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Vesper Sparrows and Western Meadowlarks Show a Mixed Response to Cattle Grazing in the Intermountain Region of British Columbia

Le Bruant vespéral et la Sturnelle de l'Ouest réagissent de façon variable au broutement dans la région intramontagnarde de la Colombie-Britannique

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ABSTRACT. Livestock grazing in the shortgrass steppe of the Intermountain region of British Columbia is predicted to have significant effects on grassland habitats and their associated ground-nesting bird communities. We tested whether grazed and ungrazed sites could be discriminated on the basis of their vegetation communities, whether the abundance of two ground-nesting bird species, Vesper Sparrow (*Pooecetes gramineus*) and Western Meadowlark (*Sturnella neglecta*), differed between grazed and ungrazed sites, and whether vegetation variables found to differ between grazed and ungrazed plots could be used to predict the abundance of the two bird species at a fine scale. Grazed sites were easily distinguishable from a site that had been ungrazed for >30 years based on the structure and composition of their vegetation communities. However, more detailed grazing categories could not be distinguished on the basis of vegetation characteristics. Despite the existence of grazing effects on vegetation structure and composition, we found no consistent differences in abundance of Vesper Sparrows and Western Meadowlarks between the grazed and ungrazed sites. However, there was weak evidence that the abundance of both species was higher at fine-scale plots (100 m radius point count station) with less bare ground and taller vegetation. Bare ground cover was lower on grazed plots, but vegetation was taller on ungrazed plots. Combined, our results suggest that low intensity grazing leads to grassland habitat change with both negative and positive effects on Vesper Sparrows and Western Meadowlarks, resulting in no net change in their broad-scale abundance.

RÉSUMÉ. On pense que le broutement du bétail dans la steppe de la région intramontagnarde de la Colombie-Britannique a des effets significatifs sur les milieux de prairie et les communautés d'oiseaux nichant au sol qui y sont associées. Nous avons testé les hypothèses suivantes : 1) Est-il possible de discriminer les sites broutés des sites non broutés à partir de leur communauté végétale? 2) L'abondance de deux espèces d'oiseaux nichant au sol, le Bruant vespéral (*Pooecetes gramineus*) et la Sturnelle de l'Ouest (*Sturnella neglecta*), diffère-t-elle selon le type de sites (broutés vs non broutés)? 3) Les variables relatives à la végétation qui diffèrent entre les sites broutés et les sites non broutés peuvent-elles servir à prévoir l'abondance des deux espèces d'oiseaux à une échelle fine? Les sites broutés ont été faciles à distinguer des sites qui n'avaient pas été broutés depuis plus de 30 ans, d'après la structure et la composition de leur communauté végétale. Toutefois, des catégories de broutement plus détaillées n'ont pas pu être déterminées à partir des caractéristiques végétales. Bien que le broutement ait des effets sur la structure et la composition végétale, nous n'avons pas trouvé de différences significatives dans l'abondance du Bruant vespéral et celle de la Sturnelle de l'Ouest entre les sites broutés et non broutés. Toutefois, selon la tendance que nous avons détectée, l'abondance des deux espèces était supérieure à l'échelle fine des parcelles (station

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d’écoute à rayon de 100 m) ayant moins de sol nu et plus de végétation haute. La proportion de sol à nu était moins grande dans les parcelles broutées, tandis que la végétation était plus haute sur les parcelles non broutées. Dans l’ensemble, nos résultats indiquent que le broutement à faible intensité modifie les milieux de prairie et que ces changements ont des effets tant positifs que négatifs sur le Bruant vespéral et la Sturnelle de l’Ouest, ce qui fait qu’à grande échelle, l’abondance de ces deux espèces ne présente aucun changement net.

Key Words: *grassland birds, grazing effects, Pooecetes gramineus, Sturnella neglecta, Vesper Sparrow, Western Meadowlark*

INTRODUCTION

North American grassland birds have been declining at a rate greater than that of any other bird group (Peterjohn and Sauer 1999, Vickery et al. 1999, Sauer et al. 2008). Habitat loss and degradation resulting from human land use have been the primary factors identified in causing the decline (Brennan and Kuvlesky 2005). Livestock grazing is one of the principal land uses in grasslands and can alter the composition, structure, and functionality of grassland habitats (Bock et al. 1993, Fleischner 1994). Several studies have found that the habitat changes associated with livestock grazing have affected grassland bird populations (reviewed in Bock et al. 1993 and Saab et al. 1995, Fondell and Ball 2004, Sutter and Richison 2005). The nature and severity of the effects of grazing on grassland birds and their habitats depend largely on the intensity, i.e., stocking rates, timing, and duration of the grazing. When the density of grazers is low, grazing can benefit grassland ecosystems by creating a patchwork of community types that support high levels of biodiversity (Fuhlendorf et al. 2006, Derner et al. 2009). However, when livestock stocking rates are high, grazing can cause uniform changes in the composition and structure of vegetation communities (Fleischner 1994). Spring and summer grazing are believed to impose greater shifts in plant species composition than grazing during the fall or winter (Mack and Thompson 1982, Bock et al. 1993, Vermeire et al. 2008). Similarly, plants are less likely to recover from the repeated defoliation associated with prolonged grazing than from a single defoliation associated with a short-term grazing regime (Kimball and Schiffman 2003).

