Rangeland Health Assessment: A Useful Tool for Linking Range Management and Grassland Bird Conservation?

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Abstract

Large-scale loss and degradation of North American native prairie coupled with sharp declines in grassland bird populations call for a clear understanding of the effects of livestock production on bird habitat selection. Grassland birds typically select breeding habitat based on a suite of structural and community vegetation features shaped by grazing. Rangeland health indices are a tool for assessing grassland structure and community composition that may offer biologists and range managers common language to achieve grassland bird recovery goals. We used point-count surveys, vegetation measures, and indices of rangeland health to examine bird-habitat relationships on native grassland in southwestern Saskatchewan for 10 grassland bird species. We used an information theoretic approach to compare the support of three hypotheses explaining variation in bird abundance as a function of local vegetation characteristics: bird abundance is best explained by 1) vegetation structure, 2) vegetation structure heterogeneity, or 3) plant community. Vegetation structure variables were present in top-ranking models (i.e., models within four Akaike information criterion units of top model) for eight species and solely comprised top-ranking models for Baird's sparrow (*Ammodramus bairdii*), chestnut-collared longspur (*Calcarius ornatus*), horned lark (*Eremophila alpestris*), McCown's longspur (*Rhynchophanes mccownii*), and savannah sparrow (*Passerculus sandwichensis*). Structural heterogeneity variables were present in top-ranked models for grasshopper sparrow (*Ammodramus savannarum*), horned lark (*Eremophila alpestris*), and western meadowlark (*Sturnella neglecta*). Plant composition variables solely comprised top-ranking models for clay-colored sparrow (*Spizella pallida*) and were present in top-ranked models for grasshopper sparrow and vesper sparrow (*Pooecetes gramineus*). Our results indicate that vegetation structure variables, namely litter mass, vegetation volume, and bare ground cover, best explain variation in bird abundance. Although the rangeland health index received little support as a predictor of bird abundance, vegetation structure components of the index could be used to communicate grazing management guidelines that maintain grassland bird habitat.

Key Words: bird abundance, grassland birds, habitat selection, rangeland health, vegetation structure, zero-inflated models

INTRODUCTION

Temperate grasslands and the biodiversity they sustain are becoming increasingly endangered. An estimated 41% of the world's native temperate grasslands and 79% of North American grasslands have been lost to cultivation for agricultural production (White et al. 2000). Those that remain support a growing human population, expanding food and fiber production, and extensive energy-sector development. Habitat loss and degradation are considered primary causes of grassland species declines worldwide (White et al. 2000). In North America, grassland birds have declined sharply over the last four decades (Askins et al. 2007; Sauer et al. 2010). Currently, 57 grassland wildlife species are considered at risk in North America, 28 of which are grassland birds (IUCN 2011).

Since livestock production is a dominant use of remaining global temperate grassland (Samson and Knopf 1994; Ramankuty et al. 2008), grazing management plays a vital role in the recovery of grassland species.

Soils, climate, topography, and disturbance (i.e., fire, grazing, and human land use) shape grassland structure, function, and diversity, creating a mosaic of habitat patches across a landscape that is home to a variety of grassland birds (Wiens 1973; Fuhlendorf and Engle 2001; Askins et al. 2007). Grassland birds show distinct preferences for the structure and composition of the plant community (Madden et al. 2000; Fisher and Davis 2010). As a result, bird species assemblages vary along a continuum of habitat features shaped by environmental conditions and disturbance such as grazing (Bock et al. 1993; Fritcher et al. 2004; Smith and Lomolino 2004; Fuhlendorf et al. 2006). Species such as horned lark (*Eremophila alpestris*) and McCown's longspur (*Rhynchophanes mccownii*) are associated with pastures under relatively heavy grazing pressure whereas species such as bobolink (*Dolichonyx oryzivorus*) and sedge wren (*Cistothorus platensis*) are associated with lightly or ungrazed grasslands and Baird's sparrow (*Ammodramus bairdii*) and Sprague's pipit (*Anthus spragueii*) occupy grasslands with intermediate grazing pressure (Knopf 1996). Grassland generalist species, such as vesper sparrow (*Pooecetes gramineus*) and savannah sparrow (*Passerculus sandwichensis*) occupy a wider

range of grassland habitats (Jones and Cornely 2002; Wheelwright and Rising 2008).

Despite debate over the ecological merit of commercial livestock grazing (Savoury 1988; Jensen 2001; Freilich et al. 2003), grazing may be used to enhance grassland bird habitat, in part via changes in the structure and function of rangeland plant communities (Fuhlendorf and Engle 2001; Derner et al. 2009). Livestock grazing may ultimately lead to a mosaic of grass species and structure that varies across time and space (Turner and Chapin 2005; Romo 2007), thereby providing habitat for a wide variety of grassland birds. Most research attempting to uncover relationships between various aspects of livestock management and grassland bird habitat selection uses bird-centric vegetation measures (Fisher and Davis 2010) that may be of little relevance to land managers. For example, Wiens pole measurements (Wiens 1969), while useful in describing bird habitat structure, may be difficult to relate to some rangeland managers and livestock producers in a meaningful way.

Rangeland assessments based on vegetation measures have long been used to determine the impact of grazing by cattle. Although range condition methods were once predominantly used to evaluate the response of grassland vegetation to grazing (Dyksterhuis 1949), the methodology could not account for the wide spectrum of vegetation dynamics that occur on rangelands, including the irreversible impacts of invasive species and soil erosion (Task Group on Unity in Concepts and Terminology Committee 1995; Briske et al. 2005). Rangeland health indices are a standard tool for assessing grassland structure and community composition and indicate how close producers are to achieving optimal grassland health on a particular ecological site defined by soil and site stability, hydrologic function, and biotic integrity (Pyke et al. 2002; Adams et al. 2005; Pellant et al. 2005). These indices may be more useful for monitoring biodiversity than other methods of range assessment based primarily on plant species composition because some species may respond more to vegetation structure. Although relationships between biodiversity and rangeland condition have been studied (Smith et al. 1996; Nelson et al. 1997; Bai et al. 2001; Fritcher et al. 2004), few studies have examined the relationship between biodiversity and rangeland health (Bradford et al. 1998; Symstad and Jonas 2011). If rangeland health indices can be used for biodiversity assessment, they may offer biologists and range managers a valuable tool to achieve grassland species conservation goals through grazing management.

