

24 **Abstract**

25 In 2006-10, effects of four different cattle stocking rates (0, 14.4, 28.8, and 43.2 animal unit
26 months) were compared, representing 0, 20, 32, and 46% utilization of vegetation by domestic
27 livestock, on vegetation structure (as indexed by visual obstruction), and songbird population and
28 apparent nest density, community composition, and diversity in a Pacific Northwest bunchgrass
29 prairie in northeastern Oregon, USA. Overall paddock-level visual obstruction decreased and
30 structural heterogeneity increased with increasing stocking rates, and those effects carried over
31 one year after grazing had ceased. Most species were able to locate nesting sites regardless of
32 differences in visual obstruction, except western meadowlark and vesper sparrow, for which
33 obstruction was lower in paddocks with higher stocking rates. Apparent nest density for
34 grasshopper sparrows was negatively affected by higher stocking rates. Grazing effects on
35 absolute songbird population density were restricted to negative effects of higher stocking rates
36 on savannah sparrows, but this relationship was not observed until one year after grazing had
37 ceased. Songbird community composition differed between control and heavily-grazed
38 paddocks, driven by an increase in the proportion of horned larks and a decrease in the
39 proportion of savannah sparrows in heavily-grazed paddocks from pre-treatment to post-
40 treatment years. Bird diversity indices were unaffected by stocking rate. Negative effects of
41 high stocking rates on densities of two species and absence of any clear positive effect for the
42 other three species suggest high stocking rates as applied in this experiment may not provide
43 suitable habitat for all grassland songbirds. The absence of negative responses of density to low
44 and moderate stocking rates suggests these grazing regimes generally provided suitable habitat
45 for all species.

46 *Keywords:* ground-nesting bird, vegetation structure, rangeland management, habitat complexity,

47 nonmetric multidimensional scaling, sustainable grazing

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63 **1. Introduction**

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

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

82 Some researchers have suggested livestock grazing can be used as a management tool to
83 facilitate particular habitat conditions for grassland birds; however, they acknowledge the effects
84 of grazing on bird habitat remain unpredictable (Derner et al., 2009). One range management
85 practice that can be manipulated is grazing intensity, which is defined as the “frequency of plant

86 defoliation” by herbivores and when increased leads to reduced stubble height and aboveground
87 plant biomass relative to ungrazed areas (Bransby et al., 1988). Grazing can enhance structural
88 heterogeneity of vegetation up to a point above which it results in more homogenous structure
89 (Ausden, 2007).

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

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

109 rates due to the creation of different numbers of nesting micro-sites suitable for each species in
110 the community.

111 **2. Materials and methods**

112 This study was conducted at The Nature Conservancy's Zumwalt Prairie Preserve (ZPP)
113 in northeastern Oregon, USA. The 13,269 ha, high elevation (average 1500 m) preserve is
114 located within the largest remaining tract of Pacific Northwest bunchgrass prairie in North
115 America, and provides breeding habitat for several species of grassland birds including:
116 savannah sparrow (*Passerculus sandwichensis*), horned lark (*Eremophila alpestris*), western
117 meadowlark (*Sturnella neglecta*), grasshopper sparrow (*Ammodramus savannarum*), and vesper
118 sparrow (*Poocetes gramineus*). Land use on and surrounding the ZPP has primarily been
119 summer livestock grazing, first by horses belonging to Native Americans beginning in the early
120 1700's, and since the late 1800's by sheep and cattle when homesteaders introduced non-native
121 grasses (e.g. *Bromus inermis*, *Phleum pratense*) as livestock forage (Bartuszevige et al., in
122 press). Currently, surrounding land use is private rangeland focused on beef production. At the
123 ZPP, upland sites are presently dominated by cool- season native species, in particular Idaho
124 fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Pseudoroegneria spicata*). Climate is
125 semi-arid and mean annual temperature is 7.4° C (Western Regional Climate Center, 2009).
126 Mean annual precipitation is 49.0 cm, with an average of 18.3 cm occurring from April through
127 July.

