

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/251520415>

Johnson TN, Kennedy PL, DelCurto T, Taylor RV. Bird community responses to cattle stocking rates in a Pacific Northwest bunchgrass prairie. *Agriculture, Ecosystems and Environment*

ARTICLE *in* AGRICULTURE ECOSYSTEMS & ENVIRONMENT · NOVEMBER 2011

Impact Factor: 3.4 · DOI: 10.1016/j.agee.2011.10.003

CITATIONS

8

READS

108

4 AUTHORS:



[Tracey N. Johnson](#)

University of Idaho

16 PUBLICATIONS 56 CITATIONS

SEE PROFILE



[Patricia L. Kennedy](#)

Oregon State University

101 PUBLICATIONS 1,190 CITATIONS

SEE PROFILE



[Tim Delcurto](#)

Oregon State University

6 PUBLICATIONS 95 CITATIONS

SEE PROFILE



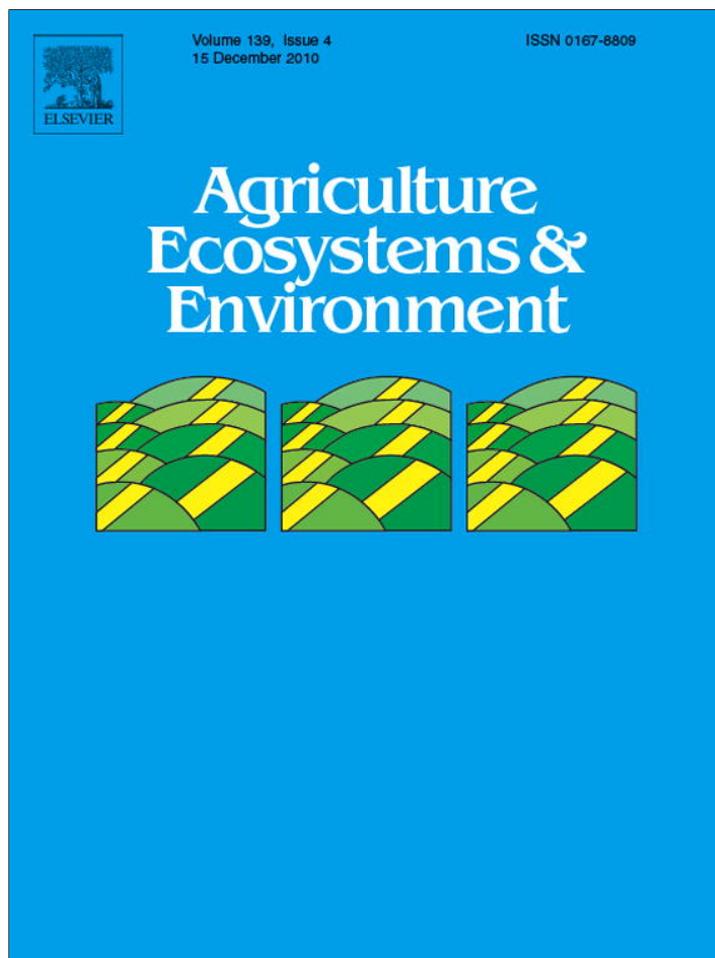
[Robert V Taylor](#)

The Nature Conservancy

22 PUBLICATIONS 85 CITATIONS

SEE PROFILE

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

Contents lists available at [SciVerse ScienceDirect](http://www.elsevier.com/locate/agee)

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Bird community responses to cattle stocking rates in a Pacific Northwest bunchgrass prairie

Tracey N. Johnson^{a,*}, Patricia L. Kennedy^a, Tim DelCurto^b, Robert V. Taylor^c^a Department of Fisheries and Wildlife and Eastern Oregon Agricultural Research Center, Oregon State University, 372 South 10th Street, Union, OR 97883, USA^b Department of Animal Science and Eastern Oregon Agricultural Research Center, Oregon State University, 372 South 10th Street, Union, OR 97883 USA^c The Nature Conservancy, 906 South River Street, Enterprise, OR 97828, USA

ARTICLE INFO

Article history:

Received 14 March 2011

Received in revised form 3 October 2011

Accepted 5 October 2011

Keywords:

Ground-nesting bird

Vegetation structure

Rangeland management

Habitat complexity

Nonmetric multidimensional scaling

Sustainable grazing

ABSTRACT

In 2006–2010, effects of four different cattle stocking rates (0, 14.4, 28.8, and 43.2 animal unit months) were compared, representing 0%, 20%, 32%, and 46% utilization of vegetation by domestic livestock, on vegetation structure (as indexed by visual obstruction), and songbird population and apparent nest density, community composition, and diversity in a Pacific Northwest bunchgrass prairie in northeastern Oregon, USA. Overall paddock-level visual obstruction decreased and structural heterogeneity increased with increasing stocking rates, and those effects carried over 1 year after grazing had ceased. Most species were able to locate nesting sites regardless of differences in visual obstruction, except western meadowlark and vesper sparrow, for which obstruction was lower in paddocks with higher stocking rates. Apparent nest density for grasshopper sparrows was negatively affected by higher stocking rates. Grazing effects on absolute songbird population density were restricted to negative effects of higher stocking rates on savannah sparrows, but this relationship was not observed until 1 year after grazing had ceased. Songbird community composition differed between control and heavily-grazed paddocks, driven by an increase in the proportion of horned larks and a decrease in the proportion of savannah sparrows in heavily-grazed paddocks from pre-treatment to post-treatment years. Bird diversity indices were unaffected by stocking rate. Negative effects of high stocking rates on densities of two species and the absence of any clear positive effect for the other three species suggest high stocking rates as applied in this experiment may not provide suitable habitat for all grassland songbirds. The absence of negative responses of density to low and moderate stocking rates suggests these grazing regimes generally provided suitable habitat for all species.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

In North America, the loss of grassland habitat from conversion to farmland, as well as management practices designed principally to maximize livestock production, has likely contributed to significant population declines of grassland-obligate wildlife including several species of grassland-breeding birds (Vickery et al., 1999; Askins et al., 2007; With et al., 2008). Large-scale loss of critical grassland habitat highlights the importance of appropriate management and conservation measures for remaining grasslands, most of which are grazed by domestic livestock (Lubowski et al., 2006; Derner et al., 2009).

Grassland-breeding songbirds may be particularly vulnerable to the effects of livestock grazing because of its influence on vegeta-

tion structure. Altered vegetation structure can influence songbird food availability through effects on invertebrate abundance or by affecting the availability of foraging sites (Vickery et al., 2001; DeBano, 2006). Additionally, changes in vegetation height, density, and life form can affect suitability of grazed areas as breeding sites for many species (Vickery et al., 2001). Where grazing occurs after a nesting attempt has been initiated, vegetative cover near the nest may be reduced, diminishing nest concealment and potentially increasing the likelihood that a nest is depredated (Johnson and Temple, 1990). Alternatively, where grazing occurs before nesting is initiated, altered vegetation structure may affect availability of suitable nest sites, influencing settlement decisions and ultimately density of breeding birds (Fondell and Ball, 2004).