Our objective was to examine the feasibility of rangeland health as a rangeland assessment tool for biodiversity. We focus on 10 grassland bird species, including three species (Sprague's pipit, chestnut-collared longspur [*Calcarius ornatus*], and McCown's longspur) currently listed under Canada's Species at Risk Act (Government of Canada 2013). Populations of these species are in decline across North America and ample research shows that livestock grazing (Bock et al. 1993) and vegetation structure (Fisher and Davis 2010) influence grassland songbird habitat selection. Furthermore, the abundance of some grassland songbirds has been used as an indicator of a healthy prairie (Environment Canada 2008). We used an information theoretic approach to assess the support of three hypotheses explaining variation in bird abundance as a function of local vegetation measures: bird abundance is best explained by 1) vegetation structure, 2) vegetation structure heterogeneity, and 3) plant community. In doing so, we aimed to elucidate how bird species compare in the niches they occupy along a gradient of rangeland health and associated vegetation characteristics.

METHODS

Study Area and Site Selection

We selected the Milk River watershed of southwestern Saskatchewan, Canada as our study area as it contains the largest tracts of remaining native prairie grazed by livestock and the highest diversity of species at risk in the province (Fig. S1; available online at http://dx.doi.org/10.2111/REM-D-12-00140.s1). The region is comprised of mixed-grass and fescue prairie communities, largely dominated by *Elymus lanceolatus* (Scribn. & Sm.) Gould, *Pascopyrum smithii* (Rydb.) Barkworth & D.R. Dewey, *Calamagrostis montanensis* (Scribn.) Vasey, *Festuca hallii* (Vasey) Piper, *Festuca saximontana* Rydb., *Hesperostipa comata ssp. comata* (Trin. & Rupr.) Barkworth, or *Hesperostipa curtiseta* (Hitchc.) Barkworth (Thorpe 2007; ITIS 2013). Approximately 70%, 20%, and 10% of the native grassland in the study is under private, provincial, or federal management, respectively. All grasslands in our study region were grazed by cattle, with the exception of Grasslands National Park. Our random selection of 140 quarter sections captured a wide range of grazing practices typical for this region. Although we did not quantify grazing intensity directly, it is reflected in the vegetation structure variables we measured.

We used ArcGIS 9.3 (Esri 2008) to stratify our random sampling based on land management categories (federal, provincial, and private) and selected 140 quarter sections of upland native prairie as indicated by either loam or solonetzic soils. We used the quarter section (i.e., 160 acres or 65 ha) as our experimental unit because it offered a suitable area for rangeland health assessments and is the typical unit by which land is sold and managed in the province (McKercher and Wolfe 1986). We restricted our selection of quarter sections to those that were native rangeland, entirely within a single management jurisdiction, and part of an upland grassland patch > 145 ha to reduce any potential confounding effects of patch size on grassland songbird abundance (Johnson and Igl 2001; Davis 2004).

Bird Abundance

We randomly positioned three point-count (Hutto et al. 1986) sampling stations 300 m apart from the center of the point count and at least 100 m from edges within each quarter section. In 2009 and 2010, trained surveyors conducted one 5-min, 100-m radius point count at each survey location from 26 May to 3 July. Surveyors recorded singing males upon first detection inside and outside of the 100-m-radius circle. Surveys took place from 0.5 h before sunrise until 4 h after sunrise and during mornings with wind < 20 km · h^{-1} and no precipitation. We constrained survey conditions to reduce variability in bird detection among counts (Rotella et al. 1999). We measured or estimated distance to each bird (Buckland et al. 2001) and

recorded bird detections within three equal time periods during the survey period (Farnsworth et al. 2002). We used the sum of male birds aurally detected within 100 m over all three point counts as an index of abundance. We used only those individuals detected by song to estimate the number of territorial males breeding in each quarter section because we could not reliably separate females from nonsinging males for most species.

Imperfect Detection

Potential detection biases associated with point-count surveys used to estimate bird abundance have undergone much criticism (Alldredge et al. 2007a, 2007b, 2008; Efford and Dawson 2009; but see Johnson 2008). Inference based on bird counts adjusted for imperfect detection is considered an improvement over unadjusted counts (Buckland et al. 2001). Therefore, we used distance (Buckland et al. 2001) and removal sampling (Farnsworth et al. 2002) to attempt to account for the probability of detecting a cue once it is given and the probability that a cue is given when the observer is present, respectively.

We used the program Distance 6.0 Release 2 (Thomas et al. 2009) for species with > 45 detections and modeled probability of detection for each species without covariates using the conventional distance sampling (CDS) engine and with observer and time of day as covariates using the multiple-covariate distance sampling (MCDS) engine (Marques et al. 2007). In both analyses we binned counts based on distance intervals deemed appropriate by previous studies (i.e., 0–20 m, 20–30 m, 30–40 m, 40–50 m, 50–75 m, 75–100 m; Rotella et al. 1999). To remove outliers and facilitate model fitting, we right-truncated count data to 100 m for each species (i.e., $g[w]=0.1$; Buckland et al. 2001). We assessed model fit based on Akaike information criterion (AIC) value, χ^2 goodness of fit, and visual assessment of detection and probability distribution functions.

We used R statistical software 2.14.1 (R Development Core Team 2011) and package RMARK 2.1.0 (Laake 2012) to estimate detection probabilities via removal sampling (Farnsworth et al. 2002). We examined the relationship between capture history and our treatment parameters of interest (e.g., rangeland health, litter, etc.). We fit closed-capture Huggins models (Huggins 1989) in RMARK using candidate models comprised of grouping variables (i.e., year, season) or individual covariates (i.e., minutes from sunrise, wind speed, cloud cover, and observer). We selected the most parsimonious model based on AIC and goodness of fit (Burnham and Anderson 2002).

