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Nest-site selection and productivity of Vesper Sparrows breeding in grazed habitats

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ABSTRACT. Livestock grazing in the shortgrass steppe of the Intermountain region of British Columbia may have a negative impact on ground-nesting birds, but evidence of such an impact is lacking. We examined nest-site selection and productivity of ground-nesting Vesper Sparrows (*Pooecetes gramineus*) across sites with different grazing histories. From 2006 to 2008, we monitored Vesper Sparrow nests and measured vegetation characteristics known to be affected by grazing within nest patches. We used an information-theoretic approach to test the relative importance of grazing-affected vegetation variables as predictors of nest-site selection, nest survival, and nestling condition. Vesper Sparrows selected nest sites with greater cover of late-seral grass species that decrease in occurrence in response to grazing (i.e., “decreasers”) than was available in random patches in the same territories. Daily nest survival was also lower for nests surrounded by shorter vegetation (odds ratio = 1.12). However, “decreaser” cover was not associated with either of the two indices of productivity measured (daily nest survival probability and nestling condition). In addition, vegetation height, although an important driver of success, was not linked with nest-site selection, and no vegetation-cover variable was positively associated with productivity, despite nest concealment being central to our predictions. This suggests that predation risk for nests in areas with shorter vegetation was being elevated through some factor unrelated to concealment. Our results show that grazing reduced both the availability of suitable habitat for and nesting success of Vesper Sparrows, indicating that grazing could pose a threat to population persistence at a broader scale and could potentially contribute to observed declines. Additional research is needed to determine if grazing guidelines in the Intermountain region of British Columbia should be amended, better enforced, or both to prevent regional declines in populations of ground-nesting grassland birds.

RESUMEN. **Selección del lugar de anidación y productividad en *Pooecetes gramineus* anidando en hábitats de pastoreo**

El pastoreo de ganado en pastos de estepa corta en la región inter montañosa de British Columbia pueden tener un impacto negativo sobre las aves que anidan en el suelo, pero la evidencia de este impacto es inexistente. Examinamos la selección de lugares de anidación y productividad de *Pooecetes gramineus* que anida en el suelo a través de lugares con diferentes historias de pastoreo. Entre el 2006 y el 2008 monitoreamos nidos de *Pooecetes gramineus* y medimos las características conocidas de la vegetación que son afectadas por el pastoreo entre los parches de los nidos. Usamos una aproximación de información teórica para poner a prueba la importancia relativa de las variables de la vegetación que son afectadas por el pastoreo como pronosticadores de selección del lugar de anidación, supervivencia del nido y condición del polluelo. *Pooecetes gramineus* selecciono lugares de anidación con una mayor cobertura de buenas especies de pastos que disminuyeron en frecuencia en respuesta al pastoreo (i.e., “reductores”), comparado a lo que estaba disponible en parche aleatorios en el mismo territorio. La supervivencia diaria de los nidos también fue baja para los nidos que estaban rodeados por vegetación más corta (tasa de probabilidad = 1.12). Sin embargo, los ‘reductores’ de cobertura no estuvieron asociados con ninguno de los dos indicies de medidas de productividad (la supervivencia diaria del nido y la condición del polluelo). Adicionalmente, la altura de la vegetación a pesar de que es un importante guía del éxito, no estuvo relacionada con la selección del lugar de anidación y ninguna variable de cobertura de vegetación estuvo asociada positivamente con la productividad, a pesar de que el camuflaje del nido era central a nuestras predicciones. Esto sugiere que el riesgo de depredación para nidos en aéreas con vegetación más baja fue evaluado a través de factores que no estaban relacionados con el ocultamiento. Nuestros resultados mostraron que el pastoreo reduce tanto la disponibilidad de hábitat adecuado para el éxito de anidación de *Pooecetes gramineus*, indicando que el pastoreo puede representar una amenaza en poblaciones que persisten a escalas amplias y potencialmente puede contribuir a las disminuciones observadas. Investigaciones adicionales son necesarias para determinar si los protocolos de pastoreo en la región inter montañosa de British Columbia deberían corregirse, mejorar su consecución o ambas para prevenir disminuciones regionales en las poblaciones de aves que anidan en el suelo en las praderas.