128 *2.1. Experimental design*

129 To evaluate predictions, a randomized complete block design with one factor (livestock
130 grazing) and four grazing treatment levels (stocking rate) was used. All study plots were rested
131 from grazing for two years prior to the start of our 4 y experiment. Blocking controlled for

132 potential environmental heterogeneity created by variation in historical grazing management. In
133 2006, fences were erected around 160 ha blocks, and within each block, four 40 ha paddocks
134 were partitioned. Pre-treatment data on vegetation structure and songbird population density
135 (see section 2.3) were collected in each paddock during May-July 2006. In 2007 and 2008, cattle
136 grazed paddocks from 21 May to 3 July and 29 May to 9 July, respectively. Each of the four
137 blocks contained one replicate paddock of each randomly assigned stocking rate ($n = 4$ replicates
138 of each stocking rate; Table 1). Stocking rates corresponding to each grazing intensity treatment
139 were developed using cattle forage utilization data previously collected at the ZPP (DelCurto and
140 Williams, unpublished results; Table 1). The moderate treatment was based on stocking rates
141 used by area ranchers (40% forage removal). The three other grazing treatments were designed
142 to represent light (20%), heavy (60%), or no grazing (control) of vegetation by cattle. In each
143 year, 48 yearling heifers and 192 cow-calf pairs were stratified by age and body condition, and
144 randomly assigned to a grazing treatment (Wyffels 2009). Actual forage utilization values for
145 each stocking rate are presented in Table 1. Timing of grazing coincided with the growing
146 period of dominant grass species at the site and the peak period of reproductive activity for
147 grassland songbirds. In 2009, data on post-treatment responses were recorded during May-July,
148 when no grazing occurred in study paddocks.

149 2.2. *Sampling methods*

150 To evaluate vegetation structure in paddocks grazed at different stocking rates, paddock-
151 level estimates of visual obstruction (VO) were measured during the passerine breeding season
152 in each year. Visual obstruction is correlated with aboveground biomass in grasslands and
153 represents a measure of the vertical height and density of vegetation (Robel et al., 1970; Damiran
154 et al., 2007). Evaluation of changes in vegetation structure was limited to VO because this

155 parameter was expected to be most influenced by stocking rate in the near-term, and it is easily
156 measured over large areas. Visual obstruction was measured using a Robel pole held
157 perpendicular to the ground, where an observer recorded the height of the lowest visible dm from
158 4 m away and 1 m off the ground (Robel et al., 1970). From 26 June to 24 July in the pre-
159 treatment year and post-treatment year, two VO measurements were taken 1.5 m away from each
160 of 36 vegetation sampling points systematically placed within each paddock ($n = 72$
161 measurements). During the two treatment years (2007-08), paddock-level VO was measured at
162 10 m intervals along eight 100 m transects within each paddock ($n = 80$ measurements) within 24
163 h after cattle were removed from paddocks. Transects were stratified randomly by physiographic
164 characteristics in each paddock to account for differences in vegetation biomass, and thus
165 vegetation structure, and included hilltops, swales, rocky outcroppings, and slopes. Distribution
166 of transects among physiographic classes was not standardized, but depended on the number of
167 different physiographic features present within each paddock. Structural heterogeneity was
168 measured as the coefficient of variation of paddock-level VO.

169 To estimate bird population density, 5 min fixed radius point counts were conducted
170 (Ralph et al., 1995) using distance-sampling from mid-May to early July from 2006-09. Each
171 paddock contained 16 point transects systematically placed at 150 m intervals, but excluded a 16
172 m buffer around the inner edge of each paddock to minimize potential fence line effects on bird
173 surveys. Each point was visited twice in 2006, and three times in 2007-09. Point counts were
174 conducted by five different observers over the four years of the study. Surveys were conducted
175 from 06:30 to 10:30 (PST) in all years, and surveys were never conducted during periods of
176 precipitation, fog, or winds exceeding 5.3 m/s. All birds seen or heard within 75 m were

177 recorded. Distance from the observer to the location each bird was first detected was estimated
178 to the nearest meter using a laser range finder.

179 Grassland songbird nests were counted by dragging a 25 m rope between two observers
180 across vegetation and then intensively searching areas from which adult birds flushed (Winter et
181 al., 2003). Each paddock was systematically searched in its entirety three times in 2007 and
182 twice in 2008 from 1 May to 25 July. Nests were also located opportunistically during
183 vegetation surveys. To evaluate nest-site selection, VO was measured at nests once a nesting
184 attempt was complete ($n = 157$ nests in 2007, $n = 115$ in 2008; no nest data are available for
185 2006 and 2009). Nest-level VO was measured by inserting a Robel pole into the nest cup and
186 recording VO once from each cardinal direction. The four VO values were then averaged to
187 obtain one value for each nest.