Vegetation Assessment

Previous work suggests grassland bird habitat selection is mediated by grassland structure (e.g., litter, vegetation volume, bare ground cover), heterogeneity in structure, and plant community composition (Wiens 1974b; Rotenberry 1985; Fuhlendorf et al. 2006). We selected predictor variables from the rangeland health index that we considered important for grassland birds, including litter mass (kg·ha^{-1}); percentage of cover of bare ground, club moss, lichen, and shrub; and proportional biomass of individual plant species. In addition,

we selected vegetation features not directly included in the overall rangeland health index that may be important to grassland birds, including vegetation volume (Robel et al. 1970), plant species richness, and structural heterogeneity (Wiens and Rotenberry 1981; Fuhlendorf et al. 2006; Fisher and Davis 2010).

We collected all vegetation measurements in 24 plots (20 cm×50 cm) distributed regularly along the lines between the three bird point-count locations. In each plot, we estimated the percentage that each plant species contributed to total plant biomass within the plot; we used these data to calculate species richness. We measured vegetation volume using a Robel pole with 2.5-cm increments (Toledo et al. 2008) and estimated 100% obscurity to the nearest centimeter in all cardinal directions. All measurements were assessed from 4 m away at a height of 1 m (Robel et al. 1970). We visually estimated litter mass (kg·ha^{-1}) by hand-raking to collect all dead plant material (e.g., standing stems, fallen stems, leaf material, and partially decomposed material) within the plot and compared this to a litter typical of the range site being evaluated (Adams et al. 2005; Saskatchewan PCAP Greencover Committee 2008). We visually estimated signs of erosion and percentage of cover of club moss (Selaginella spp.), lichen, and bare ground (i.e., any land surface not covered by vegetation). We measured shrub cover (%) using the line-intercept method (Canfield 1941) on three 100-m transects randomly located between point-count centers.

Since plant species composition is an important component of the rangeland health index, we used nonmetric multidimensional scaling (NMS) in PC-ORD 4.0 (McCune and Mefford 1999) with a Sorenson distance measure and random start configuration to reduce the dimensionality of plant species composition (74 species) to one synthetic variable for use in further analyses (McCune and Mefford 1999; Beals 2006). Ordination of the plant community largely partitioned plant species biogeographically into those typical of the Dry Mixed, Mixed Grassland, and Cypress Upland ecoregions (Thorpe 2007), or invasive species. Values from the single orthogonal axis of the NMS were used as a covariate in subsequent models.

Rangeland Health

We assigned each quarter section an index of rangeland health using the Saskatchewan Rangeland Health Index (Saskatchewan PCAP Greencover Committee 2008). Similar indices were developed in Alberta (Adams et al. 2005) and the United States (Pellant et al. 2005) and have been used in other rangeland studies (Desserud et al. 2010). We used site descriptions and visual guides outlined in the Saskatchewan Rangeland Health Index (Saskatchewan PCAP Greencover Committee 2008) to score a series of questions that reflect key indicators of rangeland health: plant species composition and structure, hydrologic function and nutrient cycling, site stability, and presence of invasive species. We assessed the plant species composition for each quarter section by comparing the proportional biomass of each species present to that of the reference community for that ecosite (Thorpe 2007). Plant communities that closely resembled the reference plant community received a "similarity index" score of 40 whereas those that showed minor, moderate, significant, or extreme

alterations from the reference plant community received a score of 30, 15, 7, or 0, respectively. We visually assessed plant structure by examining the presence of low shrubs, tall graminoids and forbs, medium graminoids and forbs, and ground-covering graminoids, forbs, moss, and lichen. If plant layers closely resembled those of the reference community, we assigned a score of 10. If one, two, or three layers were absent, we assigned a score of 7, 3, or 0, respectively. We assessed the cover and density distribution of invasive species. If no invasive species were present, we assigned a score of 5 for both cover and density distribution. If invasive species coverage was $\leq 1\%$, or $> 1\%$, we assigned a score of 3 or 0, respectively. We used a density distribution guide to rate the infestation of invasive species. Invasive species density distributions rated as low or high were assigned a score of 3 or 0, respectively. We visually assessed whether there was more soil erosion than expected for each site (e.g., hoof-shearing, pedestalling, etc.). Sites with no sign of soil movement beyond the natural extent for the site were assigned a score of 10. Sites with slight, moderate, and extreme amounts of soil movement were scored 7, 3, and 0, respectively. Sites where $\leq 10\%$ of the area was exposed soil that was management-caused received a score of 5. Sites where 10% to 20%, 20% to 50%, and $> 50\%$ of their area was management-caused exposed soil received a score of 3, 2, or 0, respectively. In compliance with the rangeland assessment methodology, we visually assessed amounts and distribution of litter $(\mathrm{kg} \cdot \mathrm{ha}^{-1})$ as described above. Sites received a score of 25 if litter amounts were evenly distributed and 65% to 100% of amounts expected under moderate disturbance. Moderately patchy litter amounts in the range of 35% to 65% of the expected amount and greatly reduced litter with $< 35\%$ of the expected amount received scores of 13 and 0, respectively. We summed scores from all questions to determine the total rangeland health score (out of 100); this final score represented rangeland that can be broadly classified as "unhealthy" (< 50), "healthy with problems" (50–75), or "healthy" (75–100).

Statistical Analysis

We used R statistical software 2.14.1 (R Development Core Team 2011) for all analyses. We checked for multicollinearity and selected predictor variables that did not demonstrate strong correlation with each other $(r^2 < 0.5)$; these included litter mass, vegetation volume, bare ground cover, shrub cover; coefficients of variation of litter mass, vegetation volume, and bare ground cover; and plant species richness, plant species composition, overall rangeland health score, and similarity index. We did not include similarity index and overall rangeland health score in the same models because they were correlated with each other $(r^2 = 0.7)$. All predictor variables were averaged to the quarter section and scaled by 0.01 to ensure model convergence.