Some researchers have suggested livestock grazing can be used as a management tool to facilitate particular habitat conditions for grassland birds; however, they acknowledge the effects of grazing on bird habitat remain unpredictable (Derner et al., 2009). One range management practice that can be manipulated is grazing intensity, which is defined as the “frequency of plant defoliation” by herbivores and when increased leads to reduced stubble height

* Corresponding author. Present address: Department of Zoology and Physiology, Box 3166, 1000 East University Avenue, University of Wyoming, Laramie, WY 82071, USA. Tel.: +1 307 766 5299; fax: +1 307 766 5625.

E-mail address: tjohns67@uwyo.edu (T.N. Johnson).

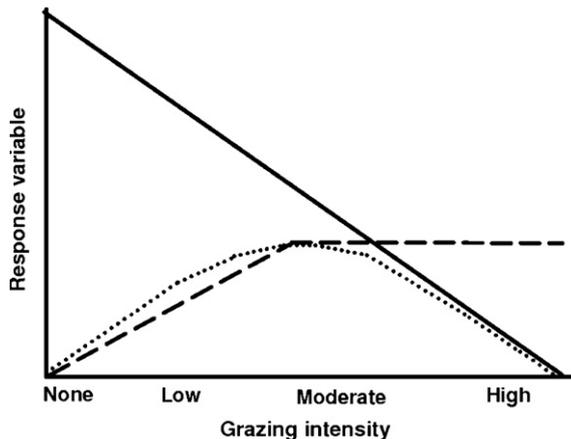


Fig. 1. Predictions of how structural heterogeneity, bird diversity, and songbird density may change in response to livestock grazing intensity. Solid line: linear response (may be negative or positive); dashed line: threshold response; dotted line: quadratic response. See text for more details.

and aboveground plant biomass relative to ungrazed areas (Bransby et al., 1988). Grazing can enhance structural heterogeneity of vegetation up to a point above which it results in more homogenous structure (Ausden, 2007).

A replicated, experimental approach was used to evaluate responses of grassland songbirds to four different cattle stocking rates. The objectives of this study were to evaluate effects of cattle stocking rate on: (1) vertical vegetation structure, (2) grassland songbird density, and (3) grassland songbird diversity and community composition. Further, a multivariate approach was used to examine the relationship between songbird community composition and vegetation structure at multiple spatial scales to enhance understanding of grassland songbird responses to grazing-induced changes in vegetation structure.

Vegetation structure was hypothesized to differ among pastures with different stocking rates, and these structural changes were predicted to affect grassland-breeding bird density and community composition. Specifically, vegetation height and density was expected to decrease linearly with higher stocking rates, but structural heterogeneity of vegetation was expected to increase in areas grazed at low to moderate stocking rates relative to ungrazed controls, and to decrease or exhibit a threshold response at high grazing intensity (Fig. 1). Bird diversity and total songbird density were expected to increase at low to moderate stocking rates and decrease at high stocking rates because of a higher number of suitable nesting and foraging sites for multiple species where structural heterogeneity is highest (Fig. 1). Single-species songbird population density was expected to be a linear function of stocking rate and could increase or decrease depending on species-specific habitat preferences (Fig. 1). Furthermore, composition of breeding bird communities was expected to differ among areas grazed at different stocking rates due to the creation of different numbers of nesting micro-sites suitable for each species in the community.

2. Materials and methods

This study was conducted at The Nature Conservancy's Zumwalt Prairie Preserve (ZPP) in northeastern Oregon, USA. The 13,269 ha, high elevation (average 1500 m) preserve is located within the largest remaining tract of Pacific Northwest bunchgrass prairie in North America, and provides breeding habitat for several species of grassland birds including: savannah sparrow (*Passerculus sandwichensis*), horned lark (*Eremophila alpestris*), western meadowlark (*Sturnella neglecta*), grasshopper sparrow (*Ammodramus savannarum*), and vesper sparrow (*Poocetes gramineus*). At the

Table 1

Grazing treatments randomly assigned to each 40-ha paddock within each block ($n = 4$) on the Zumwalt Prairie Preserve, northeastern Oregon, USA.

Treatment	Animal unit months ^b	Mean % forage utilization ^c (SD)
Control ^a	0.00	9.52 (3.05)
Low	14.4	20.18 (4.08)
Moderate	28.8	31.66 (5.72)
High	43.2	46.09 (11.68)

^a Control treatments represented no use by domestic livestock.

^b One animal unit is defined as a mature cow and calf and consumes 20 kg/d per 42 d grazing period.

^c Forage utilization was averaged over the two treatment years (2007–2008). Methods for determining forage utilization are presented in Wyffels (2009).

ZPP, upland sites are presently dominated by cool-season native species, in particular Idaho fescue (*Festuca idahoensis*) and blue-bunch wheatgrass (*Pseudoroegneria spicata*). Climate is semi-arid and mean annual temperature is 7.4 °C (Western Regional Climate Center, 2009). Mean annual precipitation is 49.0 cm, with an average of 18.3 cm occurring from April through July.

2.1. Experimental design

To evaluate predictions, a randomized complete block design with one factor (livestock grazing) and four grazing treatment levels (stocking rate) was used. All study plots were rested from grazing for 2 years prior to the start of our 4 years experiment. Blocking controlled for potential environmental heterogeneity created by variation in historical grazing management. In 2006, fences were erected around 160 ha blocks, and within each block, four 40 ha paddocks were partitioned. Pre-treatment data on vegetation structure and songbird population density (see Section 2.3) were collected in each paddock during May–July 2006. In 2007 and 2008, cattle grazed paddocks from 21 May to 3 July and 29 May to 9 July, respectively. Each of the four blocks contained one replicate paddock of each randomly assigned stocking rate ($n = 4$ replicates of each stocking rate; Table 1). Stocking rates corresponding to each grazing intensity treatment were developed using cattle forage utilization data previously collected at the ZPP (DelCurto and Williams, unpublished results; Table 1). The moderate treatment was based on stocking rates used by area ranchers (40% forage removal). The three other grazing treatments were designed to represent light (20%), heavy (60%), or no grazing (control) of vegetation by cattle. In each year, 48 yearling heifers and 192 cow-calf pairs were stratified by age and body condition, and randomly assigned to a grazing treatment (Wyffels, 2009). Actual forage utilization values for each stocking rate are presented in Table 1. Timing of grazing coincided with the growing period of dominant grass species at the site and the peak period of reproductive activity for grassland songbirds. In 2009, data on post-treatment responses were recorded during May–July, when no grazing occurred in study paddocks.

2.2. Sampling methods

To evaluate vegetation structure in paddocks grazed at different stocking rates, paddock-level estimates of visual obstruction (VO) were measured during the passerine breeding season in each year. Visual obstruction is correlated with aboveground biomass in grasslands and represents a measure of the vertical height and density of vegetation (Robel et al., 1970; Damiran et al., 2007). Evaluation of changes in vegetation structure was limited to VO because this parameter was expected to be most influenced by stocking rate in the near-term, and it is easily measured over large areas. Visual obstruction was measured using a Robel pole held perpendicular to the ground, where an observer recorded the height of the lowest visible dm from 4 m away and 1 m off the ground (Robel

et al., 1970). From 26 June to 24 July in the pre-treatment year and post-treatment year, two VO measurements were taken 1.5 m away from each of 36 vegetation sampling points systematically placed within each paddock ($n = 72$ measurements). During the two treatment years (2007–2008), paddock-level VO was measured at 10 m intervals along eight 100 m transects within each paddock ($n = 80$ measurements) within 24 h after cattle were removed from paddocks. Transects were stratified randomly by physiographic characteristics in each paddock to account for differences in vegetation biomass, and thus vegetation structure, and included hilltops, swales, rocky outcroppings, and slopes. Distribution of transects among physiographic classes was not standardized, but depended on the number of different physiographic features present within each paddock. Structural heterogeneity was measured as the coefficient of variation of paddock-level VO.

