 1988), demonstrating the benefits of retaining some idle pastures.

The probability of nest depredation almost invariably mirrored the probability of nest failure, suggesting that effects of grazing on nest survival were driven by depredation levels. Small to medium-sized mammals are key predators of passerine and duck nests (Klett et al. 1988; Miller & Knight 1993). Abundance of small mammals tends to increase as cover increases in the presence of large avian predators, but to decrease as cover increases in the presence of mammalian mesopredators (Korpimäki et al. 1996); therefore, nest predation risk may either increase or decrease with changes in grazing pressure and vegetation cover because nest predator populations are regulated not only by vegetation structure, but also by the local assemblage of predators at higher trophic levels.

Because rates of nest destruction by cattle are so low, it is difficult to estimate risks from a single study, so combining data from many studies was required to estimate these risks. However, the benefits of conducting our analyses using a large sample size are also associated with disadvantages. Numbers of exposure periods per nest, periods between nest checks, and methods of confirming whether nests were successful or failed vary among studies. Some field protocols, such as visitation close to the fledging date, may affect relative bias in estimates of nest survival rates (e.g., Stanley 2004; Etterson et al. 2007). Due to the large extent of our study, we could not control for these biases and acknowledge that some estimates of nest survival could have been

affected. While our expansive data set allowed us to evaluate effects of grazing and nest destruction on nest survival at a regional scale, detailed estimates of nest survival rates can be facilitated by short periods between visits close to the estimated fledging date (Stanley 2004) and that such field methods should be encouraged.

Most native grasslands in North America have been lost to agriculture and urbanization (Vickery et al. 1999). Population declines of many grassland birds have been linked to the conversion of rangeland to cropland (Murphy 2003) and the intensification of agriculture (NABCI US Committee 2009). Rangelands are typically the most attractive agricultural landscapes for grassland nesting birds due to their close approximation to natural grasslands and minimum human disturbance (Saab et al. 1995). Nest losses to livestock are relatively low compared with other agricultural disturbances; most reported rates in the North American literature do not exceed 10% (Supporting Information). The conservation significance of grasslands retained in well-managed rangelands, despite some losses of nests to livestock, is therefore high.

European studies have generally documented higher rates of nest destruction than North American studies (Supporting Information). Most European grasslands are more productive than native North American grasslands and have limited grazing histories (Scholtz 1975). Birds in these systems may be susceptible to nest destruction because they are exposed to high stocking rates, yet they have not evolved behavioral defenses that divert livestock away from nests (Beintema & Müskens 1987). Further, sheep represent a significant proportion of grazing livestock in Europe (Zygoyiannis 2006) and may be particularly destructive to nests (Beintema

& Müskens 1987). Grassland managers should consider livestock species when addressing risk of nest destruction.

Overall rates of nest destruction by livestock were too low to have a strong effect on nest survival and avian productivity. Implementation of measures aimed at reducing nest destruction beyond levels observed under current management practices may not have ecological or economic value, except in isolated circumstances in which heavy losses occur. Our results suggest that indirect impacts of well-managed grazing can be far-reaching and positive.

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Supporting Information

Summary of literature on nest destruction of bird nests by livestock (Appendix S1); sources of data used in this study (Appendices S2 and S3); per-region rates of nest destruction (Appendix S4), and per-species rates of nest destruction (Appendix S5) are available online. The authors are

solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Table 1. Summary of hypothesized and observed effects of livestock grazing on grassland birds.