Key words: grassland birds, grazing effects, productivity, *Pooecetes gramineus*

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Populations of North American grassland birds have been declining at a greater rate than any other bird group (Peterjohn and Sauer 1999, Sauer et al. 2008), and habitat loss and degradation have been identified as important factors in this decline (Brennan and Kuvlesky 2005). Livestock grazing is one of the principal land uses of grasslands, and has been shown to alter the composition, structure, and functionality of grassland habitats (Bock et al. 1993, Fleischner 1994). These changes have been especially prevalent in the shortgrass grasslands of the Intermountain region that are believed to have evolved in the absence of large herds of bison (Mack and Thompson 1982, Bock et al. 1993, Gayton 2003, Yeo 2005, Harrison et al. 2010). Given the significance of these habitat changes, grazing is expected to significantly impact native bird species occupying these rangelands.

Ground-nesting birds are likely to be most affected by grazing because the vegetation features on which they rely for nest substrate, nest concealment, and foliar invertebrate food sources are all potentially altered by the presence of livestock (Fondell and Ball 2004, Sutter and Ritchison 2005). However, the influence of grazing on the productivity of ground-nesting birds differs among species, depending on their nesting behaviors and habitat preferences. Species that rely on tall, robust vegetation cover for nest concealment, e.g., Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) and Upland Sandpipers (*Bartramia longicauda*; Derner et al. 2009), may be negatively affected by grazing as dominant plant species shift from robust bunchgrasses and shrubs to less robust, mat-forming grasses and forbs and vegetation height is reduced. These species may suffer increased nest-predation rates due to reduced concealment of nest sites (Ammon and Stacey 1997, Fondell and Ball 2004). Alternatively, species that are not dependent on specific structural features or that do not require overhead cover (e.g., relying instead on crypsis) may not be negatively affected by grazing-induced changes in vegetation, e.g., Mountain Plovers (*Chardrius montanus*) and Long-billed Curlews (*Numenius americanus*; Derner et al. 2009).

Vesper Sparrows (*Pooecetes gramineus*) are one of the most common and wide-ranging ground-nesting species in western grasslands (Jones and Cornely 2002), but breeding populations have been declining throughout their range (Sauer et al. 2008). Grazing-induced habitat changes that have negatively affected other grassland species (Bock et al. 1993, Saab et al. 1995, Fondell and Ball 2004, Sutter and Ritchison 2005) could also affect Vesper Sparrows. Vesper Sparrows build well-concealed ground nests under or at the base of vegetation (Jones and Cornely 2002), and nest success is positively associated with vegetation density (Wray and Whitmore 1979). This suggests that Vesper Sparrows rely on vegetation cover to conceal their nests from predators and that reduced cover caused by grazing may reduce their reproductive success.

Harrison et al. (2010) found that grazing dramatically altered many characteristics of the plant community in the Cariboo-Chilcotin region of British Columbia, Canada. Ungrazed areas had taller vegetation dominated by densely tufted or bunched-grass species like bluebunch wheatgrass (*Pseudoroegneria spicata*) and spreading needlegrass (*Achnatherum richardsonii*). Such species are good indicators of grazing pressure in this region because their occurrence decreases with grazing and they are collectively referred to as "decreasers" (see Gayton 2003). With grazing, the dominant species shifts to mat-forming grasses and forbs like Kentucky bluegrass (*Poa pratensis*) and yarrow (*Achillea millefolium*), collectively referred to as "increasers" because their occurrence increases with grazing in this region. Forb cover and cover of bare ground and biocrust (mosses and lichens) also increase with grazing (Harrison et al. 2010). Whether a plant is an "increasers" or a "decreaser" species depends primarily on its palatability to grazers and tolerance to repeated defoliation (Del-Val and Crawley 2005). Previous studies have also revealed fine-scale (territory-level) associations between Vesper Sparrow abundance and the characteristics of vegetation affected by grazing (Harrison et al. 2010). However, abundance data provide limited information about the demographic consequences of habitat change and the likely future trajectories of populations breeding in altered habitats (Van Horne 1983, Winter and Faaborg 1999). Therefore, studies involving measures of productivity are needed to determine the possible effects of grazing.