To estimate bird population density, 5 min fixed radius point counts were conducted (Ralph et al., 1995) using distance-sampling from mid-May to early July from 2006 to 2009. Each paddock contained 16 point transects systematically placed at 150 m intervals, but excluded a 16 m buffer around the inner edge of each paddock to minimize potential fence line effects on bird surveys. Each point was visited twice in 2006, and three times in 2007–2009. Point counts were conducted by five different observers over the 4 years of the study. Surveys were conducted from 06:30 to 10:30 (PST) in all years, and surveys were never conducted during periods of precipitation, fog, or winds exceeding 5.3 m/s. All birds seen or heard within 75 m were recorded. Distance from the observer to the location each bird was first detected was estimated to the nearest meter using a laser range finder.

Grassland songbird nests were counted by dragging a 25 m rope between two observers across vegetation and then intensively searching areas from which adult birds flushed (Winter et al., 2003). Each paddock was systematically searched in its entirety three times in 2007 and twice in 2008 from 1 May to 25 July. Nests were also located opportunistically during vegetation surveys. To evaluate nest-site selection, VO was measured at nests once a nesting attempt was complete ($n = 157$ nests in 2007, $n = 115$ in 2008; no nest data are available for 2006 and 2009). Nest-level VO was measured by inserting a Robel pole into the nest cup and recording VO once from each cardinal direction. The four VO values were then averaged to obtain one value for each nest.

2.3. Data analysis

Mixed models were used to evaluate trend of response variables relative to stocking rates. Response variables included paddock-level VO, structural heterogeneity of vegetation, total songbird population density, and songbird species diversity. Nest-level VO, population density and apparent nest density were additional response variables modeled separately for each species. Data were modeled using PROC MIXED in SAS System V. 9.3.1 (SAS Institute Inc., 2002–2003). The number of cattle was included as a continuous predictor and tested for linear and quadratic effects on response variables. Because initial songbird density within a paddock could influence changes in density related to grazing intensity, pre-treatment density from 2006 was used as a covariate when estimating trends in songbird population density. To address the question of whether structural heterogeneity influenced diversity or total density of songbirds in a paddock, the coefficient of variation of paddock-level VO was used as a covariate when evaluating effects on diversity and total songbird density. To evaluate the relationship between nest density and vegetation structure, mean paddock-level VO was used as a covariate when modeling effects on nest density.

Number of livestock and year were assigned as fixed effects, and block, block \times treatment and block \times year as random effects.

Year was a fixed effect because treatments could have cumulative effects over time since livestock remove vegetation every season, and the amount and distribution of remaining vegetation in year $t + 1$ depends on the amount of vegetation removed in year t . A random effect of block allows us to make inferences beyond blocks used in this study; a random effect of block \times treatment and block \times year identifies each paddock in each year as the experimental unit. Denominator degrees of freedom were estimated in each analysis using the Satterthwaite approximation method (Littell et al., 2006). Prior to testing models, correlations among all predictor variables were evaluated to ensure highly correlated variables ($|r| > 0.6$) were not included in the same model. An alpha ≤ 0.05 was considered significant. Data were log-transformed where needed to satisfy assumptions of normality and homogeneity of variance. Finally, to identify the most parsimonious model for each response variable, backward elimination of fixed-effect predictor variables was implemented based on the smallest F -value (Hocking, 1976).

Breeding bird densities were estimated using Program Distance Ver. 5 Release 5 (Thomas et al., 2005) to account for the influence of potential differences in detection probabilities among species and habitats on density estimates. Preliminary analyses included all observations and suggested no differences in detection probabilities among observers based on comparisons of point estimates and 95% confidence intervals (Ramsey and Schafer, 2002). Detection functions were fitted separately for each paddock to ensure that paddock-level density estimates did not co-vary and comparisons of songbird density could be made among treatments. Because this resulted in several species with a low number of detections, the approach outlined in Alldredge et al. (2007) was followed. Two groups of species from the community of grassland passerines that breed on the ZPP were created. A common detection function was assumed among species within a group, and pooled observations of those species were used to increase precision of density estimates. The first group included savannah sparrows, grasshopper sparrows, and vesper sparrows, and the second group included horned larks and western meadowlarks. Species assignments to a group were chosen based on similarity in behavior, plumage crypticity, and song characteristics. Other rare species were omitted from all analyses because they could potentially obscure important patterns in breeding bird density. Candidate models included uniform key function with cosine and simple polynomial adjustments, and half-normal key function with cosine, simple polynomial, or hermite polynomial adjustments. Best models were selected using goodness-of-fit tests and Akaike's Information Criterion corrected for small sample size (AIC_c; Buckland et al., 2001; Burnham and Anderson, 2002).

To describe relationships among songbird community composition, paddock-level vegetative structure, and nest-site preferences unique to each species (hereafter, species traits), data collected from point counts were analyzed using a multivariate approach. Coefficient of variation for total density for each species was moderate (96%) so density data were log-transformed to account for this variation (McCune and Grace, 2002). Subsequently, the CV for species totals decreased to $<40\%$. Transformed density data were evaluated for skewness and extreme values by comparing the standard deviation of mean Euclidean distances for each paddock to all other paddocks (McCune and Grace, 2002). One paddock was identified as an outlier in 2007; however, it was a weak outlier (2.7 standard deviations) and was therefore retained for analysis.

To determine whether there were differences in breeding bird community composition among treatments within each year, a Blocked Multi-Response Permutation Procedure (MRBP; Mielke, 1984) was conducted on the transformed data. Median alignment within blocks was used, which focuses the analysis on differences among treatments within a given experimental block and accounts for the blocking in the experimental design (McCune and