188 *2.3. Data analysis*

189 Mixed models were used to evaluate trend of response variables relative to stocking rates.
190 Response variables included paddock-level VO, structural heterogeneity of vegetation, total
191 songbird population density, and songbird species diversity. Nest-level VO, population density
192 and apparent nest density were additional response variables modeled separately for each
193 species. Data were modeled using PROC MIXED in SAS System V. 9.3.1 (SAS Institute Inc.,
194 2002-03). The number of cattle was included as a continuous predictor and tested for linear and
195 quadratic effects on response variables. Because initial songbird density within a paddock could
196 influence changes in density related to grazing intensity, pre-treatment density from 2006 was
197 used as a covariate when estimating trends in songbird population density. To address the
198 question of whether structural heterogeneity influenced diversity or total density of songbirds in
199 a paddock, the coefficient of variation of paddock-level VO was used as a covariate when

200 evaluating effects on diversity and total songbird density. To evaluate the relationship between
201 nest density and vegetation structure, mean paddock-level VO was used as a covariate when
202 modeling effects on nest density.

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

217 Breeding bird densities were estimated using Program Distance Ver. 5 Release 5
218 (Thomas et al., 2005) to account for the influence of potential differences in detection
219 probabilities among species and habitats on density estimates. Preliminary analyses included all
220 observations and suggested no differences in detection probabilities among observers based on
221 comparisons of point estimates and 95% confidence intervals (Ramsey and Schafer, 2002).
222 Detection functions were fitted separately for each paddock to ensure that paddock-level density

223 estimates did not co-vary and comparisons of songbird density could be made among treatments.
224 Because this resulted in several species with a low number of detections, the approach outlined
225 in Alldredge et al. (2007) was followed. Two groups of species from the community of
226 grassland passerines that breed on the ZPP were created. A common detection function was
227 assumed among species within a group, and pooled observations of those species were used to
228 increase precision of density estimates. The first group included savannah sparrows, grasshopper
229 sparrows, and vesper sparrows, and the second group included horned larks and western
230 meadowlarks. Species assignments to a group were chosen based on similarity in behavior,
231 plumage crypticity, and song characteristics. Other rare species were omitted from all analyses
232 because they could potentially obscure important patterns in breeding bird density. Candidate
233 models included uniform key function with cosine and simple polynomial adjustments, and half-
234 normal key function with cosine, simple polynomial, or hermite polynomial adjustments. Best
235 models were selected using goodness-of-fit tests and Akaike's Information Criterion corrected
236 for small sample size (AIC_c ; Buckland et al., 2001; Burnham and Anderson, 2002).

237 To describe relationships among songbird community composition, paddock-level
238 vegetative structure, and nest-site preferences unique to each species (hereafter, species traits),
239 data collected from point counts were analyzed using a multivariate approach. Coefficient of
240 variation for total density for each species was moderate (96%) so density data were log-
241 transformed to account for this variation (McCune and Grace, 2002). Subsequently, the CV for
242 species totals decreased to <40%. Transformed density data were evaluated for skewness and
243 extreme values by comparing the standard deviation of mean Euclidean distances for each
244 paddock to all other paddocks (McCune and Grace, 2002). One paddock was identified as an

245 outlier in 2007; however, it was a weak outlier (2.7 standard deviations) and was therefore
246 retained for analysis.

247 To determine whether there were differences in breeding bird community composition
248 among treatments within each year, a Blocked Multi-Response Permutation Procedure (MRBP;
249 Mielke, 1984) was conducted on the transformed data. Median alignment within blocks was
250 used, which focuses the analysis on differences among treatments within a given experimental
251 block and accounts for the blocking in the experimental design (McCune and Grace, 2002).
252 Stocking rate treatments were used as *a priori* groups for comparison of community
253 composition. Distances were calculated using the Euclidian measure and groups were defined by
254 treatments (each group included four paddocks). Non-metric multidimensional scaling (NMS)
255 was used to elucidate the MRBP results and evaluate the relationship between grassland-
256 breeding songbird community composition and stocking rate, year, and VO values (Kruskal,
257 1964; Mather, 1976). Data from all years were included in the MRBP analysis; however, only
258 data from 2007-09 were included in the ordination because including pre-treatment data from
259 2006 would have obscured any treatment-related patterns.