We used an information theoretic approach (Burnham and Anderson 2002) to assess the support of three hypotheses explaining variation in bird abundance as a function of local vegetation measures; bird abundance is best explained by 1) vegetation structure, 2) vegetation structure heterogeneity, or 3) plant community. Models comprised combinations of either four structural variables (hereafter structure models: litter

Table 1. Candidate vegetation structure, vegetation structure heterogeneity, and plant community models of abundance for 10 grassland bird species built on a priori hypotheses of grassland bird habitat selection.

Structure	Heterogeneity	Community
lit[1] + robel + bg + shrub	cvlit + cvrob + cvbg	comp + sim + rich
lit + robel + bg	cvlit + cvrob + cvbg	comp + rich + rh
robel + bg + shrub	cvlit + cvrob	comp + sim
lit + bg + shrub	cvlit + cvbg	sim + rich
lit + robel + shrub	cvlit + cvrob	rich + rh
lit + robel	cvlit + cvbg	comp + rich
robel + bg	cvrob + cvbg	comp + rh
bg + shrub	cvlit	sim
lit + bg	cvrob	rich
lit + shrub	cvbg	rh
robel + shrub		
robel		
bg		
shrub		
lit		

[1] lit indicates litter mass $(\mathrm{kg} \cdot \mathrm{ha}^{-1})$; robel, vegetation volume (cm^3); bg, bare ground cover (%); shrub, shrub cover (%); cvlit, litter mass heterogeneity; cvrob, vegetation volume heterogeneity; cvbg, bare ground heterogeneity; comp, plant species composition; sim, similarity index; rich, plant species richness; rh, rangeland health score.

mass, bare ground cover, vegetation volume, and shrub cover), three variables associated with structural heterogeneity (hereafter heterogeneity models: coefficients of variation for litter mass, vegetation volume, and bare ground cover), or four community variables (hereafter community models: plant species richness, plant species composition, similarity index, and overall rangeland health score). Our final suite of 35 candidate models included only main effects and subsets of all additive models for each suite of models (Table 1).

Given the high frequency of zero counts and overdispersion in our bird abundance data, we explored the fit of a suite of zero-inflated Poisson and negative binomial models against their noninflated counterparts (Wenger and Freeman 2008). A binomial generalized linear model is used to model for species occurrence, whereas species abundance can be modeled by a Poisson or negative binomial distribution (Zurr et al. 2009). We assessed zero and noninflated Poisson and negative binomial main effects models for the occurrence portion of the zero-inflated model using robel and litter, because these variables are particularly important predictors of grassland bird habitat selection (Fisher and Davis 2010). Once we identified a suitable structural model for each species occurrence, we held this component constant and varied the abundance component for all species models.

Models were ranked using AIC adjusted for small sample size (AIC$_c$; Anderson et al. 2001; Anderson 2008) and selected using χ^2 goodness of fit (Burnham and Anderson 2002). We examined residual plots to ensure that we met assumptions associated with generalized linear models. We addressed model selection uncertainty and effects of uninformative parameters using a model-averaging approach (Burnham and Anderson 2002; Arnold 2010). We model-averaged all variables within 4 AIC units of the top model and calculated their relative variable importance values (Burnham and Anderson 2002) using the MuMIn R package (Barton 2012). Although we calculated

relative variable importance values across an unequal number of models, this did not affect cumulative weights for top-ranked variables because variables in models ranked below the top-ranking models had extremely small weights. Post hoc, we combined top-ranked structure, community and heterogeneity models to explore whether a combination of a priori hypotheses ultimately improved model fit. We considered a variable an important predictor of bird abundance if the 85% confidence interval did not include zero (Arnold 2010).

RESULTS

Imperfect Detection
We had sufficient detections to analyze bird habitat relationships for the following species: Baird's sparrow, chestnut-collared longspur, clay-colored sparrow (*Spizella pallida*), grasshopper sparrow (*Ammodramus savannarum*), horned lark, McCown's longspur, savannah sparrow, Sprague's pipit, vesper sparrow, and western meadowlark (*Sturnella neglecta*).

Few detections close to 0 m of all species yielded poor goodness of fit and a problematic shape in the detection function for all distance sampling models. It is not known whether few birds detected near 0 m were due to evasive movement of birds away from the observer or a lack of bird response close to 0 m. Regardless, these results violated the assumption that all birds at 0 m are detected with certainty (i.e., $g(0)=1$; Buckland et al. 2001). Therefore, we did not adjust our data to account for potential detection error associated with distance from the observer.

Our removal sampling results showed that more birds were detected in the first interval than the second and third intervals for all species. Examination of relationships between variables related to capture history (wind speed, observer, minutes from sunrise, and cloud cover) and treatments (rangeland health, vegetation volume, litter, and species richness) yielded no outliers or patterns to warrant adjusting counts. Only abundance of chestnut-collared longspur and Sprague's pipit held potential for adjustment to account for detection probability associated with minutes from sunrise and cloud cover, respectively. However, we did not adjust our counts because it would result only in a scaling up or down of abundance without any meaningful consequences for the relationship between bird abundance and our explanatory variables. Abundance data for all other species did not require adjustment due to lack of model fit because the null model was the best-supported model, model weights were consistently low, or confidence intervals for estimates of detection probability included zero (Anderson 2008).

Bird–Vegetation Relationships
For the occurrence component of the zero-inflated model, the best-supported model for Baird's sparrow, chestnut-collared longspur, horned lark, McCown's longspur, savannah sparrow, and Sprague's pipit, occurrence was a zero-inflated negative binomial (ZINB) model with vegetation volume and litter mass as covariates (Table 2). For Baird's sparrow, savannah sparrow, and Sprague's pipit the probability of occurrence increased with greater vegetation volume and litter mass whereas the opposite

was found for chestnut-collared longspur, horned lark, and McCown's longspur. The best-supported model of occurrence for clay-colored sparrow and grasshopper sparrow was a ZINB model with vegetation volume as a covariate; the probability of occurrence for both species increased with increasing vegetation volume. The top occurrence model for vesper sparrow and western meadowlark was a ZINB model with no covariates assigned and vegetation volume, respectively. Confidence intervals for estimates of abundance of vesper sparrow and western meadowlark across all occurrence models overlapped zero.