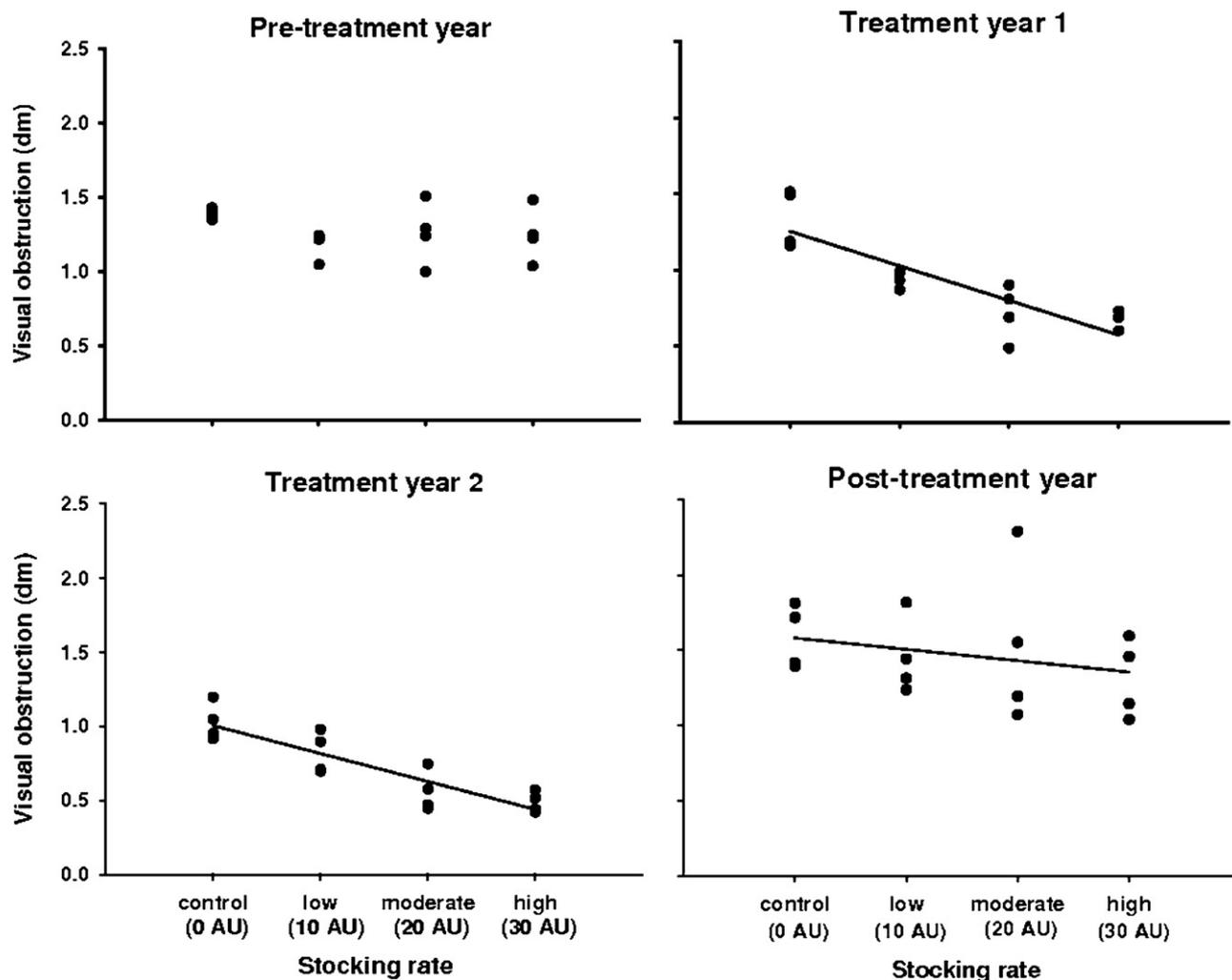


Fig. 2. Mean paddock-level visual obstruction for four stocking rates ($n=4$ replicates of each stocking rate) on the Zumwalt Prairie Preserve, northeastern Oregon, USA, 2006–2009. Significant trends from a mixed model are indicated with regression lines. AU: number of animal units.

Grace, 2002). Stocking rate treatments were used as *a priori* groups for comparison of community composition. Distances were calculated using the Euclidian measure and groups were defined by treatments (each group included four paddocks). Non-metric multidimensional scaling (NMS) was used to elucidate the MRBP results and evaluate the relationship between grassland-breeding songbird community composition and stocking rate, year, and VO values (Kruskal, 1964; Mather, 1976). Data from all years were included in the MRBP analysis; however, only data from 2007 to 2009 were included in the ordination because including pre-treatment data from 2006 would have obscured any treatment-related patterns.

Euclidean distance measurement was used for the ordination. Final dimensionality of data was assessed by evaluating final stress (where stress is a measure of departure from monotonicity between distance in original species space and distance in reduced ordination space) vs. the number of dimensions and by performing a randomization test (250 runs; McCune and Grace, 2002). To address the potential biological factors influencing patterns in breeding bird density and VO, values of paddock- and nest-level VO were overlaid onto the final ordination. Correlations of vectors from the environmental and species trait matrices with axes from the ordination represent the direction and strength of relationships. All multivariate analyses were conducted in PC-ORD Version 6.9 (McCune and Mefford, 2009).

3. Results

There was a significant year-by-treatment interaction effect for mean paddock-level VO ($F_{3,33} = 6.70$, $P < 0.01$). There was no pre-existing trend in paddock-level VO the year before cattle grazed (2006: $\beta = -0.004$, $t = -1.12$, $df = 42.8$, $P = 0.27$; Fig. 2). After cattle were allowed to graze for 6 weeks at different intensities, decreased VO corresponding to increased stocking rate was observed at the paddock level in both treatment years (2007: $\beta = -0.02$, $t = -6.28$, $df = 42.8$, $P < 0.0001$; 2008: $\beta = -0.02$, $t = -5.20$, $df = 42.8$, $P < 0.0001$). Post-treatment data indicated the difference in paddock-level VO among treatments remained at least 1 year after grazing ceased (2009: $\beta = -0.008$, $t = -2.08$, $df = 42.8$, $P = 0.04$). There were significant quadratic ($F_{1,10} = 5.03$, $P = 0.05$) and linear year-by-treatment interaction effects ($F_{3,33} = 3.95$, $P = 0.02$) for structural heterogeneity. No pre-existing differences in structural heterogeneity were detected before cattle were allowed to graze (2006: $\beta = 0.74$, $t = 1.97$, $df = 15.3$, $P = 0.07$). Heterogeneity increased with increasing stocking rate in the first year of grazing ($\beta = 1.56$, $t = 4.13$, $df = 15.3$, $P < 0.001$) and the second year of grazing ($\beta = 1.56$, $t = 4.15$, $df = 15.3$, $P < 0.001$). Post-treatment data indicated a carryover effect of stocking rate and there was higher structural heterogeneity in paddocks that had been grazed at a higher stocking rate at least 1 year after grazing ceased (2009: $\beta = 1.30$, $t = 3.34$, $df = 15.3$, $P < 0.01$). Over all years, however, the final model suggested a quadratic effect