Grassland habitats in western North America range from the tallgrass prairies in the east, through to mid-height mixed grass steppe in the central plains, and shortgrass steppe in the Intermountain region of the west (Bock et al. 1993). Following the Pleistocene, bison were most prevalent in the tallgrass prairies, and are believed to have been almost entirely absent within the shortgrass steppe of the Intermountain region (Mack and Thompson 1982). It is hypothesized that, because the shortgrass grasslands of the Intermountain region evolved in the absence of large herds of bison, communities in this region became dominated by perennial bunchgrasses that are poorly equipped to withstand sustained grazing pressure (Mack and Thompson 1982, Milchunas et al. 1988). While native ungulate grazers such as elk (*Cervus elaphus*) were historically abundant in the shortgrass steppe, they ranged more broadly and thus exerted more diffuse grazing pressure than bison and cattle, providing less selective pressure for resiliency against grazing (Painter 1995, Kimball and Schiffman 2003). Following the introduction of cattle, Intermountain grassland communities have experienced loss of biological soil crusts, i.e., biocrust, reduction in cover of perennial grasses and forbs, and increases in the cover of shrubs and non-native grasses and forbs (Mack and Thompson 1982, Bock et al. 1993, Gayton 2003). Given these dramatic changes in vegetation structure and composition following the introduction of cattle in the Intermountain region, grazing is expected to significantly affect native bird species occupying these rangelands.

Saab et al. (1995) conducted a meta-analysis of 31 studies that surveyed birds within grazed and ungrazed habitats in shrubsteppe and grassland steppe ecosystems in the Western United States, and found that 9 of 13 ground-nesting species surveyed trended toward lower abundance in grazed versus ungrazed habitats. Ground-nesting birds are likely to be most affected by grazing because the vegetation features that they rely on for nest substrate, nest concealment, and foliar invertebrate food sources are all potentially altered by the presence of livestock (Sutter and Richison 2005, Walsberg 2005). Ground-nesting birds are expected to be similarly affected by grazing at the northern extent of the Intermountain region in British Columbia. However, few studies have been conducted at the northern edge of the region. A study by Krannitz and Rohner (2000) in the sagebrush-dominated South Okanagan region of British Columbia found no direct effects of grazing history on two species of ground-nesting birds, Vesper Sparrows (*Pooecetes gramineus*), and Western Meadowlarks (*Sturnella neglecta*), but no studies have been conducted within the grass-dominated Cariboo-Chilcotin region further north. We therefore examined the response of two common ground-nesting birds, Vesper Sparrows and Western Meadowlarks, to habitat changes caused by cattle grazing in the Cariboo-Chilcotin region of British Columbia. We first quantified differences in vegetation structure and composition between plots with different grazing histories to identify characteristic changes in vegetation communities associated with grazing. We then examined whether the abundance of the two species differed between plots characterized by different grazing histories. Finally, we assessed the vegetation features found to characterize plots with different grazing histories as individual and combined predictors of the abundance of Vesper Sparrows and Western Meadowlarks at a finer (100 m radius point count station) scale. This allowed us to identify the fine-scale drivers of larger scale patterns of abundance in the two species.

METHODS

Field methods

Study area

This study was conducted in the grasslands of the Cariboo-Chilcotin region of British Columbia, which are sparsely populated and used primarily for domestic livestock production. Small herds of native ungulate grazers such as mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*) are also present in the study area. Average cattle stocking rates in this region are estimated at 1.2 AUM/ha (animal unit months per hectare), and do not exceed 3.3 AUM/ha (C. Mumford and W. Hayes-van Vliet, *personal communication*). The timing and duration of grazing in the region are variable. This study was conducted at three sites, all less than 70 km apart. Junction Sheep Range Provincial Park (JSRPP) is on a plateau above the junction of the Chilcotin and Fraser Rivers, Churn Creek Protected Area (CCPA) is on a western plateau above the Fraser River, and the OK Ranch (OKR) is on an eastern plateau above the Fraser River. We established between one and four study plots at each site that varied in current and historical grazing (Table 1). Plot-specific information on stocking rates and the timing and duration of grazing was not available. Instead, the relative intensity of grazing in currently grazed areas was inferred based on a visual assessment of the predominant seral stage, i.e., ecological condition. Visual identification of seral stages was performed under the guidance of a provincial range ecologist. Early seral stages were associated with the highest grazing intensity, mixed seral stages were associated with moderate grazing intensity, and late seral stages were associated with the lowest intensity grazing. Although this limits the degree to which the results of this study can be applied to specific grazing systems and extrapolated to other areas, it still provides a useful indication of how current grazing practices affect bird populations in the area, and determines whether grazing must be more carefully managed. Four study plots occurred at OKR (Table 1). Two plots were grazed at a higher intensity (RT and DF), a third was grazed at a moderate intensity (BBS), and a fourth had been ungrazed for 15 years (RTC). Three study plots occurred at CCPA. One plot was grazed at a higher intensity (WCF), a second was grazed at a moderate intensity (LCM), and a third plot was grazed at a lower intensity (GP). Because JSRPP has not been grazed by cattle in over 30 years, it acts as an ungrazed reference.

Study species

Both Vesper Sparrows and Western Meadowlarks are short-distance migrants that inhabit grassland habitats during both wintering and breeding periods (Jones and Cornely 2002, Davis and Lanyon 2008). Both species build their nests on the ground, and establish and defend multipurpose territories (Jones and Cornely 2002, Davis and Lanyon 2008). Breeding populations of both species have been declining throughout their range with significant annual rates of decline of -1.0 and -0.9% for Vesper Sparrows and Western Meadowlarks, respectively,

Table 1. A description of the sites, plots, and point count stations used to study the associations between grazing history, vegetation patterns, and Vesper Sparrow and Western Meadowlark abundance within the Cariboo-Chilcotin region of British Columbia.