We examined how grazing-induced changes in vegetation influenced nest-site selection and productivity (daily nest survival and nestling condition) of Vesper Sparrows. We used an information-theoretic approach to determine if grazing affected Vesper Sparrow nest-site selection and productivity. We hypothesized that Vesper Sparrows (1) might benefit from the additional concealment and foliar invertebrates (food) provided by increased cover of forbs and mat-forming grass species, i.e., "increasers" species (grazing-positive hypothesis), (2) would depend on specific structural features of native, late-seral tufted and bunched grass species, i.e., "decreaser" species, and tall vegetation, and productivity would decline in response to the effects of grazing on these variables (grazing-negative hypothesis), or (3) would not be affected by changes in vegetation that result from grazing (no-effect hypothesis).

METHODS

Our study was conducted in the grasslands of the Cariboo-Chilcotin region of British Columbia that are used primarily for domestic livestock production. Small herds of native ungulate grazers/browsers (mule deer, *Odocoileus hemionus*, and bighorn sheep, *Ovis canadensis*) are also present in the study area. Cattle-stocking rates in this region average ~1.2 animal unit months per hectare (AUM/ha), and do not exceed 3.3 AUM/ha (C. Mumford and W. Hayes-van Vliet, pers. comm.). The timing and duration of grazing in the region vary. Our study was conducted at two sites less than 70 km apart. Junction Sheep Range Provincial Park (JSRPP 51°46′35.92″N 122°25′31.41″W) is on a plateau above the junction of the Chilcotin and Fraser rivers, and the OK Ranch (OKR 51°16′5.29″W 122°1′37.55″W) is on an eastern plateau above the Fraser River. JSRPP (206 ha) had not been grazed by cattle for over 30 yr. OKR was subdivided into plots that varied in current and historical grazing intensity; two plots (75 and 135 ha) were grazed at a higher intensity, a third (82 ha) at a moderate intensity, and a fourth (77 ha) had not been grazed for 15 yr. The diversity in grazing histories across study plots allowed us to examine Vesper Sparrow nest-site selection and productivity across a broad range of vegetation conditions.

Monitoring reproductive success. We monitored OKR for breeding Vesper Sparrows from 2006 to 2008, and JSRPP was monitored in 2007 and 2008. Nests were located and monitored following BBIRD protocols (Martin et al. 1997). Territories were identified by recording the locations of singing males, and nest searching was focused in the vicinity of bird activity, including singing, nest building, and carrying food for young. When found, nests were monitored (mean nest check interval = 3.7 d) until they either failed or young fledged. If fledglings were not observed, nestlings were assumed to have fledged if a nest was empty no fewer than eight days after hatching, there were no signs of predation, and parents were observed carrying food or heard making contact calls with mates or fledglings. Another sign of fledging was the presence of feces on nest rims. Nests were assumed to have been predated if they were empty before nestlings were old enough to have fledged (i.e., seven days). Other signs of predation included holes in a nest or eggs and the remains of nestlings. Where observational data for a nest were incomplete, dates of clutch initiation, hatching, and fledging were calculated based on an assumed incubation period of 12 d and nestling period of nine days (Jones and Cornely 2002). When possible, we measured mass and tarsus length of 4-d-old nestlings.