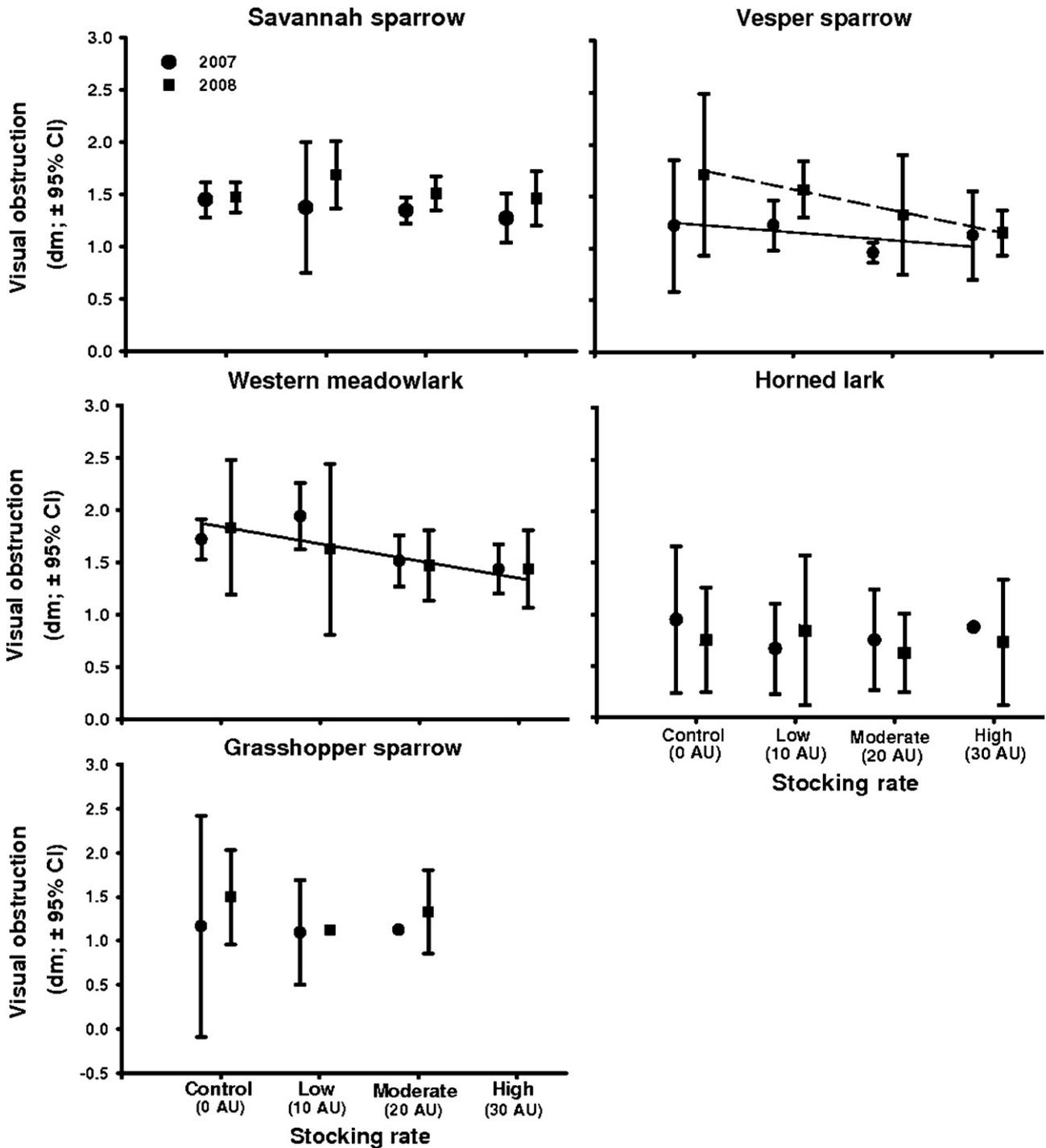


Fig. 3. Mean nest-level visual obstruction for five species of songbird nesting in paddocks exposed to four experimental stocking rates in 2007–2008 on the Zumwalt Prairie Preserve, northeastern Oregon, USA. Significant trends from a mixed model are indicated with regression lines. AU: number of animal units.

of stocking rate on structural heterogeneity where heterogeneity increased from controls to moderate stocking rates, but decreased at the highest stocking rate.

There were significant effects of year ($F_{1,3} = 18.13, P = 0.02$) and stocking rate ($F_{1,53} = 18.37, P < 0.0001$) on nest-level VO for vesper sparrows (Fig. 3). Nest-level VO for vesper sparrows was lower in 2007 ($\bar{x} = 1.17 \text{ dm} \pm 0.07 \text{ dm, SE}$) than in 2008 ($\bar{x} = 1.41 \text{ dm} \pm 0.06 \text{ dm, } t = -3.36, \text{ df} = 3, P = 0.04$), but decreased with higher stocking rates similarly in both years ($\beta = -0.01, t = -4.29, \text{ df} = 53, P < 0.0001$). There was a significant effect of stocking rate on nest-level VO for western meadowlarks ($F_{1,23} = 7.36, P = 0.01$;

VO at the nest decreased similarly in both treatment years with increased stocking rate ($\beta = -0.01, t = -2.71, \text{ df} = 23, P = 0.01$). There were no significant effects of stocking rate or year on nest-level VO for savannah sparrows, horned larks, and grasshopper sparrows.

3.1. Population and apparent nest density

Estimated songbird population density within each paddock ranged from 0 to 1.93 individuals per ha for each species (Appendix A), and total population density ranged from 0.73 to 3.0 individuals per ha. There were significant year-by-treatment interaction

effects ($F_{2,21.6} = 3.92, P = 0.04$) and pre-treatment density effects ($F_{1, 8.79} = 9.27, P = 0.01$) on savannah sparrow density, which was negatively correlated with higher stocking rates only after grazing had ceased (2009: $\beta = -0.03, t = -2.24, df = 14.6, P = 0.04$). Pre-treatment density explained 20.1% of the variation in savannah sparrow density. Vesper sparrow and horned lark density was affected by pre-treatment density (vesper sparrow: $F_{1,12} = 8.69, P = 0.01$; horned lark: $F_{1,13.7} = 7.87, P = 0.01$), but stocking rate was not included in the final model for either species. Pre-treatment density explained 18.7% of the variation in vesper sparrow density and 38.8% of the variation in horned lark density. There were no significant effects of any predictor variable on grasshopper sparrow or western meadowlark population density. Total density (all species combined) was affected by year ($F_{3,9} = 12.2, P < 0.01$) but not stocking rate. Total density was higher in 2006 than any other year of the study (2006–2007: mean difference = 0.47 individuals per ha, $t = 4.04, df = 9, P < 0.01$; 2006–2008: mean difference = 0.69 individuals, $t = 5.92, df = 9, P < 0.001$; 2006–2009: mean difference = 0.41 individuals, $t = 3.50, df = 9, P < 0.01$). All other years were similar to each other in total density.

Over 2 years, 275 nests were located (158 in 2007 and 117 in 2008). Savannah sparrow nests were most common ($n = 92$), followed by vesper sparrow ($n = 76$), western meadowlark ($n = 45$), horned lark ($n = 44$), and grasshopper sparrow ($n = 18$; Appendix A). Grasshopper sparrow apparent nest density decreased with increased stocking rate ($F_{1,11} = 6.97, P = 0.02$; $\beta = -0.02, t = -2.39, P = 0.04$) and no grasshopper sparrow nests were located in the high stocking rate treatment (Appendix A). The effect of stocking rate on western meadowlark apparent nest density depended on year ($F_{1,11} = 4.97, P = 0.05$). In 2007, there was a positive effect of stocking rate on meadowlark nest density ($\beta = 0.02, t = 2.28, P = 0.03$), but in 2008 there was no effect ($\beta = -0.01, t = -0.56, P = 0.58$). There were no significant effects of stocking rate or year on savannah sparrow, vesper sparrow, or horned lark apparent nest density.

3.2. Community composition

The MRBP showed differences in patterns of breeding bird community composition among treatments during the second treatment year and 1 year post-treatment (Table 2). Pairwise comparisons of all stocking rates by year revealed the relationship between heavily grazed paddocks (high) and ungrazed paddocks (control) dominated patterns in differences in community composition among treatments. This difference was driven by a decrease in relative density of savannah sparrows (from 56% of the bird community in 2006 to 36% in 2009) and an increase in relative density of horned larks (from 19% in 2006 to 38% in 2009) in heavily-grazed (high) paddocks from the pre-treatment to post-treatment year. There was also evidence that patterns of community composition differed between controls and lightly grazed (low) treatments 1 year after grazing ceased, but there were no clear directional changes for any one species across years that is responsible for this pattern. Homogeneity within treatment groups that differed in composition was fairly high ($A = 0.19–0.38$). Songbird diversity ranged from 0.91 to 1.60 (Shannon Diversity Index), and there were no significant effects of stocking rate or year on diversity.