Vegetation structure variables were present in top-ranking models (i.e., models within 4 AIC units of top model) for eight species and solely comprised top-ranking models for 5 of 10 species (Baird's sparrow, chestnut-collared longspur, McCown's longspur, savannah sparrow, and Sprague's pipit; Table 2). Litter mass was an important predictor of Baird's sparrow, chestnut-collared longspur, horned lark, McCown's longspur, and savannah sparrow abundance (Table 3). Baird's sparrow and savannah sparrow abundance increased with litter mass, whereas chestnut-collared longspur, horned lark, and McCown's longspur abundance decreased (Fig. 1A). Vegetation volume was an important predictor of Baird's sparrow, chestnut-collared longspur, grasshopper sparrow, horned lark, McCown's longspur, and Sprague's pipit abundance (Table 3). Abundance of Baird's sparrow, grasshopper sparrow, and Sprague's pipit increased with vegetation volume whereas chestnut-collared longspur, horned lark, and McCown's longspur abundance decreased. Baird's sparrow abundance increased sharply from 0.05 cm to 0.15 cm then rose slowly, whereas McCown's longspur abundance decreased sharply from 0.05 cm to 0.2 cm and declined slowly thereafter (Fig. 1B). Bare ground cover explained variation in abundance for Baird's sparrow, horned lark, McCown's longspur, and savannah sparrow (Tables 2 and 3). Abundance of McCown's longspur and horned lark steadily increased with bare ground cover whereas Baird's sparrow and savannah sparrow abundance steadily decreased (Fig. 1C). Shrub cover influenced the abundance of clay-colored sparrow, grasshopper sparrow, McCown's longspur, and savannah sparrow but its effect was more variable than other structural covariates. Abundance of clay-colored, grasshopper, and savannah sparrows increased with shrub whereas McCown's longspur abundance decreased (Table 3).

Species richness, species composition, similarity index or the overall rangeland health index were present in top-ranking models for only clay-colored, grasshopper, and vesper sparrows and heterogeneity variables were present in top models for only grasshopper sparrow, horned lark, and western meadowlark (Table 2). Rangeland health was not a strong predictor of bird abundance as confidence intervals overlapped zero for all species. Model-averaged estimates of abundance indicated that plant species richness or heterogeneity of vegetation structure were important predictors of abundance for clay-colored sparrow, grasshopper sparrow, horned lark, vesper sparrow, and western meadowlark (Table 3). Species richness was an important predictor of abundance for clay-colored, grasshopper, and vesper sparrows (Table 3); clay-colored sparrow and vesper sparrow abundance increased with species richness whereas grasshopper sparrow decreased (Fig. 1D). Grasshop-

Table 2. Final ranking of candidate models relating bird abundance to vegetation characteristics for 10 grassland bird species on 140 quarter sections in southwestern Saskatchewan. Only those models with AIC_c values lower than the null model are presented. Species common name, model rank and structure, number of model parameters (K), log likelihood values (log[L]), AIC_c values of the null model and top-ranked models ($\Delta AIC_c \leq 4$), delta AIC_c values (Δi), and AIC_c weights (w_i) are presented; Zero-inflated models are presented as abundance component | occurrence component.

Species	Rank	Model structure[1]	K	log(L)	AIC_c	Δ_i	w_i
Baird's sparrow	1	lit + bg + robel | robel + lit	7	−525.1	1 066.8	0.0	0.27
	2	lit + bg | robel + lit	6	−526.3	1 067.1	0.3	0.23
	3	lit + robel + bg + shrub | robel + lit	8	−524.3	1 067.3	0.5	0.21
	4	lit + bg + shrub | robel + lit	7	−525.8	1 068.3	1.5	0.13
	5	lit + robel | robel + lit	6	−527.3	1 069.0	2.2	0.09
	6	robel + bg | robel + lit	7	−526.4	1 069.4	2.6	0.07
	23	1 | robel + lit[2]	4	−535.2	1 080.7	13.9	0.0
Chestnut-collared longspur	1	lit + robel | robel + lit	6	−652.4	1 319.3	0.0	0.37
	2	lit + robel + shrub | robel + lit	7	−651.9	1 320.5	1.1	0.21
	3	lit + robel + bg | robel + lit	7	−652.4	1 321.4	2.0	0.14
	4	lit | robel + lit	5	−654.9	1 322.1	2.8	0.09
	5	lit + robel + bg + shrub | robel + lit	8	−651.9	1 322.5	3.2	0.07
	6	lit + bg | robel + lit	6	−654.4	1 323.3	4.0	0.05
	27	1 | robel + lit[2]	4	−665.1	1 340.5	21.2	0.0
Clay-colored sparrow	1	rich | robel	4	−163.4	337.1	0.0	0.31
	2	rich + rh | robel	5	−163.3	339.0	1.9	0.12
	3	comp + rich | robel	5	−163.3	339.0	1.9	0.12
	4	sim + rich | robel	5	−163.4	339.2	2.1	0.11
	5	shrub | robel	4	−165.3	340.9	3.8	0.05
	6	comp + rich + rh | robel	6	−163.3	341.1	3.9	0.04
	12	1 | robel[2]	3	−167.4	343.0	5.9	0.0
Grasshopper sparrow	1	sim + rich | robel	5	−107.7	227.8	0.0	0.21
	2	rich | robel	4	−109.6	229.5	1.7	0.09
	3	comp + sim + rich | robel	6	−107.7	229.8	2.0	0.08
	4	cvlit + cvrob | robel	5	−108.8	229.9	2.1	0.07
	5	cvlit + cvbg | robel	5	−108.9	230.1	2.3	0.07
	6	cvbg | robel	4	−110.2	230.7	2.9	0.05
	7	rich + rh | robel	5	−109.2	230.7	2.9	0.05
	8	cvlit + cvrob + cvbg | robel	6	−108.1	230.7	2.9	0.05
	9	robel + shrub | robel	5	−109.3	231.0	3.2	0.04
	10	cvrob + cvbg | robel	5	−109.3	231.0	3.2	0.04
	11	cvrob | robel	4	−110.5	231.3	3.5	0.04
	12	comp + rich | robel	5	−109.6	231.6	3.8	0.03
	21	1 | robel[2]	3	−113.0	234.2	6.4	0.0
Horned lark	1	lit + robel + bg | robel + lit	7	−562.1	1 140.7	0.0	0.23
	2	cvbg | robel + lit	5	−564.4	1 141.1	0.4	0.19
	3	cvrob + cvbg | robel + lit	6	−563.6	1 141.6	0.9	0.15
	4	lit + robel | robel + lit	6	−564.1	1 142.7	2.0	0.09
	5	lit + robel + bg + shrub | robel + lit	8	−562.1	1 142.9	2.1	0.08
	6	cvlit + cvbg | robel + lit	6	−564.3	1 143.0	2.3	0.07
	7	robel + bg | robel + lit	6	−564.5	1 143.4	2.7	0.06
	8	cvlit + cvrob + cvbg | robel + lit	7	−563.5	1 143.6	2.9	0.06
	24	1 | robel + lit[2]	4	−578.3	1 167.0	26.2	0.0
McCown's longspur	1	lit + robel + bg + shrub | robel + lit	8	−332.2	683.2	0.0	0.34
	2	lit + robel + shrub | robel + lit	7	−334.0	684.6	1.4	0.17
	3	robel + bg + shrub | robel + lit	7	−334.3	685.2	2.0	0.12
	4	lit + robel + bg | robel + lit	7	−334.4	685.4	2.1	0.12
	5	lit + robel | robel + lit	6	−335.7	685.9	2.7	0.09
	6	robel + shrub | robel + lit	6	−335.7	686.0	2.7	0.09
	29	1 | robel + lit[2]	4	−347.3	704.7	21.5	0.0