Site	Plot	Code	Area (ha)	Grazing history	# grassland point count stations (100 m radius)
OK Ranch	Big Bar South	BBS	82	Grazed moderate intensity	14
	Race Track	RT	79	Grazed high intensity	14
	Race Track Control	RTC	77	Ungrazed for 15 yrs	14
	Dry Farm	DF	135	Grazed high intensity	23
Churn Creek Protected Area	Golden Plateau	GP	78	Grazed low intensity	14
	West Churn Flats	WCF	91	Grazed high intensity	15
	Little Churn Mountain	LCM	87	Grazed moderate intensity	16
Junction Sheep Range Provincial Park		JSR	206	Ungrazed for >30 yrs (reference)	34
Total			834		144

from 1966-2007 (Sauer et al. 2008). Within British Columbia, the rate of decline has been less severe for Vesper Sparrows (-0.6%, non-significant), but more severe for Western Meadowlarks (-1.5%, significant; Sauer et al. 2008). Habitat loss and degradation due to grazing is one factor that is commonly blamed for the decline of grassland birds (reviewed in Bock et al. 1993 and Saab et al. 1995, Fondell and Ball 2004, Sutter and Richison 2005). Tree encroachment due to long-term fire suppression is an additional factor that is limiting habitat availability in the area, but that is not being explicitly examined in this study. While these two species are widespread grassland generalists, and are potentially less vulnerable to grazing effects than are rarer or endemic species, they are two of only four commonly occurring grassland-nesting species present in the region. Savannah Sparrows (*Passerculus sandwichensis*) and Horned Larks (*Eromophila alpestris)* are also present, though at significantly lower densities. The influence of different landscape uses on population trends has also been identified as a research priority for both species (Jones and Cornely 2002, Davis and Lanyon 2008).

Bird surveys

In 2007, we established 278 point count stations in a grid pattern, 250 m apart, across the eight plots. Of these 278, 144 stations were classed as ‘grassland’, with less than 50% tree cover, and were therefore used for this study. Vesper Sparrows and Western Meadowlarks were surveyed at the point count stations in 2007 and 2008. Bird surveys were conducted at point count stations according to standard point count protocols (Ralph et al. 1993, British Columbia Ministry of Environment 1999). Three rounds of point counts were conducted at each site from mid-May until mid-July.

Point counts were conducted between 5:00 and 10:00 am, or occasionally until 11:00 am if the day was cool and birds were still singing after 10:00 am. In rainy or windy weather, point counts were cancelled or delayed until weather improved. Point counts at each station were conducted for six minutes. All Vesper Sparrows and Western Meadowlarks seen or heard within a 100 m radius were recorded. Because all three survey rounds were conducted within the breeding season, when any birds detected should have been territory-holders, we used the round with the maximum number of birds detected for analysis, assuming that the maximum was the best representation of the actual number of breeding birds present.

Vegetation surveys

Vegetation at each point count station was surveyed once in either 2007 or 2008. Vegetation surveys were not conducted in both years due to time constraints. Because we did not expect significant changes in the relationships between vegetation and bird abundance between the two years, we opted to maintain spatial replication rather than reduce the number of stations surveyed in order to maintain temporal replication. The height of herbaceous growth was measured at the centre and at 1, 3, 5, and 10 m from the centre of the station in the four cardinal directions. Daubenmire surveys were completed in eight locations per point count station, two per cardinal direction at 10 m and 50 m from center of point count stations. The percent cover of all plant species, as well as ground cover within four categories, bare ground, biocrust, grass, and forbs, was estimated within a 20 cm by 50 cm frame (Daubenmire 1959). Biocrust consists of lichens and mosses and plays an important role in moisture retention (Bowker et al. 2008).

Statistical analysis

Part 1: Grazing category discrimination on the basis of vegetation characteristics

We first determined whether point count stations with five different grazing histories, currently grazed - high, moderate, and low, ungrazed for 15 years, and ungrazed for >30 years, could be correctly distinguished on the basis of their vegetation characteristics using discriminant function analyses (DFAs). We then asked whether a simplified two-category classification scheme, grazed and ungrazed for >30 years, would result in better discrimination. In both cases, separate DFAs were used to assess whether plots could be discriminated based on 1) ‘general cover’, i.e., percentage of cover of grass, forb, bare ground, and biocrust, 2) ‘structure and composition’, i.e., average height, grass diversity, and forb diversity, and 3) ‘cover of species known to be affected by grazing’, i.e., percentage of cover of species known to increase with grazing, or ‘increasers’, and species known to decrease with grazing, or ‘decreasers’ (Gayton 2003). Jackknifed classification matrices were produced to demonstrate the percentage of plots that were correctly allocated to their true grazing category, using a leave-one-out classification method. All DFAs were performed using Systat 12 (Systat Software, Inc., San Jose, California, USA).

Part 2: Response of Vesper Sparrows and Western Meadowlarks to grazing

We examined whether abundance of Vesper Sparrows and Western Meadowlarks at point count stations could be explained by the complex grazing history at the stations, currently grazed – high, moderate, and low, ungrazed for 15 years, and ungrazed for >30 years, or by a simplified grazing history, grazed and ungrazed for >30 yrs, using an information-theoretic approach. We evaluated the relative support for the two grazing history candidate models and a null, or no predictors, model. Generalized linear models with a Poisson distribution and a log link (proc GENMOD, SAS 9.2) were used to generate AIC$_c$ estimates corresponding to each hypothesis (SAS Institute Inc., Cary, North Carolina, USA). We confirmed that the Poisson distribution was appropriate by calculating the variance inflation factor ($\hat{c}$, or deviance/df) of the global model in each candidate set, and confirming that the data was not over inflated (Burnham and Anderson 2002). The two years were analyzed separately so that each point count station was in an analysis only once, to avoid pseudoreplication. AIC values corrected for small sample sizes (AIC$_c$) were used in all analyses (Burnham and Anderson 2002). AIC$_c$ weights (AICW), were used to assess the relative support for each of the models. Pseudo (Nagelkerke) *r*-squared estimates were used as an additional measure to approximate the proportion of variability in the data that was accounted for by each model. Summed AICWs and AIC weighted parameter estimates (PE) and their associated unconditional standard errors (SE$_u$) were also computed to assess the support for and relative effects of the parameters present in the best-supported models (Burnham and Anderson 2002).