Ordination of the paddock-level dataset of transformed total density yielded a 3-dimensional solution (final stress = 7.5, instability < 0.00001) and total $R^2 = 0.96$ (axis 1: $R^2 = 0.15$; axis 2: $R^2 = 0.65$; axis 3: $R^2 = 0.16$). The R^2 value represents the variance in the original distance matrix represented in ordination space. Paddock-level VO and the variation in paddock-level VO are at opposite ends of axis 1, suggesting that axis 1 represents a gradient of paddock-level vegetation structure where higher VO is correlated with less variability in VO (Fig. 4 and Table 3). Axis 2 separates mean nest-level VO and the variability in nest-level VO and represents a gradient of

Table 2

Results of a blocked multi-response permutation procedure comparing ground-nesting songbird community composition at the Zumwalt Prairie Preserve, northeastern Oregon, USA.

Treatment comparison	Year	T ^a	A ^b	P-value
Control vs. low	2006	-0.65	0.04	0.27
	2007	0.40	-0.04	0.66
	2008	-0.33	0.03	0.37
	2009	-1.55	0.23	0.07
Control vs. moderate	2006	0.56	-0.07	0.67
	2007	0.67	-0.05	0.73
	2008	0.61	-0.04	0.71
	2009	-0.46	0.06	0.28
Control vs. high	2006	0.57	-0.05	0.69
	2007	0.54	-0.06	0.70
	2008	-1.93	0.19	0.04*
	2009	-2.33	0.38	0.03*
Low vs. moderate	2006	0.87	-0.15	0.82
	2007	0.91	-0.09	0.82
	2008	0.16	-0.02	0.50
	2009	1.11	-0.13	0.87
Low vs. high	2006	1.76	-0.15	0.97
	2007	1.06	-0.13	0.86
	2008	0.37	-0.05	0.57
	2009	0.98	-0.10	0.84
Moderate vs. high	2006	1.07	-0.13	0.87
	2007	-0.46	0.02	0.31
	2008	-0.56	0.05	0.26
	2009	-0.53	0.04	0.23

^a $T = (\delta - m_\delta) / s_\delta$, where δ = the weighted mean within-group distance, m_δ = mean of δ under the null hypothesis, and s_δ = standard deviation of δ under the null hypothesis.

^b Chance-corrected within-group agreement, describing within-group similarity; cf. McCune and Grace (2002).

* Statistically significant differences in group composition.

local-scale vegetation structure where higher values of mean nest-level VO are correlated with less variability in vegetation structure at the nest site (Fig. 4 and Table 3). Treatments did not show a strong association with any axis, although paddocks grazed with the highest stocking rates were concentrated at the upper end of axis 2 (Fig. 4 and Table 3). Vesper sparrows and horned larks had strong associations with shorter and more heterogeneous vegetation at the nest level. Savannah sparrows and grasshopper sparrows had strong associations with taller and less heterogeneous structure at the paddock level (Table 3). Western meadowlarks and grasshopper sparrows had strong associations with axis 3. However, because axis 3 did not capture any environmental or species trait variables

Table 3

Correlations of each variable with axes obtained from a non-metric multidimensional scaling ordination of ground-nesting songbird densities at the Zumwalt Prairie Preserve, northeastern Oregon, USA. Year = 2007 and 2008.

Variable	Correlation coefficient	
	Axis 1	Axis 2
Year	0.21	0.21
Stocking rate	-0.22	0.23
<i>Species</i>		
Savannah sparrow	0.66	-0.63
Vesper sparrow	-0.05	0.90
Western meadowlark	0.29	-0.26
Horned lark	0.26	0.87
Grasshopper sparrow	0.69	0.16
<i>Visual obstruction (VO)</i>		
Paddock-level VO	0.39	-0.27
Paddock-level VO coefficient of variation	-0.39	0.42
Nest-level VO	0.05	-0.59
Nest-level VO coefficient of variation	-0.57	0.97

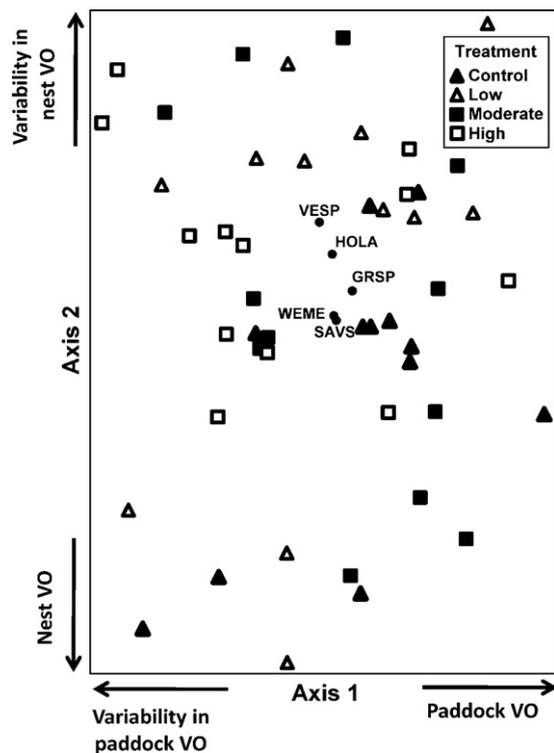


Fig. 4. Ordination of paddocks (2007–2009) in species space using non-metric multidimensional scaling. Arrows along axes represent relationships of environmental (paddock-level visual obstruction; VO) and species trait (nest-level VO) variables with each axis: VO (dm). Species codes: VESP (vesper sparrow); HOLA (horned lark); GRSP (grasshopper sparrow); WEME (western meadowlark); SAVS (savannah sparrow).

included in the NMS, the third axis was excluded from the graphic presentation for ease of interpretation.

4. Discussion

Decreased vegetation height and density (as indexed by visual obstruction) at the paddock-level was consistent with predictions and results reported from similar studies of grazing intensity (Salo, 2003; Townsend and Fuhlendorf, 2010). A similar magnitude of effect of stocking rate was observed on paddock-level vegetation structure in both treatment years, although spring 2007 was relatively dry (total precipitation in May and June was >2.5 cm below the 36 years average), whereas 2008 was wet and cool (Hansen et al., 2010) resulting in markedly lower visual obstruction overall. These results suggest the effect of cattle stocking rate on vegetation structure is a general response even under varying climatic conditions, plant phenology, and primary productivity.

Significant quadratic effects of stocking rate over all years support predictions that structural heterogeneity is highest at moderate stocking rates and lower at heavily-grazed and ungrazed paddocks. However, pre-treatment data suggest less heterogeneity in vegetation structure existed in paddocks randomly selected for high intensity grazing before grazing commenced, and this likely influenced the response pattern. Further, the relationship depended on year and responses during and after treatment years were linear and positive. Thus, we interpret these results as evidence that stocking rate has a linear effect on structural heterogeneity at the observed forage utilization levels. High stocking rates in this study did not result in more homogeneous vegetation structure than moderate stocking rates as predicted under a quadratic response. Higher structural heterogeneity with increasing stocking rate suggests forage consumption by cattle within a paddock is not

uniform across the paddock, which is consistent with the idea that grazers often “patch graze” by preferentially grazing some areas repeatedly while others are left ungrazed until forage availability is low (Willms et al., 1988; Coghénour, 1991). This suggests that ample forage was still available even under the highest stocking rate during the 6-week grazing period. However, grazing later in the growing season could result in homogenized vegetation structure at higher stocking rates if vegetation does not have time to recover from defoliation before dormancy occurs.