Vegetation surveys. We examined the potential effects of grazing on nest-site selection by comparing characteristics of nest sites and available sites in the same territories. Available sites were chosen by randomly selecting a direction and distance up to 100 m from nests. At each nest site or random site, we characterized ground cover within a 5-m radius circle centered on nests (or random locations) by dividing the circle into four sections and visually estimating the percent covered by litter, biocrust, bare ground, grass, and forbs in each section (following BBIRD protocol; Martin et al. 1997). The point-intercept method was used to identify and estimate the cover of plant species at 50-cm intervals along 5-m transects in the four cardinal directions from the center (Gayton 2003). The maximum height of vegetation at 1, 3 and 5 m from nests in each cardinal direction was also measured. At each nest site (or random site), slope and aspect were also recorded.

We also evaluated whether grazing affected reproductive success through its influence on vegetation by evaluating grazing-affected vegetation characteristics as predictors of daily nest survival probability and nestling condition. Characteristics of nest sites were also measured and included in both analyses to evaluate the relative importance of grazing-affected vegetation parameters versus physical characteristics that do not change with grazing.

Statistical analyses. Of the vegetation variables measured, forb cover, collective cover of "decreaser" and "increaser" species, and vegetation height were used in our analyses because these variables vary in response to grazing (Harrison et al. 2010). Forb cover and 'increaser' cover were higher in grazed than ungrazed areas (Harrison et al. 2010). These were central to our grazing-positive hypothesis and were grouped as grazing-positive variables. Vegetation height and "decreaser" cover were lower in grazed areas (Harrison et al. 2010). These were central to our grazing-negative hypothesis and were grouped as grazing-negative variables. The influence of slope and aspect on Vesper Sparrow productivity was not expected to be affected by grazing. Slope and aspect were therefore included in our analyses as grazing-independent variables.

Nest age, date, and clutch size have often been found to influence productivity (e.g., Hõrak et al. 1999, Davis 2005, Grant et al. 2005), so were also included as predictors in our analyses. Nest age and date for each exposure interval (i.e., number of days between nest checks) were calculated as the mid-point of the interval. For nests with uncertain fates, the last date when nest status was known was used as the termination date (Manolis et al. 2000). The termination date affected the length of the final exposure interval. Daily nest survival estimates were derived from a logistic function, modeled using the logistic exposure method (Shaffer 2004).

We used an information-theoretic approach to determine if Vesper Sparrow nest-site selection and two indices of productivity (daily nest survival and nestling condition) were affected by grazing. We tested the relative importance of grazing-affected vegetation variables as predictors of nest-site selection, nest survival, and nestling condition by comparing models including those variables with models including variables describing physical characteristics of the nest-site, and with null models containing no nest-site measures. We also controlled for additional temporal and biological factors by including date (exposure interval midpoint), a quadratic polynomial of nest age (age + age^2), and clutch size as base variables in the daily nest survival analysis, and date (nestling mass and tarsus measurement date) and clutch size as base variables in the nestling-condition analysis. Each candidate set included a null model and models with all combinations of the predictor variables, creating eight candidate models for each analysis, each composed of one null model (base variables only), three single predictor models (grazing-positive, grazing-negative, and physical), four two-predictor models, and one global model including all three predictors.

All analyses were performed with SAS version 9.2 (SAS Institute Inc., Cary, NC). Conditional logistic regressions (proc LOGISTIC with strata term) stratified by territory ID were used to generate AIC estimates for models predicting nest-site selection. Including territory ID as a strata term allowed us to link the nest and random plots from the same territory, rather than treating them as independent. The logistic exposure method (proc GENMOD) was used to generate estimates for models predicting daily nest survival probability (Shaffer 2004). Each interval between nest visits was treated as a single observation in the analysis. The response variable was survival or failure during the interval. AIC calculations for daily nest survival incorporated the effective sample size (n-effective = number of exposure days where nests were successful + the number of intervals where nests failed; Rotella et al. 2004). General linear models (proc GLM) were used to generate estimates for models predicting nestling condition. Nestling condition was an index derived from the residual of nestling mass regressed on tarsus and was averaged by nest (Brown 1996). AIC values corrected for small sample sizes (AIC_c) were used in all analyses (Burnham and Anderson 2002). Models were ranked according to their AIC weights (w_is). Summed w_is (relative variable importance), model-averaged coefficients, and unconditional 95% confidence limits (CLs) were computed to assess the relative importance of individual variables (Burnham and Anderson 2002). Coefficients in the nest-site selection and nest survival analyses were converted to odds ratios (Hosmer and Lemeshow 2000). Variables were considered important if present in models with ΔAICs < 2.0, and had coefficients or odds ratios with 95% CLs that did not bound zero (for coefficients) or one (for odds ratios).