Table 2. Continued.

Species	Rank	Model structure[1]	K	log(L)	AIC_c	Δ_i	w_i
Savannah sparrow	1	lit + bg + shrub | robel + lit	7	−375.4	767.3	0.0	0.39
	2	lit + bg | robel + lit	6	−377.5	769.5	2.1	0.13
	3	lit + robel + bg + shrub | robel + lit	8	−375.4	769.5	2.1	0.13
	4	lit + shrub | robel + lit	6	−377.6	769.6	2.3	0.12
	29	1 | robel + lit[2]	4	−392.0	794.3	27.0	0.0
Sprague's pipit	1	robel | robel + lit	5	−433.5	879.4	0.0	0.31
	2	robel + shrub | robel + lit	6	−433.1	880.7	1.3	0.16
	3	robel + bg | robel + lit	6	−433.3	881.0	1.7	0.14
	4	lit + robel | robel + lit	6	−433.5	881.4	2.0	0.12
	5	robel + bg + shrub | robel + lit	7	−432.9	882.4	3.0	0.07
	6	lit + robel + shrub | robel + lit	7	−433.0	882.7	3.3	0.06
	7	lit + robel + bg | robel + lit	7	−433.1	882.8	3.4	0.06
	16	1 | robel + lit[2]	4	−439.5	889.3	9.9	0.0
Vesper sparrow	1	comp + rich | 1	4	−303.0	616.3	0.0	0.52
	2	comp + rich + rh | 1	5	−302.9	618.1	1.8	0.21
	3	comp + sim + rich | 1	5	−302.9	618.2	1.9	0.20
	17	1 | 1[2]	2	−311.1	628.4	12.1	0.0
Western meadowlark	1	cvlit | robel	4	−213.8	437.9	0.0	0.16
	2	cvlit + cvrob | robel	5	−213.1	438.5	0.6	0.12
	4	1 | robel[2]	3	−215.9	439.9	2.1	0.1

[1]lit indicates litter mass (kg · ha^{-1}); robel, vegetation volume (cm^3); bg, bare ground cover (%); shrub, shrub cover (%); cvlit, litter mass heterogeneity; cvrob, vegetation volume heterogeneity; cvbg, bare ground heterogeneity; comp, plant species composition; sim, similarity index; rich, plant species richness; rh, rangeland health score.
[2]Null model.

per sparrow abundance decreased on rangeland characterized by greater heterogeneity of vegetation structure in general (Table 3). Horned lark abundance was greatest in areas characterized by lower heterogeneity of bare ground cover and western meadowlark abundance was greatest in areas characterized by increasing heterogeneity of litter (Table 3).

Combining top models from each hypothesis (i.e., vegetation structure, structural heterogeneity, and plant community) provided little improvement in model fit across species (Table S1, available online at http://dx.doi.org/10.2111/REM-D-12-00140.s2). Combined models were within 2 AIC units of the best single model for all but vesper sparrow and horned lark. Model fit was improved for these species by the addition of two vegetation structure variables: vegetation volume ($\Delta AIC_c = -3.8$) and heterogeneity of bare ground cover ($\Delta AIC_c = -4.0$).

DISCUSSION

Our findings are consistent with previous research identifying vegetation structure as an important predictor of grassland bird abundance. We demonstrate that while rangeland health itself is not a strong predictor of bird abundance, structural components used to assign this index are. Since abundance varies with vegetation features by bird species, our results provide further evidence that landscape-level spatial heterogeneity in vegetation structure is necessary for the recovery of the grassland bird community (Samson and Knopf 1996; Fuhlendorf et al. 2006; Askins et al. 2007). Widespread adoption of livestock production strategies that maximize economic gains

through moderate grazing (Ritten et al. 2010) may reduce heterogeneity of vegetation structure and thereby limit the amount of available habitat for a number of species (Derner et al. 2009; Toombs and Roberts 2009). A mosaic of vegetation structure on rangelands is necessary to maximize grassland bird diversity and abundance at both the local and landscape scales (Fritcher et al. 2004; Fuhlendorf et al. 2006; Madden et al. 2000).