Many birds were able to locate and choose nesting sites with similar structure regardless of differences in paddock-level vegetation structure; however, western meadowlarks and vesper sparrows were the exception. These results may be explained by temporal or spatial overlap between nesting activity or nest sites and grazing by cattle. Vesper sparrows had mean clutch initiation dates in early June (2007: 9 June; 2008: 5 June; T. Johnson, unpublished results). A typical 21 d nesting cycle for this species resulted in nesting attempts which were completed (on average) near the end of June and during the latter half of the grazing period, when treatment effects on vegetation structure were most evident (T. Johnson, unpublished results). This pattern was distinct from that of other species, which initiated 7–10 d earlier or later.

Spatial rather than temporal overlap between nest sites and grazed patches may explain the observed pattern for western meadowlarks. Western meadowlarks preferred nest sites in mesic areas with moderate litter cover, relatively high vegetative cover compared to other species present at the study site, and show no avoidance of vegetation communities dominated by non-native forage grasses (Dechant et al., 2003c). Livestock in this study preferred non-native grasses which were often restricted to deep-soiled swales, where water availability and vegetative cover is likely to be higher, over patches that were exclusively native bunchgrasses (Wyffels, 2009; S. Wyffels, personal communication). If patches dominated by non-native grasses offer the vegetative structure required by meadowlarks for nesting, overlap between cattle diet and meadowlark site choice could explain the negative effect of stocking rate on visual obstruction at meadowlark nests.

Western meadowlark nest density did not decrease in response to lower visual obstruction at the nest in paddocks with higher stocking rates, although density showed a weak negative association with habitat characteristics associated with heavier grazing. Additional years of livestock grazing at these experimental stocking rates could clarify whether the change in meadowlark nest density between years is the beginning of a trend towards decreased nest or population density under higher stocking rates.

Differences in avian community composition between control and heavily-grazed paddocks during the second treatment year were partially driven by decreases in the relative density of savannah sparrows in paddocks with high stocking rates. A similar negative effect of high grazing pressure on savannah sparrow density has been reported from previous studies, although effects of light-to-moderate grazing have been variable and are likely attributable to variability in stocking rates common to observational studies (Anstey et al., 1995; Bélanger and Picard, 1999).

Both horned larks and vesper sparrows prefer relatively short, sparse vegetation for nesting (Dechant et al., 2003a; Dinkins et al., 2003; this study). However, shorter vegetation and more heterogeneity at the paddock level created by higher stocking rates did not result in significant increases in the absolute density of either species as predicted. Timing of nesting relative to timing of grazing may partially explain this pattern. Horned larks at our study site began breeding earlier than other species, and many nests were initiated before cattle were introduced to paddocks. The majority of vesper sparrows selected nest sites before effects of grazing on vegetation structure were apparent. Furthermore, changes in absolute densities of these two species may have been too small to detect,

but taken together represented a significant shift in community composition.

Similar densities of grasshopper sparrow nests in paddocks that experienced lower levels of grazing pressure suggests lower grazing intensities may be suitable for this species. However, the lack of any nests in heavily-grazed paddocks suggests a threshold response to grazing intensity by grasshopper sparrows. Negative effects of high grazing intensity and variability in vegetation structure on grasshopper sparrow density have been described in other studies (reviewed in Dechant et al., 2003b). Although we cannot exclude the possibility that there were simply lower detection rates of grasshopper sparrow nests in heavily-grazed paddocks, this explanation is unlikely because we: (1) standardized nest-searching effort among all paddocks, and (2) likely had higher nest detection rates in more heavily-grazed paddocks due to lower overall visual obstruction. Most detections of grasshopper sparrows in heavily-grazed paddocks were of males (97%), whereas in low- and moderately grazed paddocks males made up a slightly smaller proportion of detections (90% and 87%, respectively), suggesting there could have been differences in mate-pairing success among grazing treatments. Low pairing success can be indicative of low resource availability (Probst and Hayes, 1987; Zanette, 2001), and because grasshopper sparrows showed an affinity for relatively tall vegetation and low structural heterogeneity, heavily-grazed paddocks may represent areas of limited resources for this species.

There was no support for the hypothesis that more structural heterogeneity translated into higher bird diversity. These results are consistent with a study by Wiens (1974) where no relationships between structural heterogeneity and bird diversity were observed in multiple types of grasslands. The intrinsically low diversity of grassland songbird communities may limit the range of diversity values possible in grasslands, and may make detection of significant relationships between structural heterogeneity and diversity difficult (Wiens, 1974). The absence of a significant relationship between bird diversity and structural heterogeneity as measured by a gradient of visual obstruction alone does not preclude a significant relationship between bird diversity and a multivariate structural gradient (Tews et al., 2004). Because vertical structural heterogeneity is highly constrained in grasslands, ground-nesting birds may use additional cues when making settlement decisions and visual obstruction may not be the most critical feature of structural heterogeneity (Roth, 1976). In addition, the effects of structural heterogeneity may not be apparent at the spatial scale of this experiment (40 ha).

Acknowledgements

Support for this work was provided by the National Research Initiative of the USDA Cooperative State Research, Education, and Extension Service, Grant 2006-35101-16572, The Nature Conservancy, Oregon State University, The Oregon Zoo, Prairie Biotic Research, Inc., The Cornell Lab of Ornithology, The Garden Club of America, Sigma-Xi Grants-in-Aid of Research, and The Wildlife Society, Oregon Chapter. P. Shephard, L.J. Nichols, A. Freeman, and J. Fields assisted with project logistics. D. Dail, C. Pereira, and J. Fontaine provided advice on statistical analysis. S. DeBano, L. Nagy, K. Dugger, D. Pyke, and R. Miller assisted with study design and provided editorial comments which significantly improved the manuscript. We thank numerous field technicians for assistance with data collection, especially A. Lueders and E.B. Rodrigues.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2011.10.003.