RESULTS

Nest-site selection. We located 125 Vesper Sparrow nests and paired them with an equal number of random points in the same

Table 1. Descriptive statistics for vegetation measures known to increase (grazing-positive) or decrease (grazing-negative) in occurrence under grazing pressure in the Cariboo-Chilcotin region of British Columbia (Harrison et al. 2010), plus two physical (grazing-independent) measures ($N = 125$ nest site-random site pairs).

	Nest patches			Random patches		
Variable	Mean	95% CL	Range	Mean	95% CL	Range
Grazing positive						
Increaser cover (%)	24.5	21.4–27.5	0–82.5	26.1	22.8–29.3	0–80.0
Forb cover (%)	17.6	15.8–19.4	2.3–56.0	16.9	15.0–18.8	1.0–60.0
Grazing negative						
Decreaser cover (%)	12.9	11.1–14.6	0–40.0	10.4	8.8–11.9	0–40.0
Plant height (cm)	19.1	17.4–20.8	4.9–55.5	18.8	16.9–20.8	4.4–61.2
Physical						
Slope (degrees)	6.6	5.9–7.4	0–22.0	6.1	5.5–6.8	0–17.0
Aspect[c] [cos(degrees–45) +1]	0.97	0.85–1.09	0–2.00	0.99	0.87–1.12	0–2.00

[a]Increaser cover (%) = % of vegetation plots covered by plant species known to increase in occurrence with grazing.
[b]Decreaser cover (%) = % of vegetation plots covered by plant species known to decrease in occurrence with grazing.
[c]Values near 0 are SE and near 2 are NW.

territories. Grazing-negative and grazing-positive vegetation characteristics and physical features were measured for all 125 nest-random pairs (Table 1). Of eight models evaluated as predictors of Vesper Sparrow nest-site selection, the model including only the grazing-negative term received the most support, with no model containing another term receiving a ΔAIC <2.0 (Table 2). Within the grazing-negative term, the "decreaser"-cover variable had the greatest importance, with 95% CLs for its odds ratio that did not bound one (Table 3). Nest sites had greater cover of late-seral bunched and tufted grass species that tend to decline in response to grazing (i.e., "decreasers") than random sites (mean difference in percent cover = 2.60 [0.73 – 4.47], [95% CLs]).

Daily nest survival. We monitored and made all vegetation measurements for 75 nests. These nests were checked 274 times, with nests recorded as having either survived or failed. The total number of exposure days was 1063, and the number of exposure intervals where nests failed was 16, yielding an effective sample size of 1079 (i.e., n-effective = 1063 + 16 = 1079). Of 75 nests, 53% were successful, 30% failed, and 17% had unknown fates. Of 23 nests that failed, 16 were predated (70%), six were abandoned (25%), and one was trampled by livestock (5%).

Of the eight models evaluated as predictors of daily nest survival, four models that included the grazing-negative term were the highest ranked, with ΔAICs < 2.2 (Table 2). Although the grazing-positive and physical terms were both present in models with ΔAICs < 2.0, the relative importance of variables in those terms was not high and the 95% CLs of their odds ratios bounded one (Table 3). Within the grazing-negative term, vegetation height had the greatest importance, with 95% CLs that did not bound one (Table 3). The probability of a Vesper Sparrow nest surviving a given day was greater when a nest site had taller vegetation (Fig. 1).