The rangeland health index received little support as a predictor of bird abundance. Although litter mass and bare ground are important to grassland birds (Fisher and Davis 2010), the categories used to estimate structural components of the rangeland health index may be too broad to explain variation in bird abundance. For example, our measures of litter that ranged from 8 kg · ha^{-1} to 1 121 kg · ha^{-1} were assigned to three categories for the rangeland health index (Saskatchewan PCAP Greencover Committee 2008). Although these categories may be useful for assessing rangelands, they may be too coarse to adequately relate bird abundance to rangeland health. Furthermore, shrub cover and density receive only 10 points in the rangeland health index and vegetation volume is not explicitly considered, yet both are known predictors of grassland bird abundance (Fisher and Davis 2010). Finally, plant community composition comprises 60% of the rangeland health index but it is not as important to bird habitat selection as vegetation structure (Fisher and Davis 2010; this study), which is allotted 40%. High rangeland health values are thought to represent improved ecological processes and better habitat quality for wildlife (Saskatchewan PCAP Greencover Committee 2008). This may only hold true for wildlife species whose habitat requirements are more closely linked to plant species composi-

Table 3. Model-averaged parameter estimates and relative variable importance values calculated over top-ranking models ($\Delta AIC_c \leq 4$) for abundance of 10 grassland bird species in southwestern Saskatchewan. Variable rank and name, cumulative weight of variable over top models (w_+), model-averaged parameter estimate (β^e), and unconditional standard error (U.SE) are presented.

Species	Rank	Variable[1]	w_+	β^e	U.SE
Baird's sparrow	1	lit	1.00	0.072[2]	0.03
	2	bg	0.84	−4.274[2]	1.93
	3	robel	0.64	1.198[2]	0.70
	4	shrub	0.41	−3.870	3.24
		Intercept	—	1.156[2]	0.23
Chestnut-collared longspur	1	lit	1.00	−0.120[2]	0.03
	2	robel	0.85	−1.354[2]	0.62
	3	shrub	0.30	2.861	2.89
	4	bg	0.28	0.478	1.09
		Intercept	—	2.181	2.89
Clay-colored sparrow	1	rich	0.94	7.387[2]	2.77
	2	comp	0.22	−7.600	19.59
	3	rh	0.22	−0.458	1.15
	4	sim	0.15	−0.239	1.25
	5	shrub	0.06	14.207[2]	7.42
		Intercept	—	−2.771[2]	1.04
Grasshopper sparrow	1	rich	0.56	−10.800[2]	4.05
	2	sim	0.35	−2.924[2]	1.50
	3	cvbg	0.25	0.319[2]	0.18
	4	cvrob	0.25	−3.315[2]	1.99
	5	cvlit	0.23	−1.190[2]	0.68
	6	comp	0.13	4.242	25.37
	7	rh	0.06	1.254	1.35
	8	robel	0.05	3.058[2]	1.13
	9	shrub	0.05	28.129[2]	13.89
		Intercept	—	2.057	2.28
Horned lark	1	cvbg	0.51	−0.349[2]	0.07
	2	robel	0.49	−2.479[2]	0.74
	3	lit	0.43	−0.067[2]	0.03
	4	bg	0.40	2.130[2]	1.04
	5	cvrob	0.22	0.585	0.46
	6	cvlit	0.14	−0.53[2]	0.14
	7	shrub	0.09	0.299	3.26
		Intercept	—	1.860[2]	0.23
McCown's longspur	1	robel	1.00	−6.876[2]	2.09
	2	shrub	0.78	−11.684[2]	5.92
	3	lit	0.77	−0.279[2]	0.15
	4	bg	0.63	2.982[2]	1.80
		Intercept	—	2.063[2]	0.34
Savannah sparrow	1	lit	1.00	0.115[2]	0.04
	2	bg	0.84	−4.324[2]	2.21
	3	shrub	0.83	6.697[2]	3.22
	4	robel	0.17	−0.053	0.88
		Intercept	—	0.320[2]	0.20
Sprague's pipit	1	robel	1.00	2.177[2]	0.67
	2	shrub	0.32	−3.145	3.51
	3	bg	0.29	−1.828	2.54
	4	lit	0.25	−0.16[2]	0.03
		Intercept	—	0.761[2]	0.18

Table 3. Continued.

Species	Rank	Variable[1]	w_+	β^e	U.SE
Vesper sparrow	1	comp	1.00	−43.977[2]	14.95
	2	rich	1.00	7.322[2]	1.96
	3	rh	0.22	−0.354	0.70
	4	sim	0.21	0.307	0.77
		Intercept	—	−2.332[2]	0.70
Western meadowlark	1	cvlit	1.00	0.727[2]	0.37
	2	cvrob	0.35	−1.406	1.16
	3	cvbg	0.18	−0.053	0.15
		Intercept	—	−1.259[2]	0.66

[1] lit indicates litter mass (kg · ha^{-1}); robel, vegetation volume (cm^3); bg, bare ground cover (%); shrub, shrub cover (%); cvlit, litter mass heterogeneity; cvrob, vegetation volume heterogeneity; cvbg, bare ground heterogeneity; comp, plant species composition; sim, similarity index; rich, plant species richness; rh, rangeland health score.

[2] Model parameter estimates with 85% confidence limits that do not include zero.

tion than vegetation structure, such as shrub–steppe birds (Wiens and Rotenberry 1981), or in cases where vegetation structure and composition are highly correlated.