Effect	Description or mechanism	Reference
<i>Positive</i>		
modified vegetation structure	shorter or patchier vegetation is more suitable for some ground nesters	Muchai et al. 2002*, Fondell & Ball 2004*
reduced nest predator abundance	grazed area less suitable for some predator species	Stanley 2010
decreased predator efficiency	increased vegetation heterogeneity decreases predator search efficiency	Bowman & Harris 1980
nest concealment	nests placed non-randomly beside cattle or horse dung may be better concealed from predators	Allen 1980, Derner et al. 2009
increased alternative prey availability	grazed area supports other prey species that are preferred over ground nesters by local predators, reducing nest predation rates on ground nesters	Ackerman 2002*
increased food availability	grazed area supports more desirable invertebrate or plant food sources	Atkinson et al. 2005
<i>Negative</i>		

degraded grassland	heavily grazed area is habitat for only a few species	Smith 1940*, Owens & Myres 1973*
avoidance of livestock	birds avoid nesting in actively grazed areas	Kirsch 1969*, Hart et al. 2002*
decreased nest protection	grazing strips remove protective vegetation, exposing nests to the elements and predators and increases risk of being trampled	Beintema and Müskens 1987, Paine et al. 1996*, Fondell & Ball 2004, Walsberg 2005
increased nest predator abundance	grazed area is more suitable for some predator species	Koper & Schmiegelow 2007
increased predator efficiency	decreased vegetation heterogeneity or height at heavy grazing intensity increases predator search efficiency	Muchai et al. 2002, Sutter & Ritchison 2005
decreased alternative prey availability	alternative prey species prefer ungrazed areas, so ground nesters are the main source of prey in grazed areas	Ackerman 2002
decreased food availability	grazed area supports fewer desirable invertebrate or plant food sources	Smith 1940
brood parasite attraction	livestock attract Brown-Headed Cowbirds	Goguen & Mathews 2001*
nest abandonment	birds flushed by livestock or whose nests have been exposed after the vegetative cover has been removed by grazing may abandon their nests	Temple et al. 1999*

increased risk of nest discovery	birds flushed by livestock attract predators to their nests	Hart et al. 2002*, Walsberg 2005
direct nest destruction	trampling nests, dislodging nests from low shrubs, lying on nests, crushing nests with muzzles, defecating on nests, kicking eggs or young out of nests, consuming eggs or young	Pennington 1992*, Paine et al. 1996*, Rohrbaugh et al. 1999*, Churchwell et al. 2005*, Nack & Ribic 2005*

*Studies containing empirical evidence.

Table 2. Odds ratios describing comparative effects of ecogroup, grassland type, order, nest placement, grazing system, stocking rate, and grazing intensity on rates of apparent nest destruction (direct destruction by cattle or cattle-induced abandonment) of grassland bird nests in Canada, based on 18 data sets (Supporting Information).

Parameter	Trials ^a	Estimate ^b	Confidence limits	<i>p</i>
Ecogroup ^c	Palouse Grassland vs. Prairie Grassland	3.282	1.127 to 9.559	0.029
	Prairie Grassland vs. St. Lawrence Lowlands	0.021	0.006 to 0.070	<0.0001
	Parkland Transition vs. Prairie Grassland	4.544	3.016 to 6.848	<0.0001
	Palouse Grassland vs. Parkland Transition	0.503	0.122 to 2.078	0.342
	Parkland Transition vs. St. Lawrence Lowlands	0.049	0.015 to 0.163	<0.0001
	Palouse Grassland vs. St. Lawrence Lowlands	0.093	0.018 to 0.478	0.004
Grassland type	native vs. seeded	1.361	0.789 to 2.349	0.268
Order	duck vs. passerine	0.423	0.271 to 0.662	0.000
	shorebird vs. passerine	0.240	0.093 to 0.622	0.003
	duck vs. shorebird	2.052	0.617 to 6.824	0.241
Nest placement	ground vs. above ground	1.944	0.879 to 4.299	0.101
Grazing system	rotational vs. seasonal	1.419	0.963 to 2.093	0.077
Stocking rate	AUM/ha	1.057	0.703 to 1.588	0.791

Stocking rate x order	AUM/ha*duck vs. AUM/ha*passerine	1.854	1.066 to 3.224	0.029
	AUM/ha*shorebird vs. AUM/ha*passerine	1.804	0.274 to 11.892	0.540
	AUM/ha*duck vs. AUM/ha*shorebird	1.028	0.154 to 6.870	0.977
Grazing intensity	light vs. heavy	0.145	0.054 to 0.389	0.0001
	moderate vs. heavy	0.312	0.139 to 0.699	0.005
	light vs. moderate	0.466	0.205 to 1.056	0.067

^a AUM = animal unit month and represents the expected amount of forage a 1000 lb (~450 kg) cow with calf will consume in 1 month.