Nestling condition. Mass and tarsus measurements were recorded for nestlings in 37 nests. Although the model containing the grazing-positive and grazing-negative terms received the greatest level of support, the null model was ranked second (within 2.0 ΔAIC units of the top-ranked model), indicating that the grazing-affected vegetation variables contributed little additional predictive power (Table 2). In addition, the 95% CLs for coefficients for all variables in the grazing-affected vegetation terms bounded zero, indicating they had little importance in predicting nestling condition (Table 3).

DISCUSSION

Our study provides partial support for the grazing-negative hypothesis that predicts that

Table 2. AIC ranking of three sets of candidate models that predict Vesper Sparrow nest-site selection (used vs. random), daily nest survival, and nestling condition as a function of variables measured at nest sites. Listed are the five highest ranked models (out of eight), plus the null models.

Model[a]	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]
Nest-site selection				
1. Used = grazing (-)	4	170.66	0.00	0.67
2. Used = grazing (-) + physical	6	173.36	2.70	0.17
3. Used = grazing (+) + grazing (-)	6	174.64	3.98	0.09
4. Used = grazing (+) + grazing (-) + physical	8	177.11	6.45	0.03
5. Used = (null)	2	177.34	6.67	0.02
Daily nest survival				
1. Survival = biological + temporal + grazing (+) + grazing (-)	10	130.70	0.00	0.46
2. Survival = biological + temporal + grazing (-) + physical	10	132.43	1.74	0.19
3. Survival = biological + temporal + grazing (-)	8	132.50	1.80	0.19
4. Survival = biological + temporal + grazing (+) + grazing (-) + physical	12	132.86	2.16	0.16
5. Survival = biological + temporal + physical	8	142.43	11.73	0.00
8. Survival = biological + temporal (null)	6	145.71	15.01	0.00
Nestling condition				
1. Condition = biological + temporal + grazing (+) + grazing (-)	8	128.06	0.00	0.56
2. Condition = biological + temporal (null)	4	129.98	1.92	0.21
3. Condition = biological + temporal + grazing (-)	6	131.68	3.62	0.09
4. Condition = biological + temporal + physical	6	132.90	4.84	0.05
5. Condition = biological + temporal + grazing (+)	6	133.45	5.39	0.04

[a]The grazing-negative (-) and positive (+) terms included variables found in a previous study (Harrison et al. 2010) to vary in occurrence in response to grazing. Grazing (-) included vegetation height and "decreaser" cover, and grazing (+) included forb cover and "increaser" cover. The physical term included slope and aspect. The biological term included clutch size, for both nest survival and condition, and a quadratic polynomial of nest age, for nest survival only. The temporal term included date.
[b]The number of estimated parameters in the model including the variance.
[c]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.
[d]The difference between the AIC_c of each model and that of the most parsimonious model.
[e]The weight of evidence for the model relative to the other models in the candidate set.

Vesper Sparrows select nest sites based on specific structural features of late-seral bunched or densely tufted grass species and on vegetation height, and that productivity is reduced by alteration of those variables caused by grazing. The hypothesis was only partially supported because Vesper Sparrows selected nest sites with greater cover of late-seral bunched and tufted grass species that decrease in response to grazing (Harrison et al. 2010), and daily survival was lower for nests surrounded by shorter vegetation. However, contrary to the hypothesis, late-seral grass (decreaser) cover was not associated with either of the two indices of productivity measured, and vegetation height, although apparently important for nest success, was not linked with nest-site selection. In addition, no vegetation-cover variable was positively associated with success, despite nest concealment being central to our predictions. This suggests that predation risk in areas with shorter vegetation was elevated through some factor unrelated to concealment.