References

- Allredge, M.W., Pollock, K.H., Simons, T.R., Shriner, S.A., 2007. Multiple-species analysis of point count data: a more parsimonious modelling framework. *Journal of Applied Ecology* 44, 281–290.
- Anstey, D.A., Davis, S.K., Duncan, D.C., Skeel, M., 1995. Distribution and Habitat Requirements of Eight Grassland Songbird Species in Southern Saskatchewan. Saskatchewan Wetland Conservation Corporation, Regina, Saskatchewan, 11 pages.
- Askins, R.A., Chávez-Ramírez, F., Dale, B.C., Haas, C.A., Herkert, J.R., Knopf, F.L., Vickery, P.D., 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. *Ornithological Monographs* 64, 1–46.
- Ausden, M., 2007. *Habitat Management for Conservation: A Handbook of Techniques*. Oxford University Press, New York.
- Bélanger, L., Picard, M., 1999. Cattle grazing and avian communities of the St. Lawrence River Islands. *Journal of Range Management* 52, 332–338.
- Bransby, D.I., Conrad, B.E., Dicks, H.M., Drane, J.W., 1988. Justification for grazing intensity experiments: analyzing and interpreting grazing data. *Journal of Range Management* 41, 274–279.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, New York.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second ed. Springer, New York.
- Coghenour, M.B., 1991. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *Journal of Range Management* 44, 530–542.
- Damiran, D., DelCurto, T., Darambazar, E., Clark, A.A., Kennedy, P.L., Taylor, R.V., 2007. Visual obstruction: weight technique for estimating production on northwestern bunchgrass prairie rangelands. In: *Proceedings of Western Section, American Society of Animal Science*, vol. 58, pp. 225–228.
- DeBano, S., 2006. Effects of livestock grazing on aboveground insect communities in semi-arid grasslands of southeastern Arizona. *Biodiversity and Conservation* 15, 2547–2564.
- Dechant, J.A., Dinkins, M.F., Johnson, D.H., Igl, L.D., Goldade, C.M., Euliss, B.R., 2003a. Effects of Management Practices on Grassland Birds: Vesper Sparrow. Northern Prairie Wildlife Research Center, Jamestown, ND, Northern Prairie Wildlife Research Center Online. <http://www.npwr.usgs.gov/resource/literatr/grasbird/vesp/vesp.htm> (accessed 02.06.10).
- Dechant, J.A., Sondreal, M.L., Johnson, D.H., Igl, L.D., Goldade, C.M., Nenneman, M.P., Euliss, B.R., 2003b. Effects of Management Practices on Grassland Birds: Grasshopper Sparrow. Northern Prairie Wildlife Research Center, Jamestown, ND, Northern Prairie Wildlife Research Center Online. <http://www.npwr.usgs.gov/resource/literatr/grasbird/grsp/grsp.htm> (accessed 02.06.10).
- Dechant, J.A., Sondreal, M.L., Johnson, D.H., Igl, L.D., Goldade, C.M., Zimmerman, A.L., Euliss, B.R., 2003c. Effects of Management Practices on Grassland Birds: Western Meadowlark. Northern Prairie Wildlife Research Center, Jamestown, ND, Northern Prairie Wildlife Research Center Online. <http://www.npwr.usgs.gov/resource/literatr/grasbird/weme/weme.htm> (accessed 02.06.10).
- Dermer, J.D., Lauenroth, W.K., Stapp, P., Augustine, D.J., 2009. Livestock as ecosystem engineers for grassland bird habitat in the western Great Plains of North America. *Rangeland Ecology and Management* 62, 111–118.
- Dinkins, M.F., Zimmerman, A.L., Dechant, J.A., Parkin, B.D., Johnson, D.H., Igl, L.D., Goldade, C.M., Euliss, B.R., 2003. Effects of Management Practices on Grassland Birds: Horned Lark. Northern Prairie Wildlife Research Center, Jamestown, ND, Northern Prairie Wildlife Research Center Online. <http://www.npwr.usgs.gov/resource/literatr/grasbird/hola/hola.htm> (accessed 02.06.10).
- Fondell, T.F., Ball, I.J., 2004. Density and success of bird nests relative to grazing on western Montana grasslands. *Biological Conservation* 117, 203–213.
- Hansen, J.D., Taylor, R.V., Jansen, V.S., 2010. Zumwalt Weather and Climate Annual Report, Available at: <http://conserveonline.org/workspaces/ZumwaltPrairieWorkspace/documents/zumwalt-weather-and-climate-annual-report-2006/view.html>.
- Hocking, R.R., 1976. The analysis and selection of variables in linear regression. *Biometrics* 32, 1–49.
- Johnson, R.G., Temple, S.A., 1990. Nest predation and brood parasitism of tallgrass prairie birds. *Journal of Wildlife Management* 54, 106–111.
- Kruskal, J.B., 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29, 115–129.
- Litell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., Schabenberger, O., 2006. *SAS for Mixed Models*, second ed. SAS Institute Inc., North Carolina.
- Lubowski, R.N., Vesterby, M., Bucholtz, S., Baez, A., Roberts, M.J., 2006. Major Uses of Land in the United States, 2002. U.S. Department of Agriculture, Economic Research Service, Economic Information Bulletin No. EIB-14.
- Mather, P.M., 1976. *Computational Methods of Multivariate Analysis in Physical Geography*. John Wiley & Sons, London.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software, Glendon Beach, OR, USA.
- McCune, B., Mefford, M.J., 2009. PC-ORD Multivariate Analysis of Ecological Data. Version 6.91 Beta. MjM Software, Glendon Beach, OR, USA.
- Mielke Jr., P.W., 1984. Meteorological applications of permutation techniques based on distance functions. In: Krishnaiah, P.R., Sen, P.K. (Eds.), *Handbook of Statistics*, vol. 4. Elsevier Science Publishers, The Hague, The Netherlands, pp. 813–830.

- Probst, J.R., Hayes, J.P., 1987. Pairing success of Kirtland's warblers in marginal versus suitable habitat. *Auk* 104, 234–241.
- Ralph, C.J., Sauer, J.R., Droege, S., 1995. Monitoring bird populations by point counts. United States Department of Agriculture, Forest Service, Pacific Southwest Research Station Gen. Tech. Rep. PSW-GTR-149, 187 pages.
- Ramsey, F.L., Schafer, D.W., 2002. *The Statistical Sleuth*, second ed. Duxbury, Pacific Grove, CA.
- Robel, R.J., Briggs, J.N., Dayton, A.D., Hulbert, L.C., 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23, 295–297.
- Roth, R.R., 1976. Spatial heterogeneity and bird species diversity. *Ecology* 57, 773–782.
- Salo, E.D., 2003. Effects of grazing intensity and temporal application of grazing treatments on nongame birds in North Dakota mixed-grass prairie. MS Thesis. South Dakota State University, 87 pages.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31, 79–92.
- Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B., Marques, T.A., 2005. Distance 5.0. Release 5. Research Unit for Wildlife Population Assessment. University of St. Andrews, UK, <http://www.ruwpa.st-and.ac.uk/distance/>.
- Townsend, D.E., Fuhlendorf, S.D., 2010. Evaluating relationships between spatial heterogeneity and the biotic and abiotic environments. *American Midland Naturalist* 163, 351–365.
- Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J., Brown, V.K., 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology* 38, 647–664.
- Vickery, P.D., Tubaro, P.L., Cardoso Da Silva, J.M., Peterjohn, B.G., Herkert, J.R., Cavalcanti, R.B., 1999. Conservation of grassland birds in the western hemisphere. *Studies in Avian Biology* 19, 2–26.
- Western Regional Climate Center, 2009. Enterprise 20 NNE, Oregon. Western Regional Climate Center, Oregon Climate Summaries Website: <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?oren20> (accessed 04.08.09).
- Wiens, J.A., 1974. Habitat heterogeneity and avian community structure in North American grasslands. *American Midland Naturalist* 91, 195–213.
- Willms, W.D., Dormaar, J.F., Schaalje, G.B., 1988. Stability of grazed patches on rough fescue grasslands. *Journal of Range Management* 41, 503–508.
- Winter, M., Hawks, S.E., Shaffer, J.A., Johnson, D.H., 2003. Guidelines for finding nests of passerine birds in tallgrass prairie. *Prairie Naturalist* 35, 197–211.
- With, K.A., King, A.W., Jensen, W.E., 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation* 141, 3152–3167.
- Wyffels, S., 2009. Influence of stocking density on grazing beef cattle performance, diet composition, foraging efficiency, and diet quality on a late-spring early-summer native bunchgrass prairie. MS Thesis. Oregon State University, 124 pages.
- Zanette, L., 2001. Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. *Journal of Avian Biology* 32, 38–46.