Part 3: Response of Vesper Sparrows and Western Meadowlarks to vegetation characteristics

We used an information-theoretic approach to assess whether vegetation characteristics reflecting 1) general cover, 2) structure and composition, and 3) species known to be affected by grazing predicted Vesper Sparrow and Western Meadowlark abundance at point count stations. Separate candidate model sets were developed for each of the three vegetation groups. Each candidate set included a null model and models with all combinations of the vegetation variables. Because none of the variables included within a single analysis were correlated ($r < 0.4$), each combination represented a biologically realistic hypothesis. Separate analyses did not need to be conducted for the two years because each point count was only in the analysis once. Vegetation sampling and bird surveys occurred together in only one of the two years. Year was not included in the models because we were interested in consistent vegetation effects only. Also, because the vegetation surveys on each plot were not split evenly between the two years, i.e., some plots were sampled disproportionately in one of the two years, the addition of a year term would have incorporated site effects. Generalized linear models (proc GENMOD) run with Poisson distributions and log links were used to generate AIC_c estimates for each model.

RESULTS

Part 1: Grazing category discrimination on the basis of vegetation

The percentage of plots correctly classified according to the five grazing histories, currently grazed – high, moderate, and low, ungrazed for 15 years, and ungrazed for >30 years, was low (<51%) for all three analyses, indicating that vegetation cover could not be used to distinguish between plots with a range of grazing histories (Table 2). Successful discrimination could only be achieved using a simplified grazing history, grazed and ungrazed for >30 years (Table 3).

General cover

Seventy-two percent of the plots were correctly classified into the grazed and ungrazed categories using percent cover of grasses, forbs, bare ground, and biocrust. However, forbs, bare ground, and biocrust differed most between the two categories (Table 3). Grazed plots had 35% less bare ground and 29% less biocrust than ungrazed plots and 74% greater cover of forbs (Table 3).

Structure and composition

Sixty-eight percent of the plots were correctly classified into the grazed and ungrazed categories using vegetation height, grass diversity, and forb diversity. However, height differed most between the two categories (Table 3). Grazed plots had 24% lower average vegetation height than ungrazed plots (Table 3).

Cover of species known to be affected by grazing

Eighty-five percent of the plots were correctly classified into the grazed and ungrazed categories using percent cover of ‘increaser’ and ‘decreaser’ species. Grazed plots had 46% lower cover of ‘decreaser’ species and 400% higher cover of ‘increaser’ species than ungrazed plots (Table 3).

Part 2: Response of Vesper Sparrows and Western Meadowlarks to grazing

For Vesper Sparrows, the grazing history models did not predict abundance in 2007 significantly better than the null model (Table 4). There were no clear differences in abundance between plots with different grazing histories (PEs ± SE_us bounded zero for all history classes; Fig. 1a). For Western Meadowlarks, the ‘complex grazing history’ model was the best predictor of abundance in 2007, indicating that there were differences in abundance between plots with five different grazing histories (Table 5). However, grazing history was clearly not the factor that was driving the differences in abundance between the plots (Fig. 1b). Abundance was higher at the ungrazed reference than at the currently grazed – moderate (PE: -1.63 ± 0.63 [SE_u]) and low intensity plots with no Meadowlarks present, but similar between the reference and the currently grazed – higher intensity (PE: -0.14 ± 0.32 [SE_u]) and ungrazed for 15 yrs (PE: 0.08 ± 0.42 [SE_u]) plots. The null model was the best predictor of abundance in 2008 for both species, indicating that there were no differences in Vesper Sparrow or Western Meadowlark abundance between plots with different grazing histories (Tables 4 and 5, Fig. 1a,b). The combined results from 2007 and 2008 indicate that there was no consistent effect of

Table 2. Plot means and 95% confidence intervals for the 11 vegetation variables included in the discriminant function analyses distinguishing between plots with five different grazing histories (n = 144).

	Grazed high		Grazed moderate		Grazed low		Ungrazed 15 yrs		Ungrazed > 30 yrs	
	Mean	*95% C.I.*	*Mean*	*95% C.I.*	*Mean*	*95% C.I.*	*Mean*	*95% C.I.*	*Mean*	*95% C.I.*
general % cover										
% cover bare	10.94	8.33 - 13.60	10.41	7.40 - 13.40	12.85	9.86 - 15.80	1.90	0.76 - 3.04	15.74	11.60 - 19.80
% cover forb	15.21	12.90 - 17.60	21.89	17.70 - 26.10	23.27	19.60 - 26.90	22.88	18.96 - 26.79	10.96	9.55 - 12.40
% cover grass	31.00	28.20 - 33.30	27.61	24.80 - 30.40	19.71	15.0 - 23.60	28.82	25.08 - 32.56	27.68	25.30 - 30.00
% cover biocrust	19.29	15.50 - 23.10	16.43	12.50 - 20.30	40.54	33.70 - 47.40	18.59	9.34 - 27.84	29.60	26.10 - 33.10
structure and composition										
height	10.90	9.43 - 12.40	13.82	11.40 - 16.20	9.07	7.69 - 10.50	20.67	17.09 - 24.25	16.76	15.10 - 18.40
grass diversity	1.43	1.07 - 1.79	1.36	1.25 - 1.47	0.97	0.82 - 1.12	1.05	0.87 - 1.24	1.01	0.92 - 1.91
forb diversity	1.60	1.45 - 1.75	1.73	1.59 - 1.87	1.16	0.93 - 1.38	2.00	1.86 - 2.13	1.77	1.62 - 1.91
% cover of known grazing-affected species										
% cover increasers	24.91	20.60 - 29.20	25.83	21.80 - 29.80	22.56	18.60 - 26.5	28.01	21.44 - 34.57	5.21	3.91 - 6.51
% cover decreasers	7.92	5.70 - 10.10	7.67	5.17 - 10.20	7.10	5.04 - 9.15	9.85	6.94 - 12.76	14.93	12.70 - 17.10

grazing history on Vesper Sparrow or Western Meadowlark abundance at the plot level, and that plot-level variation in abundance was driven by site rather than grazing effects.