Apparent disconnects between selection and success. Vesper Sparrows in our study selected nest sites with greater cover of late-seral (decreaser) grass species than was available in their territories, but "decreaser" cover was not linked with success. There are several possible explanations for this finding. First, although not related to either of the two productivity indices we measured, "decreaser" cover may be linked with some other measure of productivity (e.g., seasonal or lifetime fecundity). For example, Chalfoun and Martin (2007) examined habitat selection and nest success of Brewer's Sparrows (*Spizella breweri*) in Montana, and found that conclusions regarding relationships between preference and reproductive success depended

Table 3. Relative variable importance values (summed AIC weights), and AIC-weighted odds ratios (nest-site selection and nest survival) or coefficients (nestling condition) with 95% confidence limits for each variable evaluated as a predictor of nest-site selection, daily nest survival, and nestling condition in Vesper Sparrows. Bolded are variables with 95% CLs that did not bound one (for odds ratios) or zero (for coefficients).

	Nest-site selection		Daily nest survival[a]		Nestling condition	
Variable	Relative variable importance	Odds ratio (95% CL)	Relativee variable importance	Odds ratio (95% CL)	Relative variable importance	Coefficient (95% CL)
Biological						
Nest age (days)			**1.00**	**0.32 (0.13–0.82)**		
Nest age^2 (days)			**1.00**	**1.02 (1.00–1.04)**		
Clutch size			1.00	1.06 (0.51–2.18)	1.00	−0.31 (-0.93–0.32)
Temporal						
Date (Julian days)			1.00	1.03 (0.99–1.07)	1.00	−0.02 (-0.05–0.01)
Grazing positive						
Increaser cover (%)	0.13	1.00 (0.99–1.00)	0.62	1.02 (0.99–1.06)	0.62	−0.02 (-0.04–0.01)
Forb cover (%)	0.13	1.00 (0.99–1.01)	0.62	0.98 (0.95–1.01)	0.62	0.01 (-0.01–0.04)
Grazing negative						
Decreaser cover (%)	0.96	**1.03 (1.00–1.06)**	1.00	1.00 (0.96–1.05)	0.70	−0.03 (-0.07–0.01)
Plant height (%)	0.96	0.99 (0.97–1.02)	**1.00**	**1.12 (1.05–1.19)**	0.70	−0.01 (-0.05–0.03)
Physical						
Slope (degrees)	0.21	1.01 (0.99–1.03)	0.35	1.02 (0.96–1.09	0.10	−0.01 (-0.01–0.01)
Aspect (- is SE, + is NW)	0.21	0.98 (0.90–1.07)	0.35	0.87 (0.62–1.23)	0.10	−0.01 (-0.07–0.04)

[a]Daily nest survival probability (S) was modeled as log (S / [1 – S]) = Intercept + ($\text{Coefficient}_i \times \text{Variable}_i$) +$\cdots$ ($\text{Coefficient}_n \times \text{Variable}_n$).

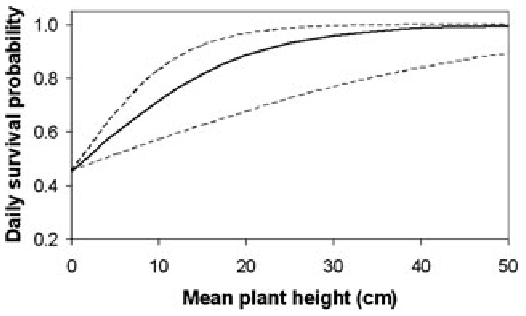

Fig. 1. Predicted daily nest-survival rate (S) for Vesper Sparrows relative to nest-patch vegetation height. The solid line denotes fitted values from a logistic exposure model ($\log (S / [1 - S]) = \text{Intercept} + (\text{Weighted Coefficient}_i \times \text{Variable}_i) + \cdots (\text{Weighted Coefficient}_n \times \text{Variable}_n)$) using AIC weighted (i.e., model-averaged) coefficients, a range of values for height, and constant (mean) values for all other variables. Dashed lines are upper and lower 95% confidence limits.