260 Euclidean distance measurement was used for the ordination. Final dimensionality of
261 data was assessed by evaluating final stress (where stress is a measure of departure from
262 monotonicity between distance in original species space and distance in reduced ordination
263 space) versus the number of dimensions and by performing a randomization test (250 runs;
264 McCune and Grace, 2002). To address the potential biological factors influencing patterns in
265 breeding bird density and VO, values of paddock- and nest-level VO were overlaid onto the final
266 ordination. Correlations of vectors from the environmental and species trait matrices with axes

267 from the ordination represent the direction and strength of relationships. All multivariate
268 analyses were conducted in PC-ORD Version 6.9 (McCune and Mefford, 2009).

269 3. Results

270 There was a significant year-by-treatment interaction effect for mean paddock-level VO
271 ($F_{3,33} = 6.70$, $P < 0.01$). There was no pre-existing trend in paddock-level VO the year before
272 cattle grazed (2006: $\beta = -0.004$, $t = -1.12$, $df = 42.8$, $P = 0.27$; Fig. 2). After cattle were allowed
273 to graze for six weeks at different intensities, decreased VO corresponding to increased stocking
274 rate was observed at the paddock level in both treatment years (2007: $\beta = -0.02$, $t = -6.28$, $df =$
275 42.8 , $P < 0.0001$; 2008: $\beta = -0.02$, $t = -5.20$, $df = 42.8$, $P < 0.0001$). Post-treatment data
276 indicated the difference in paddock-level VO among treatments remained at least one year after
277 grazing ceased (2009: $\beta = -0.008$, $t = -2.08$, $df = 42.8$, $P = 0.04$). There were significant
278 quadratic ($F_{1,10} = 5.03$, $P = 0.05$) and linear year-by-treatment interaction effects ($F_{3,33} = 3.95$, P
279 $= 0.02$) for structural heterogeneity. No pre-existing differences in structural heterogeneity were
280 detected before cattle were allowed to graze (2006: $\beta = 0.74$, $t = 1.97$, $df = 15.3$, $P = 0.07$).
281 Heterogeneity increased with increasing stocking rate in the first year of grazing ($\beta = 1.56$, $t =$
282 4.13 , $df = 15.3$, $P < 0.001$) and the second year of grazing ($\beta = 1.56$, $t = 4.15$, $df = 15.3$, $P <$
283 0.001). Post-treatment data indicated a carryover effect of stocking rate and there was higher
284 structural heterogeneity in paddocks that had been grazed at a higher stocking rate at least one
285 year after grazing ceased (2009: $\beta = 1.30$, $t = 3.34$, $df = 15.3$, $P < 0.01$). Over all years, however,
286 the final model suggested a quadratic effect of stocking rate on structural heterogeneity where
287 heterogeneity increased from controls to moderate stocking rates, but decreased at the highest
288 stocking rate.

289 There were significant effects of year ($F_{1,3} = 18.13, P = 0.02$) and stocking rate ($F_{1,53} =$
290 18.37, $P < 0.0001$) on nest-level VO for vesper sparrows (Fig. 3). Nest-level VO for vesper
291 sparrows was lower in 2007 ($\bar{x} = 1.17 \text{ dm} \pm 0.07 \text{ dm, SE}$) than in 2008 ($\bar{x} = 1.41 \text{ dm} \pm 0.06 \text{ dm,}$
292 $t = -3.36, \text{ df} = 3, P = 0.04$), but decreased with higher stocking rates similarly in both years ($\beta = -$
293 0.01, $t = -4.29, \text{ df} = 53, P < 0.0001$). There was a significant effect of stocking rate on nest-level
294 VO for western meadowlarks ($F_{1,23} = 7.36, P = 0.01$); VO at the nest decreased similarly in both
295 treatment years with increased stocking rate ($\beta = -0.01, t = -2.71, \text{ df} = 23, P = 0.01$). There were
296 no significant effects of stocking rate or year on nest-level VO for savannah sparrows, horned
297 larks, and grasshopper sparrows.