Part 3: Response of Vesper Sparrows and Western Meadowlarks to vegetation characteristics

General cover

Bare ground was the best predictor of both Vesper Sparrow and Western Meadowlark abundance (Tables 6 and 7), with a summed AICW of over 0.9 for both species and parameter estimates of -0.003 ± 0.007 (SE_u) and -0.014 ± 0.017 (SE_u) for Vesper Sparrows and Western Meadowlarks, respectively. There was a weak indication that the abundance of both Vesper Sparrows and Western Meadowlarks was higher where there was less bare ground (Fig. 2a,b).

Structure and composition

Vegetation height was the best predictor of both Vesper Sparrow and Western Meadowlark abundance (Tables 6 and 7), with a summed AICW of over 0.9 for both species and parameter estimates of 0.006 ± 0.010 (SE_u) and 0.009 ± 0.022 (SE_u) for Vesper Sparrows and Western Meadowlarks, respectively. There was a weak indication that the abundance of both Vesper Sparrows and Western Meadowlarks was higher where vegetation was taller (Fig. 2c,d).

Cover of species known to be affected by grazing

Neither the cover of species known to decrease with grazing nor the cover of species known to increase with grazing predicted the abundance of Vesper

Table 3. Plot means and 95% confidence intervals for the 11 vegetation variables included in the discriminant function analyses distinguishing grazed plots from the ungrazed for >30 years reference (n = 144).

	Grazed		Ungrazed	
	Mean	*95% C.I.*	*Mean*	*95% C.I.*
general % cover				
% cover bare	10.25	8.59 - 11.92	15.74	11.60 - 19.80
% cover forb	19.03	17.20 - 20.88	10.96	9.55 - 12.40
% cover grass	28.25	26.60 - 29.89	27.68	25.30 - 30.00
% cover biocrust	21.14	18.30 - 24.03	29.60	26.10 - 33.10
structure and composition				
height	12.76	11.50 - 14.00	16.76	15.10 - 18.40
grass diversity	1.30	1.13 - 1.48	1.01	0.92 - 1.91
forb diversity	1.63	1.53 - 1.72	1.77	1.62 - 1.91
% cover of known grazing-affected species				
% cover increasers	25.26	22.80 - 27.74	5.21	3.91 - 6.51
% cover decreasers	8.00	6.69 - 9.31	14.93	12.70 - 17.10

Sparrow or Western Meadowlark (Tables 6 and 7). Both variables had summed AICWs of less than 0.6 and weak parameter estimates with SE_us that bounded zero.

DISCUSSION

Our study is one of the first to evaluate grazing effects on grassland birds in the Intermountain region of British Columbia. We found that, although grazing was associated with significant changes in the structure and composition of vegetation communities, there were no differences in the abundance of Vesper Sparrows and Western Meadowlarks in grazed and ungrazed areas. Both species showed fine-scale selection for two vegetation characteristics that were affected by grazing, but neither of the two relationships was strong, and one of the selected variables was positively affected by grazing whereas the other was negatively affected by grazing, resulting in no net difference in the use of grazed versus ungrazed habitats by the two species.

Effects of grazing on vegetation structure and composition

The dramatic differences in vegetation structure and composition that we found between grazed and ungrazed sites were largely in keeping with what has been reported in other studies from the Intermountain region (Mack and Thompson 1982, Bock et al. 1993, Gayton 2003). We confirmed that species identified as ‘increasers’ or ‘decreasers’ in provincial range management guidelines (Gayton 2003) actually demonstrated predicted associations

Table 4. AIC ranking of sets of candidate models that predict Vesper Sparrow abundance as a function of plot-level grazing history. Complex grazing history included five history classes (currently grazed at a high, moderate, and low intensity, ungrazed for 15 yrs, and ungrazed for >30 yrs), and simplified grazing history included two classes (grazed, and ungrazed for >30 yrs). Listed are models that received strong support (ΔAICc < 2.0), plus the null models.

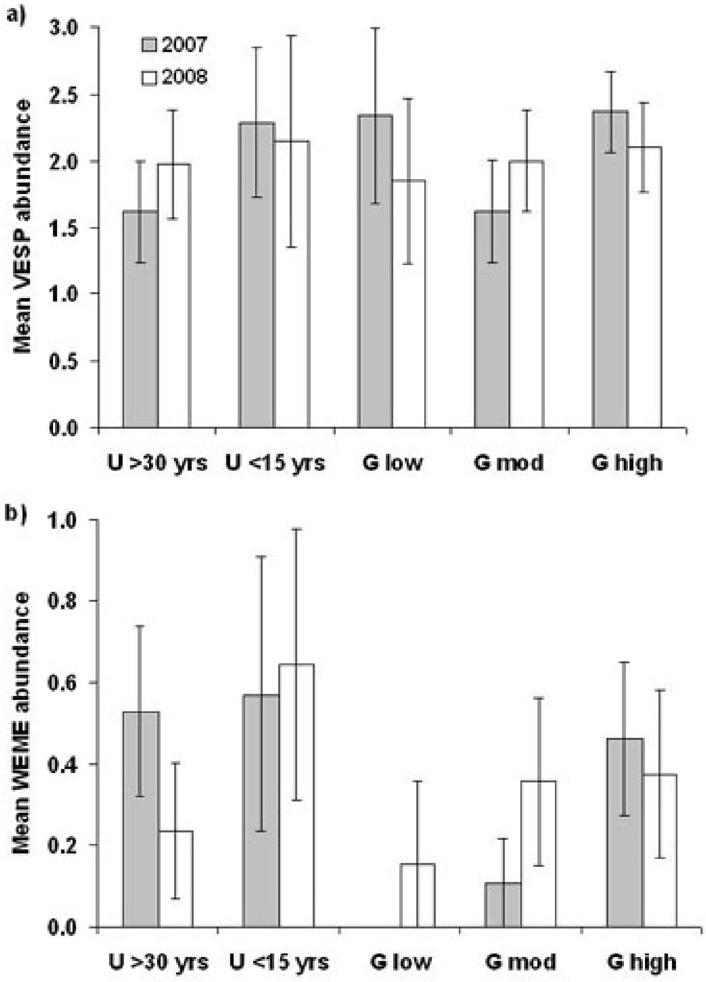
Model	$N^{\dagger}$	$K^{\ddagger}$	$\mathrm{AIC}_c^{\S}$	$\Delta\mathrm{AIC}_c^{|}$	$\mathrm{AICW}^{\P}$	Pseudo $r^{2\#}$
2007						
1. vesp = simple grazing history	144	3	456.51	0.00	0.49	0.03
2. vesp = complex grazing history	144	6	457.39	0.88	0.31	0.07
3. vesp = null	144	2	458.31	1.80	0.20	0.00
2008						
1. vesp = null	133	2	423.14	0.00	0.73	0.00
2. vesp = simple grazing history	133	3	425.19	2.05	0.26	0.00
3. vesp = complex grazing history	133	6	431.32	8.18	0.01	0.00