^b Values converted to odds ratio represent the probability that nest destruction is the same between the 2 variables in a trial. Values >1 imply nest destruction is more likely within or for the first variable; values <1 imply that nest destruction is less likely within or for the first variable.

^c As classified in Table 4.

Table 3. Effects of grazing intensity on apparent nest destruction (direct destruction by cattle or cattle-induced abandonment) of grassland bird nests in Canada.*

Species	No. studies	Grazing Intensity					
		Light		Moderate		Heavy	
		<i>n</i>	% take	<i>n</i>	% take	<i>n</i>	% take
All ducks	9	151	0a,b	2545	0.8a	76	15.8b
Blue-winged Teal	6	60	0a	425	0.7a	33	6.1b
Northern Shoveler	5	24	0a	446	1.1a	6	33.3b
All passerines	9	1046	0.9	1250	1.7	211	3.3
Sprague's Pipit	7	269	0.7a	56	5.4b	4	25.0b
Savannah Sparrow	7	470	0.4	134	1.5	12	8.3
Clay-colored Sparrow	6	29	3.4a	241	2.9a,b	6	0b
Vesper Sparrow	7	127	2.4	166	1.2	101	3.0
Chestnut-collared Longspur	5	34	0a	381	0.5a,b	26	3.8b
All shorebirds	6	43	0	538	0.2	53	3.8

*Data represents 15 data sets from 8 ecoregions in Canada. Number of nests (*n*) reflects only the nests for each species for which grazing intensity values were available. Percent estimates are based on number of nests trampled relative to number of nests surveyed. Within each row, % take values with different superscript letters are significantly different ($p < 0.05$).

Table 4. Effects of stocking rate (animal unit months per hectare, AUM/ha) on apparent nest destruction (direct destruction by cattle or cattle-induced abandonment) of grassland bird nests in Canada.*

Species	No. studies	Parameter	Estimate	Confidence limits	<i>p</i>
All ducks	7	AUM/ha	2.019	1.390 to 2.931	<0.001
Blue-winged Teal	5	AUM/ha	2.171	1.272 to 3.702	0.004
Northern Shoveler	4	AUM/ha	3.838	1.534 to 9.602	0.004
All passerines	6	AUM/ha	0.943	0.697 to 1.275	0.702
Sprague's Pipit	4	AUM/ha	2.092×10^{12}	12.756 to 3.430×10^{32}	0.031
		AUM/ha*AUM/ha	5.169×10^{-8}	2.901×10^{-14} to 0.092	0.022
Savannah Sparrow	6	AUM/ha	2.883	1.241 to 6.700	0.014
Clay-colored Sparrow	6	AUM/ha	0.001	6.646×10^{-7} to 0.852	0.045
Vesper Sparrow	5	AUM/ha	1.437	0.931 to 2.218	0.101

*Estimates and confidence limits are converted to odds ratios. For brevity, non-linear relationships are shown only when significant ($p < 0.05$).