298 3.1. Population and apparent nest density

299 Estimated songbird population density within each paddock ranged from 0 – 1.93
300 individuals per ha for each species (Appendix A), and total population density ranged from 0.73
301 – 3.0 individuals per ha. There were significant year-by-treatment interaction effects ($F_{2,21.6} =$
302 3.92, $P = 0.04$) and pre-treatment density effects ($F_{1, 8.79} = 9.27, P = 0.01$) on savannah sparrow
303 density, which was negatively correlated with higher stocking rates only after grazing had ceased
304 (2009: $\beta = -0.03, t = -2.24, \text{ df} = 14.6, P = 0.04$). Pre-treatment density explained 20.1% of the
305 variation in savannah sparrow density. Vesper sparrow and horned lark density was affected by
306 pre-treatment density (vesper sparrow: $F_{1,12} = 8.69, P = 0.01$; horned lark: $F_{1,13.7} = 7.87, P =$
307 0.01), but stocking rate was not included in the final model for either species. Pre-treatment
308 density explained 18.7% of the variation in vesper sparrow density and 38.8% of the variation in
309 horned lark density. There were no significant effects of any predictor variable on grasshopper
310 sparrow or western meadowlark population density. Total density (all species combined) was
311 affected by year ($F_{3,9} = 12.2, P < 0.01$) but not stocking rate. Total density was higher in 2006

312 than any other year of the study (2006-2007: mean difference = 0.47 individuals per ha, $t = 4.04$,
313 $df = 9$, $P < 0.01$; 2006-2008: mean difference = 0.69 individuals, $t = 5.92$, $df = 9$, $P < 0.001$;
314 2006-2009: mean difference = 0.41 individuals, $t = 3.50$, $df = 9$, $P < 0.01$). All other years were
315 similar to each other in total density.

316 Over two years, 275 nests were located (158 in 2007 and 117 in 2008). Savannah
317 sparrow nests were most common ($n = 92$), followed by vesper sparrow ($n = 76$), western
318 meadowlark ($n = 45$), horned lark ($n = 44$), and grasshopper sparrow ($n = 18$; Appendix A).
319 Grasshopper sparrow apparent nest density decreased with increased stocking rate ($F_{1,11} = 6.97$,
320 $P = 0.02$; $\beta = -0.02$, $t = -2.39$, $P = 0.04$) and no grasshopper sparrow nests were located in the
321 high stocking rate treatment (Appendix A). The effect of stocking rate on western meadowlark
322 apparent nest density depended on year ($F_{1,11} = 4.97$, $P = 0.05$). In 2007, there was a positive
323 effect of stocking rate on meadowlark nest density ($\beta = 0.02$, $t = 2.28$, $P = 0.03$), but in 2008
324 there was no effect ($\beta = -0.01$, $t = -0.56$, $P = 0.58$). There were no significant effects of stocking
325 rate or year on savannah sparrow, vesper sparrow, or horned lark apparent nest density.

326 3.2. Community composition

327 The MRBP showed differences in patterns of breeding bird community composition
328 among treatments during the second treatment year and one year post-treatment (Table 2).
329 Pairwise comparisons of all stocking rates by year revealed the relationship between heavily
330 grazed paddocks (high) and ungrazed paddocks (control) dominated patterns in differences in
331 community composition among treatments. This difference was driven by a decrease in relative
332 density of savannah sparrows (from 56% of the bird community in 2006 to 36% in 2009) and an
333 increase in relative density of horned larks (from 19% in 2006 to 38% in 2009) in heavily-grazed
334 (high) paddocks from the pre-treatment to post-treatment year. There was also evidence that

335 patterns of community composition differed between controls and lightly grazed (low)
336 treatments one year after grazing ceased, but there were no clear directional changes for any one
337 species across years that is responsible for this pattern. Homogeneity within treatment groups
338 that differed in composition was fairly high ($A = 0.19 - 0.38$). Songbird diversity ranged from
339 $0.91 - 1.60$ (Shannon Diversity Index), and there were no significant effects of stocking rate or
340 year on diversity.