Distinct patterns in the relationship between bird abundance and structural features related to rangeland health in our study echo those previously established in the literature (Bock et al. 1993; Madden et al. 2000; Fisher and Davis 2010) and outline the range of habitat conditions required by the grassland bird community. Baird's, grasshopper, and savannah sparrows and Sprague's pipit, whose abundances generally increased with vegetation cover, are typical of lightly to moderately grazed dry mixed grasslands (Madden et al. 2000; Wheelwright and Rising 2008). Horned lark, chestnut-collared longspur, and McCown's longspur, whose abundance decreased with greater amounts of vegetative cover and increased with bare ground cover, are typically associated with moderate to heavy grazing (With 1994b; Beason 1995; Davis et al. 1999). This partitioning of the grassland bird community along a continuum of habitat features may be attributed to its evolution with grazing by large herbivores on the northern Great Plains (Knopf 1996) and the subsequent niches resulting from the heterogeneity in vegetation structure, competitors, and prey (Wiens 1973). We did not find strong relationships between structural variables related to rangeland health and abundance for vesper sparrow or western meadowlark. Both species occupy a wide range of grassland types (Jones and Cornely 2002; Davis and Lanyon 2008) and the variation of vegetation structure represented in our study likely fell within their niche requirements.

Although vegetation structure was an important predictor of abundance in our study, our results suggest that plant species richness and within-habitat heterogeneity are also important for some species. Plant species richness and within-habitat heterogeneity are not considered important drivers of grassland bird abundance, nor are they frequently examined in field studies (Fisher and Davis 2010). Our results are consistent with others in that grasshopper sparrow was associated with somewhat homogenous litter cover and vegetation height (Wiens 1973) and patchy bare ground (Vickery 1996) whereas horned lark was associated with homogenous bare ground cover (Beason 1995). Plant species
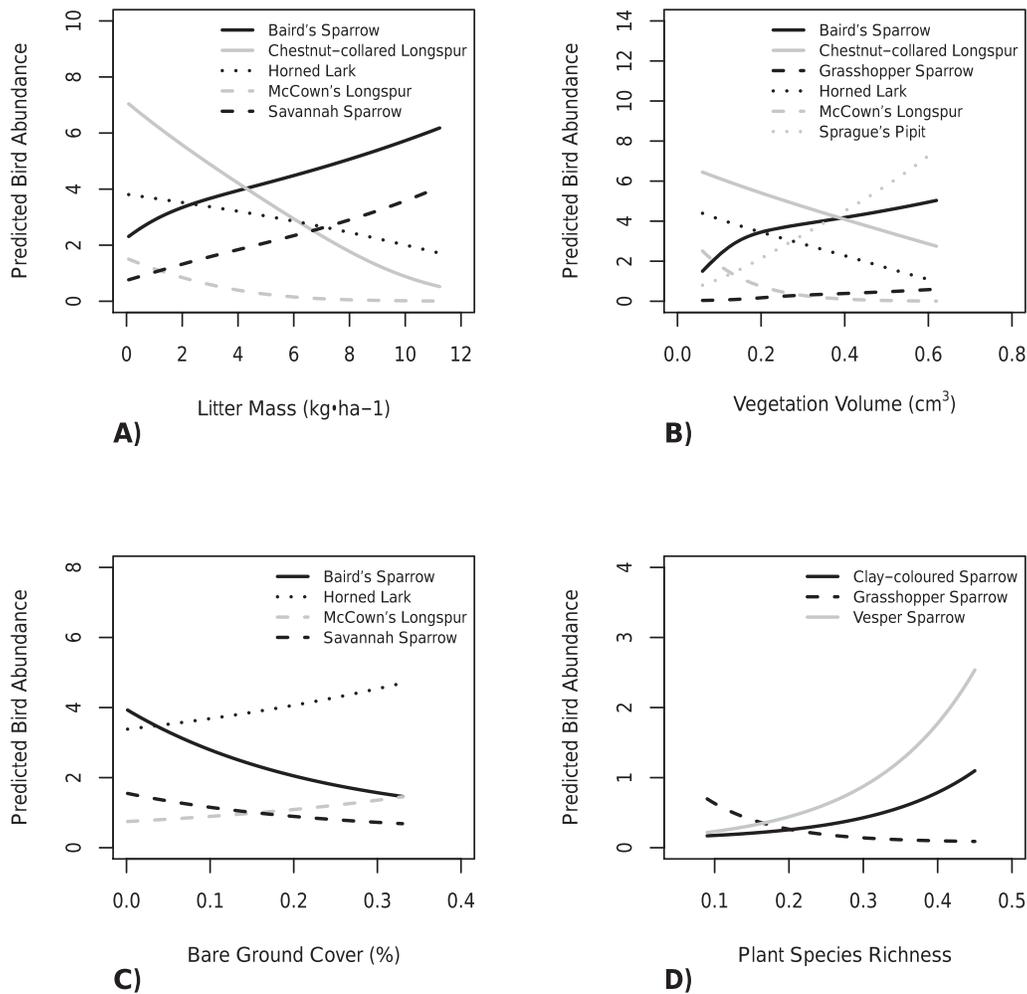
Figure 1. Relationships between predicted bird abundance and covariates where 85% confidence intervals do not include zero: **A,** litter mass (kg · ha^{-1}); **B,** vegetation volume (cm); **C,** bare ground cover (%); and **D,** plant species richness for nine species of grassland birds. Each x-axis represents the range of values recorded in the field, scaled by 0.01 to ensure model convergence. Model averaged estimates and unconditional standard errors for relationships are reported in Table 3.

richness may represent greater structural complexity (Fisher and Davis 2010) or food availability (Wiens 1969; Rodenhouse 1981; Wiens and Rotenberry 1981; Sample 1989) whereas structural heterogeneity may provide a range of available shelter, nesting, or foraging sites (Wiens 1974a, 1974b; Fuhlendorf et al. 2006).

IMPLICATIONS

We demonstrate that although rangeland health itself is not a strong predictor of bird abundance, structural components used to assign this index are. If the rangeland health index is to be used to assess bird habitat, we recommend that it be altered to reflect the importance of vegetation structure. For example, greater value could be attributed to refined categories of litter, and vegetation volume (Robel et al. 1970) could be added to the rangeland health index. We advocate for future research that examines relationships between rangeland health and grassland biodiversity and determines the extent to which indices of rangeland health are currently used by rangeland

managers on private and public lands and whether using such measures would be feasible for private livestock producers.

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