Table 5. Estimated nest survival rate and probability of depredation of grassland bird nests under three grazing intensities and in ungrazed habitat.^a

Species	Grazing intensity ^b	<i>n</i>	Overall nest survival rate (95% CI)	Daily nest survival rate (95% CI)	Overall probability of nests not depredated (95% CI)	Daily probability of nests not depredated (95% CI)
All ducks	UG	1730	0.234 (0.020)a	0.958 (0.002)a	0.260 (0.022)a	0.961 (0.002)a
	G	2860	0.166 (0.012)b	0.948 (0.002)b	0.193 (0.014)b	0.953 (0.002)b
	UG	1730	0.234 (0.020)a	0.958 (0.002)a	0.260 (0.022)a	0.961 (0.002)a
	M	634	0.173 (0.024)b	0.950 (0.004)b	0.194 (0.026)b	0.953 (0.004)b
Gadwall	UG	337	0.285 (0.052)a	0.965 (0.004)a	0.303 (0.054)a	0.966 (0.004)a
	G	454	0.225 (0.042)a	0.958 (0.006)a	0.242 (0.044)a	0.960 (0.004)a
	UG	337	0.285 (0.052)a	0.965 (0.004)a	0.303 (0.054)a	0.966 (0.004)a
	M	191	0.212 (0.066)a	0.957 (0.008)a	0.239 (0.070)a	0.960 (0.008)a
Mallard	UG	279	0.172 (0.046)a	0.951 (0.008)a	0.199 (0.050)a	0.955 (0.006)a
	G	612	0.117 (0.024)b	0.940 (0.006)b	0.145 (0.028)a	0.946 (0.006)a

	UG	279	0.172 (0.046)a	0.951 (0.008)a	0.199 (0.050)a	0.955 (0.006)a
	M	116	0.139 (0.070)a	0.945 (0.014)a	0.145 (0.070)a	0.946 (0.014)a
Blue-winged Teal	UG	618	0.255 (0.036)a	0.961 (0.004)a	0.276 (0.038)a	0.963 (0.004)a
	G	1047	0.178 (0.024)b	0.95 (0.004)b	0.210 (0.026)b	0.955 (0.004)b
	UG	618	0.255 (0.036)a	0.961 (0.004)a	0.276 (0.038)a	0.963 (0.004)a
	M	197	0.168 (0.054)b	0.949 (0.010)b	0.180 (0.058)b	0.951 (0.008)b
Northern Shoveler	UG	288	0.232 (0.050)a	0.958 (0.006)a	0.266 (0.054)a	0.962 (0.006)a
	G	549	0.180 (0.032)a	0.951 (0.006)a	0.206 (0.036)a	0.955 (0.004)a
	UG	288	0.232 (0.050)a	0.958 (0.006)a	0.266 (0.054)a	0.962 (0.006)a
	M	237	0.197 (0.052)a	0.953 (0.008)a	0.219 (0.056)a	0.956 (0.008)a
Northern Pintail	UG	108	0.143 (0.068)a	0.944 (0.012)a	0.196 (0.080)a	0.950 (0.012)a
	G	342	0.124 (0.036)a	0.940 (0.008)a	0.160 (0.042)a	0.944 (0.008)a
	UG	108	0.143 (0.068)a	0.944 (0.012)a	0.196 (0.080)a	0.950 (0.012)a

	M	173	0.134 (0.054)a	0.939 (0.012a	0.159 (0.060)a	0.944 (0.012)a
Passerines	UG	449	0.293 (0.046)a	0.954 (0.006)a	0.364 (0.052)a	0.962 (0.006)a
	L	233	0.035 (0.022)b	0.879 (0.022)b	0.041 (0.026)b	0.885 (0.020)b
	M	439	0.313 (0.048)a	0.956 (0.006)a	0.430 (0.054)a	0.968 (0.004)a
	H	40	0.362 (0.168)a	0.962 (0.018)a	0.456 (0.184)a	0.970 (0.016)a
Sprague's Pipit	UG	449	0.293 (0.046)a	0.954 (0.006)a	0.364 (0.052)a	0.962 (0.006)a
	G	1404	0.252 (0.026)a	0.948 (0.004)a	0.325 (0.028)a	0.958 (0.004)a
	UG	43	0.532 (0.168)a	0.975 (0.012)a	0.602 (0.170)a	0.980 (0.010)a
	L	100	0.037 (0.036)b	0.877 (0.034)b	0.049 (0.044)b	0.886 (0.032)b
	M	52	0.460 (0.142)a	0.969 (0.012)a	0.614 (0.150)a	0.981 (0.010)a
	H	1	—	—	—	—
	UG	43	0.532 (0.168a	0.975 (0.012a	0.602 (0.170a	0.980 (0.010a
	G	180	0.274 (0.078b	0.949 (0.010b	0.340 (0.088b	0.958 (0.010b
Clay-colored Sparrow	UG	29	0.177 (0.138)a	0.927 (0.032)a	0.293 (0.186)a	0.948 (0.026)a