[†] The sample size.
[‡] The number of estimated parameters in the model including the variance.
[§] A measure of the level of fit of the data to the model weighted by the number of variables in the model, corrected for small sample sizes.
[|] The difference between the AIC_c of each model and that of the most parsimonious model.
[¶] The likelihood of the model given the data, relative to the other models in the candidate set .
[#] The proportion of variability in the data that is accounted for by the model. Pseudo r^2 = Nagelkerke's r^2.

with grazing in our study area; cover of species in the ‘increaser’ category was higher in the grazed plots, and cover of ‘decreasers’ was higher in the ungrazed plot. Mack and Thompson (1982) and Yeo (2005) also reported decreases in cover of native bunchgrass species and increases in cover of rhizomatous Kentucky bluegrass (*Poa pratensis*), which were key components of our decreaser and increaser categories, respectively. Grazing also reduced the average height of vegetation, and the amount of biocrust and bare ground, and increased the overall forb cover. Height reduction is a common effect of grazing (e.g., Page et al. 1978, Fuhlendorf et al. 2006), and Mack and Thompson (1982) and Yeo (2005) reported decreases in cover of biocrust in grazed areas. Our finding that grazing resulted in less bare ground was somewhat counterintuitive in that cattle break up the biocrust, creating an expectation that grazed sites would have more bare ground than ungrazed sites (Mack and Thompson 1982, Yeo 2005, Bowker et al. 2008). However, bare ground exposed by cattle is rapidly colonized by early-seral grass and forb species, e.g., the mat-forming Kentucky bluegrass, when grazing intensity is low enough to allow it, resulting in less bare ground on the grazed than the ungrazed plots.

Despite the significant changes in vegetation that we found in association with grazing, plots with five different grazing histories could not be discriminated on the basis of vegetation characteristics. The poor discrimination between the more detailed set of grazing histories could be a consequence of the great spatial heterogeneity in the intensity of grazing within our grazed sites. The relatively low number of cattle present on the grazed

Fig. 1. Mean abundance by point count of a) Vesper Sparrows (VESP) and b) Western Meadowlarks (WEME) in five grazing categories (currently grazed at a high, moderate, and low intensity, ungrazed for 15 yrs, and ungrazed for >30 yrs). Error bars are 95% confidence intervals. (2007: n = 144, 2008: n = 133.)



sites, less than 3.3 AUM/ha, and the variability of the terrain allowed some areas to nearly escape grazing effects, whereas others were targeted by cattle and experienced dramatic changes in vegetation. The finer scale of the point count station vegetation surveys allowed that heterogeneity to be captured, resulting in point count station means that varied widely within grazing categories, and making accurate designation of the stations to their grazing categories, which were assigned at a plot level, impossible. No other studies from the Intermountain region examined grazing effects across a similar range of history classes.

Effects of vegetation structure and composition on grassland bird numbers

We found evidence for associations between individual vegetation variables and bird abundance at the point count scale for both Vesper Sparrows and Western Meadowlarks. Both species showed

Table 5. AIC ranking of sets of candidate models that predict Western Meadowlark (WEME) abundance as a function of plot-level grazing history. Complex grazing history included five history classes (currently grazed at a high, moderate, and low intensity, ungrazed for 15 yrs, and ungrazed for >30 yrs), and simplified grazing history included two classes (grazed, and ungrazed for >30 yrs). Listed are models that received strong support (ΔAICc < 2.0), plus the null models.

Model	N[†]	K[‡]	AIC$_c$[§]	ΔAIC$_c$[|]	AICW[¶]	Pseudo r^2[#]
2007						
1. weme = complex grazing category	144	5	223.14	0.00	0.86	0.10
2. weme = simple grazing category	144	3	227.70	4.57	0.09	0.03
3. weme = null	144	2	228.51	5.37	0.06	0.00
2008						
1. weme = null	133	2	201.33	0.00	0.54	0.00
2. weme = simple grazing category	133	3	201.87	0.54	0.41	0.01
3. weme = complex grazing category	133	5	206.05	4.72	0.05	0.02

[†] The sample size.
[‡] The number of estimated parameters in the model including the variance.
[§] A measure of the level of fit of the data to the model weighted by the number of variables in the model, corrected for small sample sizes.
[|] The difference between the AIC$_c$ of each model and that of the most parsimonious model.
[¶] The likelihood of the model given the data, relative to the other models in the candidate set .
[#] The proportion of variability in the data that is accounted for by the model. Pseudo r^2 = Nagelkerke's r^2.

weak associations with two habitat variables: negative with percent cover of bare ground and positive with average vegetation height. Both Vesper Sparrows and Western Meadowlarks are ground-nesting species, which rely on general vegetative cover as well as vertical structure for nest concealment (Sutter and Richison 2005, Walsberg 2005). Reduced bare ground is correlated with increased general vegetative cover, which, along with general vegetative height, could increase both the concealment of nests, and the potential food available to feed nestlings (Sutter and Richison 2005, Walsberg 2005, West and Messmer 2006, Dennis et al. 2008, Zalik and Strong 2008). Higher plants of some of the more robust species are also used as song perches by both Vesper Sparrows and Western Meadowlarks.