on the reproductive metrics used. Second, because Vesper Sparrows are among the earliest migrants to arrive on their breeding grounds and begin breeding (late April to early May at our study sites; Jones and Cornely 2002), they may select sites with greater cover of bunched or densely tufted grass species because these are the only species that retain enough overwinter cover to be visible early in the breeding season, and not because they will contribute to eventual success. Third, Vesper Sparrows may have adapted their nest-site selection to minimize predation by a suite of predators found at the core of the range, but those adaptations are not beneficial at the periphery of their range where our study sites were located. Harrison and Green (2010) suggested that adaptation to predation pressures at the core of the range could explain the disconnect between vegetation structure and nesting success in a northern population of Brewer's Sparrows. Fourth, inter-annual variability in the population dynamics of Vesper Sparrow nest predators may cause selection to appear maladaptive when associations are examined over a short period when, in fact, selection does maximize some measure of productivity over the long term. Clark and Shutler (1999) found evidence in a study of several species of ducks that selection patterns that appeared disconnected from success in a given year did actually correlate weakly with success over an eight-year period.

Finally, nest success may not have been associated with any of the cover metrics we examined because incidental predation plays a major role in nest failure, making success unrelated to the relative cover of different species in the surrounding vegetation. In this case, incidental predation refers to predation by species that do not prey primarily on Vesper Sparrow eggs or nestlings, and that locate nests opportunistically when foraging. In the Cariboo-Chilcotin, snakes and small mammals prey opportunistically on Vesper Sparrow eggs and nestlings. Vickery et al. (1992) found that incidental predation by skunks played a major role in nest failure for grassland birds in Maine, and explained an otherwise puzzling lack of associations between nest predation and nest-patch vegetation structure.

Vegetation height was positively associated with nest survival in our study, but we found no association between vegetation height and nest-site selection. A possible explanation for this apparent disconnect is that we measured vegetation height after nesting rather than during the period of nest-site selection and birds could not reliably predict where vegetation would be tallest. In grazed areas, this unpredictability likely increases because grazing can result in mid-season reductions in height. Best and Rodenhouse (1984) found that mid-season tilling made the nesting success of Vesper Sparrows breeding in cultivated fields in Iowa extremely unpredictable, and attributed a disconnect between nest-site selection and success to this sudden, unpredictable change. We did not measure mid-season vegetation height, but some reduction due to grazing is likely to have occurred on grazed plots.

Predation risk unrelated to concealment. Nest survival in our study was not linked with any vegetation-cover variable measured, suggesting that concealment did not limit predation risk. In contrast, Grant et al. (2006) found that nest survival for Vesper Sparrows in North Dakota was positively associated with cover of Kentucky bluegrass, the most dominant species in our unsupported "increasers" category. In addition, Wray and Whitmore (1979) found that Vesper Sparrow nest success in West Virginia was positively associated with nest-patch vegetation density, which is likely positively correlated with concealment. We may have failed to detect a correlation between concealment and nest survival because the predator community in the

Cariboo-Chilcotin differs from those in North Dakota and West Virginia. There is a greater diversity and density of avian nest predators near the core of Vesper Sparrow's range (Sauer et al. 2008), and avian predators, due to their reliance on visual cues, are more limited by visual concealment than are snakes and small mammals (Martin 1993) that rely more on olfactory cues.

In sum, we found that Vesper Sparrows selected nest sites with greater cover of late-seral grass species (decreasers) that decrease in cover in response to grazing, and daily nest survival was lower for nests surrounded by shorter vegetation. This suggests that grazing in the Cariboo-Chilcotin region reduces both the availability of suitable habitat for and nesting success of Vesper Sparrows, indicating that grazing could pose a threat to population persistence at a broader scale. Important areas of future research include incorporating a broader-scale replication of grazing treatments and monitoring banded adults over time to estimate demographic parameters such as seasonal or lifetime fecundity and adult survival that could shed additional light on the population-level consequences of livestock grazing for Vesper Sparrows and other grassland birds.

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