	G	152	0.270 (0.074)a	0.945 (0.012)a	0.341 (0.084)a	0.954 (0.010)a
Vesper Sparrow	UG	44	0.351 (0.080)a	0.959 (0.008)a	0.438 (0.088)a	0.967 (0.008)a
	L	122	0.025 (0.024)b	0.863 (0.032)b	0.025 (0.024)b	0.863 (0.032)b
	M	39	0.352 (0.156)a	0.959 (0.016)a	0.410 (0.168)a	0.965 (0.016)a
	H	10	0.433 (0.362)a	0.967 (0.032)a	0.541 (0.384)a	0.976 (0.028)a
Savannah Sparrow	UG	169	0.351 (0.080)a	0.959 (0.008)a	0.438 (0.088)a	0.967 (0.008)a
	G	341	0.241 (0.052)b	0.945 (0.008)b	0.287 (0.058)b	0.951 (0.008)b
	UG	44	0.232 (0.134)a	0.943 (0.022)a	0.263 (0.144)a	0.948 (0.020)a
	L	5	—	—	—	—
	M	40	0.343 (0.160)b	0.958 (0.018)b	0.584 (0.190)b	0.979 (0.012)b
	H	3	—	—	—	—
Baird's Sparrow	UG	44	0.232 (0.134)a	0.943 (0.022)a	0.263 (0.144)a	0.948 (0.020)a
	G	121	0.277 (0.086)a	0.950 (0.012)a	0.394 (0.104)a	0.963 (0.010)a
Baird's Sparrow	UG	47	0.186 (0.110)a	0.935 (0.010)a	0.222 (0.124)a	0.942 (0.020)a

	L	3	—	—	—	—
	M	31	0.633 (0.204)b	0.982 (0.012)b	0.754 (0.190)b	0.989 (0.010)b
	H	3	—	—	—	—
	UG	47	0.186 (0.110)a	0.935 (0.010)a	0.222 (0.124)a	0.942 (0.020)a
	G	99	0.400 (0.110)b	0.964 (0.010)b	0.487 (0.118)b	0.972 (0.010)b
Chestnut-collared Longspur	UG	60	0.197 (0.100)a	0.952 (0.018)a	0.234 (0.112)a	0.948 (0.016)a
	L	1	—	—	—	—
	M	202	0.236 (0.062)a	0.948 (0.010)a	0.344 (0.078)a	0.961 (0.008)a
	H	20	0.354 (0.232)a	0.962 (0.024)a	0.443 (0.256)a	0.970 (0.020)a
	UG	60	0.197 (0.100)a	0.952 (0.018)a	0.234 (0.112)a	0.948 (0.016)a
	G	291	0.259 (0.054)a	0.951 (0.008)a	0.348 (0.064)a	0.962 (0.006)a

^a Values for depredation represent the probability that nests are *not* depredated. Data represents 7 data sets from 6 ecoregions in Prairie Canada. Letters next to numbers that differ within a column indicate significant differences ($p < 0.05$) in nest survival or depredation among grazing intensities for that order or species. Dashes indicate insufficient sample sizes for analysis.

^b Abbreviations: G, grazed; H, heavy; L, light; M, moderate; UG, ungrazed.

Figures:

Figure 1. Study site and nest point locations by ecoregion from 18 studies of direct cattle effects on grassland bird nests in Canada.