341 Ordination of the paddock-level dataset of transformed total density yielded a 3-
342 dimensional solution (final stress = 7.5, instability <0.00001) and total $R^2 = 0.96$ (axis 1: $R^2 =$
343 0.15 ; axis 2: $R^2 = 0.65$; axis 3: $R^2 = 0.16$). The R^2 value represents the variance in the original
344 distance matrix represented in ordination space. Paddock-level VO and the variation in paddock-
345 level VO are at opposite ends of axis 1, suggesting that axis 1 represents a gradient of paddock-
346 level vegetation structure where higher VO is correlated with less variability in VO (Fig. 4;
347 Table 3). Axis 2 separates mean nest-level VO and the variability in nest-level VO and
348 represents a gradient of local-scale vegetation structure where higher values of mean nest-level
349 VO are correlated with less variability in vegetation structure at the nest site (Fig. 4; Table 3).
350 Treatments did not show a strong association with any axis, although paddocks grazed with the
351 highest stocking rates were concentrated at the upper end of axis 2 (Fig. 4; Table 3). Vesper
352 sparrows and horned larks had strong associations with shorter and more heterogeneous
353 vegetation at the nest level. Savannah sparrows and grasshopper sparrows had strong
354 associations with taller and less heterogeneous structure at the paddock level (Table 3). Western
355 meadowlarks and grasshopper sparrows had strong associations with axis 3. However, because
356 axis 3 did not capture any environmental or species trait variables included in the NMS, the third
357 axis was excluded from the graphic presentation for ease of interpretation.

358 4. Discussion

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

368 Significant quadratic effects of stocking rate over all years support predictions that
369 structural heterogeneity is highest at moderate stocking rates and lower at heavily-grazed and
370 ungrazed paddocks. However, pre-treatment data suggest less heterogeneity in vegetation
371 structure existed in paddocks randomly selected for high intensity grazing before grazing
372 commenced, and this likely influenced the response pattern. Further, the relationship depended
373 on year and responses during and after treatment years were linear and positive. Thus, we
374 interpret these results as evidence that stocking rate has a linear effect on structural heterogeneity
375 at the observed forage utilization levels. High stocking rates in this study did not result in more
376 homogeneous vegetation structure than moderate stocking rates as predicted under a quadratic
377 response. Higher structural heterogeneity with increasing stocking rate suggests forage
378 consumption by cattle within a paddock is not uniform across the paddock, which is consistent
379 with the idea that grazers often “patch graze” by preferentially grazing some areas repeatedly
380 while others are left ungrazed until forage availability is low (Willms et al., 1988; Coghenour,

381 1991). This suggests that ample forage was still available even under the highest stocking rate
382 during the six-week grazing period. However, grazing later in the growing season could result in
383 homogenized vegetation structure at higher stocking rates if vegetation does not have time to
384 recover from defoliation before dormancy occurs.

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

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

403 cattle diet and meadowlark site choice could explain the negative effect of stocking rate on visual
404 obstruction at meadowlark nests.

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

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

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

426 these two species may have been too small to detect, but taken together represented a significant
427 shift in community composition.

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

444 There was no support for the hypothesis that more structural heterogeneity translated into
445 higher bird diversity. These results are consistent with a study by Wiens (1974) where no
446 relationships between structural heterogeneity and bird diversity were observed in multiple types
447 of grasslands. The intrinsically low diversity of grassland songbird communities may limit the
448 range of diversity values possible in grasslands, and may make detection of significant

449 relationships between structural heterogeneity and diversity difficult (Wiens, 1974). The
450 absence of a significant relationship between bird diversity and structural heterogeneity as
451 measured by a gradient of visual obstruction alone does not preclude a significant relationship
452 between bird diversity and a multivariate structural gradient (Tews et al., 2004). Because
453 vertical structural heterogeneity is highly constrained in grasslands, ground-nesting birds may
454 use additional cues when making settlement decisions and visual obstruction may not be the
455 most critical feature of structural heterogeneity (Roth, 1976). In addition, the effects of
456 structural heterogeneity may not be apparent at the spatial scale of this experiment (40 ha).

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607 Supplementary material not for publication

608 Appendix A. Mean population density (individuals per ha) and mean apparent nest density
609 (nests per ha) of grassland songbirds in paddocks with four different cattle stocking rates ($n = 4$
610 replicates of each stocking rate) on the Zumwalt Prairie Preserve, northeastern Oregon, USA.

611
612 Fig. 1. Predictions of how structural heterogeneity, bird diversity, and songbird density may
613 change in response to livestock grazing intensity. Solid line: linear response (may be negative or
614 positive); dashed line: threshold response; dotted line: quadratic response. See text for more
615 details.

616
617 Fig. 2. Mean paddock-level visual obstruction for four stocking rates ($n = 4$ replicates of each
618 stocking rate) on the Zumwalt Prairie Preserve, northeastern Oregon, USA 2006-09. Significant
619 trends from a mixed model are indicated with regression lines. AU: number of animal units.