Effects of grazing on Vesper Sparrow and Western Meadowlark numbers

While grazing caused significant changes in vegetation structure and composition, and both bird species demonstrated fine-scale selection for vegetation characteristics that were affected by grazing, differences in the abundance of the two species between plots were not related to grazing history. One possible explanation for this finding is that fine-scale habitat heterogeneity allowed birds to find suitable patches even within areas that had been partially altered by grazing. A second explanation is that the habitat conditions in grazed areas were within the range of acceptable conditions for these two generalist species and the habitat changes caused by grazing would have needed to be more dramatic to influence Western Meadowlark

Table 6. AIC ranking of three sets of candidate models that predict Vesper Sparrow (VESP) abundance at point counts as a function of three sets of vegetation variables. Listed are models that received strong support (ΔAICc < 2.0), plus the null models.

Model	*N*[†]	*K*[‡]	AIC$_c$[§]	ΔAIC$_c$[|]	AICW[¶]	Pseudo r^2[#]
VESP = general cover (16 models)						
1. vesp = bare	135	3	432.15	0.00	0.39	0.18
2. vesp = grass + bare	135	4	433.92	1.76	0.16	0.18
3. vesp = forb + bare	135	4	434.23	2.07	0.14	0.18
4. vesp = bare + bio	135	4	434.28	2.12	0.13	0.18
5. vesp = grass + forb + bare	135	5	435.91	3.75	0.06	0.18
6. vesp = grass + bare + bio	135	5	436.07	3.89	0.05	0.18
11. vesp = null	135	2	455.76	23.60	0.00	0.00
VESP = structure and composition (8 models)						
1. vesp = height	140	3	448.05	0.00	0.41	0.07
2. vesp = height + grass diversity	140	4	449.07	1.02	0.25	0.08
3. vesp = height + forb diversity	140	4	449.53	1.48	0.20	0.07
4. vesp = height + forb diversity + grass diversity	140	5	450.53	2.48	0.12	0.08
5. vesp = null	140	2	455.76	7.71	0.01	0.00
VESP = grazing-affected species (4 models)						
1. vesp = null	136	2	434.04	0.00	0.39	0.00
2. vesp = decreasers	136	3	435.32	1.28	0.21	0.01
3. vesp = increasers	136	3	435.34	1.29	0.21	0.01
4. vesp = increasers + decreasers	136	4	435.47	1.43	0.19	0.02

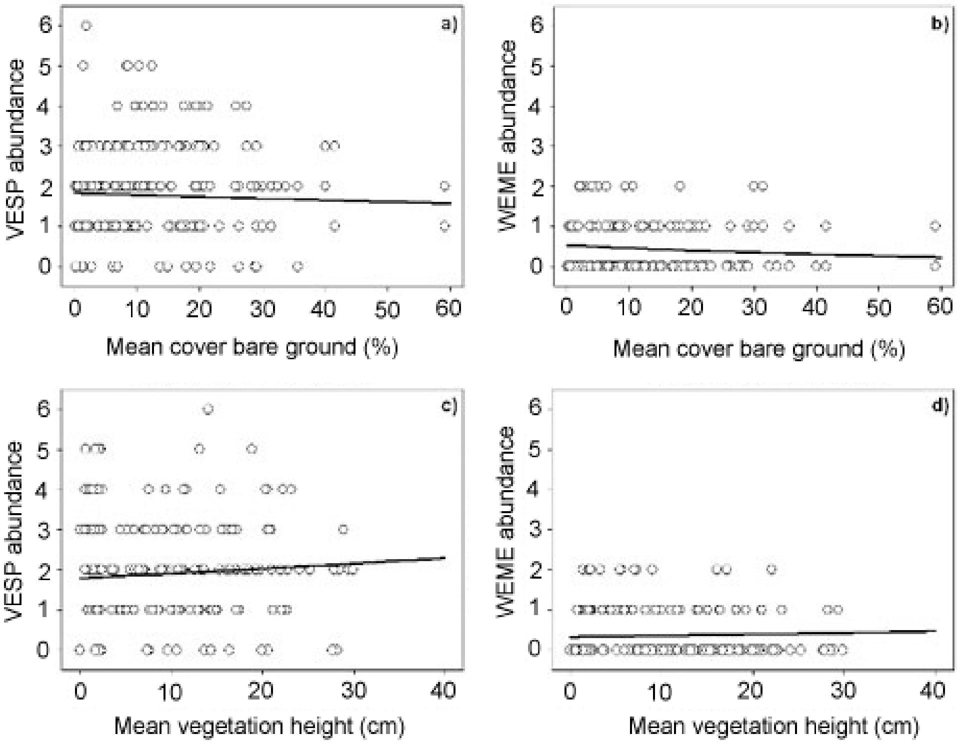
[†] The sample size.
[‡] The number of estimated parameters in the model including the variance.
[§] A measure of the level of fit of the data to the model weighted by the number of variables in the model, corrected for small sample sizes.
[|] The difference between the AIC$_c$ of each model and that of the most parsimonious model.
[¶] The likelihood of the model given the data, relative to the other models in the candidate set .
[#] The proportion of variability in the data that is accounted for by the model. Pseudo r^2 = Nagelkerke's r^2.

Table 7. AIC ranking of three sets of candidate models that predict Western Meadowlark (WEME) abundance at point counts as a function of three sets of vegetation variables. Listed are models that received strong support (ΔAICc < 2.0), plus the null models.

Model	*N*[†]	*K*[‡]	AIC$_c$[§]	ΔAIC$_c$[|]	AICW[¶]	Pseudo r^2[#]
WEME = general cover (16 models)						
1. weme = bare	135	3	225.62	0.00	0.38	0.11
2. weme = bare + bio	135	4	227.27	1.64	0.17	0.12
3. weme = grass + bare	135	4	227.61	1.98	0.14	0.12
4. weme = forb + bare	135	4	227.74	2.11	0.13	0.11
5. weme = grass + bare + bio	135	5	229.34	3.72	0.06	0.12
6. weme = forb + bare + bio	135	5	229.40	3.78	0.06	0.11
11. weme = null	135	2	236.81	11.19	0.00	0.00
WEME = structure and composition (8 models)						
1. weme = height	140	3	227.20	0.00	0.42	0.10
2. weme = height + forb diversity	140	4	227.86	0.66	0.30	0.11
3. weme = height + grass diversity	140	4	229.27	2.07	0.15	0.10
4. weme = height + forb diversity + grass diversity	140	5	229.95	2.75	0.11	0.11
8. weme = null	140	2	236.81	9.61	0.00	0.00
WEME = grazing-affected species (4 models)						
1. weme = decreasers	136	3	227.31	0.00	0.32	0.02
2. weme = null	136	2	227.54	0.23	0.29	0.00
3. weme = increasers + decreasers	136	4	227.63	0.32	0.27	0.04
3. weme = increasers	136	3	229.31	2.01	0.12	0.00

[†] The sample size.
[‡] The number of estimated parameters in the model including the variance.
[§] A measure of the level of fit of the data to the model weighted by the number of variables in the model, corrected for small sample sizes.
[|] The difference between the AIC$_c$ of each model and that of the most parsimonious model.
[¶] The likelihood of the model given the data, relative to the other models in the candidate set .
[#] The proportion of variability in the data that is accounted for by the model. Pseudo r^2 = Nagelkerke's r^2.

Fig. 2. Predicted (lines) and actual (dots) associations between Vesper Sparrow (VESP) and Western Meadowlark (WEME) abundance at point counts and vegetation variables in the general cover (a,b), and structure and composition (c,d) AIC analyses. Predicted trends were drawn using the AIC weighted (i.e., model averaged) parameter estimates, constant (mean) values for weakly supported vegetation variables, and a range of values for the best-supported variable. (n = 143.)



or Vesper Sparrow abundance. Finally, a third explanation for the similarity in the abundance of the two species between grazed and ungrazed plots is that the mixed response to grazing-affected vegetation variables that we found at a fine scale resulted in no net influence of grazing at a broad scale. The declining population trends for these two species in British Columbia may be driven by steeper declines in areas to the south of this study region where, in addition to cattle grazing, habitat has been lost to development and agricultural intensification.

CONCLUSION

Our results agree with those of many of the other studies that have examined the effects of grazing on ground-nesting grassland birds in the Intermountain region in the Western United States (reviewed in Bock et al. 1993 and Saab et al. 1995) and British Columbia (Krannitz and Rohner 2000). There are several potential reasons why livestock grazing often does not exert a strong influence on ground-nesting grassland bird numbers despite the significant changes to the vegetation community it causes. The first, as indicated by this study, is that grazing can cause both beneficial and detrimental changes in vegetation communities that result in no net difference between grazed and ungrazed habitats from the perspective of birds.

The second potential reason grazing did not influence abundance of ground-nesting birds is that relatively low-intensity grazing maintains fine-scale habitat heterogeneity that allows birds to occupy suitable habitat even within grazed areas. Several studies have found either positive or negligible effects of low- or variable-intensity grazing on bird communities, supporting the idea that grazing can create habitat heterogeneity without broad-scale degradation (Page et al. 1978, Bock and Webb 1984, Fuhlendorf et al. 2006). Studies that have found negative effects of grazing on ground-nesting grassland birds have largely been conducted in areas with higher intensity (>7.2 AUM/ha) grazing (Fondell and Ball 2004, Sutter and Richison 2005).

The third reason, is that the ungrazed treatments in virtually all of the grazing effects studies conducted were not pristine, but were instead protected from grazing for several decades, and it is possible that the most dramatic changes in bird populations associated with grazing occurred when livestock were first introduced (Bock et al. 1993). This could mean that the population sizes at the ungrazed sites are already reduced relative to the time before domestic livestock introduction (Wiens and Dyer 1975).

The fourth reason, which could also be evidenced by this study, is that some of the most abundant ground-nesting bird species in grazed grasslands are resilient grassland generalists, with the capacity to adapt to a range of ecological conditions, and show no response to different management regimes from an abundance perspective. Other studies that have evaluated Vesper Sparrow and Western Meadowlark abundance in grazed or agriculturally converted habitats suggest that these two species are resilient from an abundance perspective (Kantrud 1981, Best and Rodenhouse 1984, Fritcher et al. 2004).

Finally, the fifth potential reason that studies have often found no significant effect of grazing on ground-nesting birds in the Intermountain region is that most studies have looked at relative abundance, which could miss effects that are evident in additional measures such as relative reproductive success, e.g., nest success and nestling condition. Although abundance measures do sometimes correlate with success (Bock and Jones 2004), there are many examples of cases where abundance does not give accurate information about the relative success of birds breeding in different habitats (Van Horne 1983). It is possible, for example, that grazed habitats are of lower quality and thus result in lower average reproductive success, but that these habitats appear to be suitable for birds even though they actually are not, i.e., ecological trap scenario (Battin 2004), or that grazed habitats are filled with younger, and thus less successful birds that are competitively excluded from the more optimal ungrazed habitats (Fretwell and Lucas 1970). Conclusions cannot be made about the population-level consequences of livestock grazing for ground-nesting birds in the Cariboo-Chilcotin region of British Columbia without an examination of the relative reproductive success of birds breeding in grazed versus ungrazed habitats. We will examine the reproductive consequences of habitat selection for ground-nesting birds in the Cariboo-Chilcotin region in a subsequent paper.

Responses to this article can be read online at:
http://www.ace-eco.org/vol5/iss1/art1/responses/

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