620
621 Fig. 3. Mean nest-level visual obstruction for five species of songbird nesting in paddocks
622 exposed to four experimental stocking rates in 2007-08 on the Zumwalt Prairie Preserve,
623 northeastern Oregon, USA. Significant trends from a mixed model are indicated with regression
624 lines. AU: number of animal units.

625
626 Figure 4. Ordination of paddocks (2007-09) in species space using non-metric multidimensional
627 scaling. Arrows along axes represent relationships of environmental (paddock-level visual
628 obstruction; VO) and species trait (nest-level VO) variables with each axis: VO (dm). Species

629 codes: VESP (vesper sparrow); HOLA (horned lark); GRSP (grasshopper sparrow); WEME

630 (western meadowlark); SAVS (savannah sparrow).

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653 Table 1. Grazing treatments randomly assigned to each 40-ha paddock within each block ($n = 4$)
 654 on the Zumwalt Prairie Preserve, northeastern Oregon, USA.

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

661 ^a Control treatments represented no use by domestic livestock.

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

664 ^c Forage utilization was averaged over the two treatment years
 665 (2007-08). Methods for determining forage utilization are
 666 presented in Wyffels (2009).
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673 Table 2. Results of a blocked multi-response permutation procedure comparing ground-
 674 nesting songbird community composition at the Zumwalt Prairie Preserve, northeastern
 675 Oregon, USA. Asterisks (*) denote statistically significant differences in group
 676 composition.

677

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

Table 2 continued

	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

678 ^a $T = (\delta - m_{\delta}) / s_{\delta}$, where δ = the weighted mean within-group distance, m_{δ} = mean of δ

679 under the null hypothesis, and s_{δ} = standard deviation of δ under the null hypothesis.

680 ^b Chance-corrected within-group agreement, describing within-group similarity; cf.

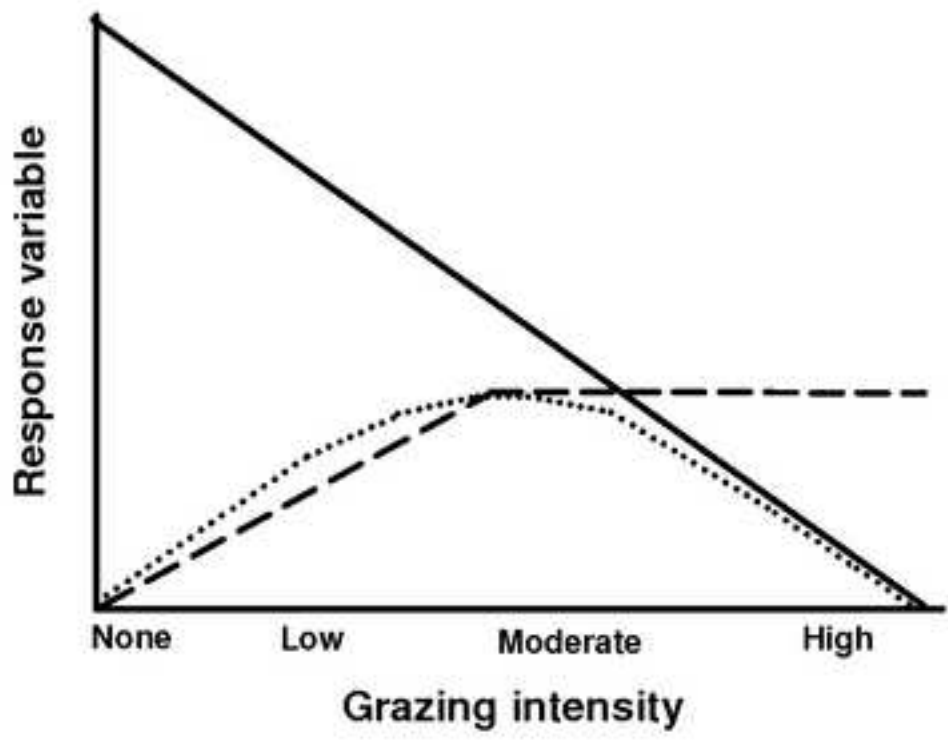
681 McCune and Grace (2002).

682 Table 3. Correlations of each variable with axes obtained from a non-metric multidimensional
 683 scaling ordination of ground-nesting songbird densities at the Zumwalt Prairie Preserve,
 684 northeastern Oregon, USA. Year = 2007 and 2008.

685

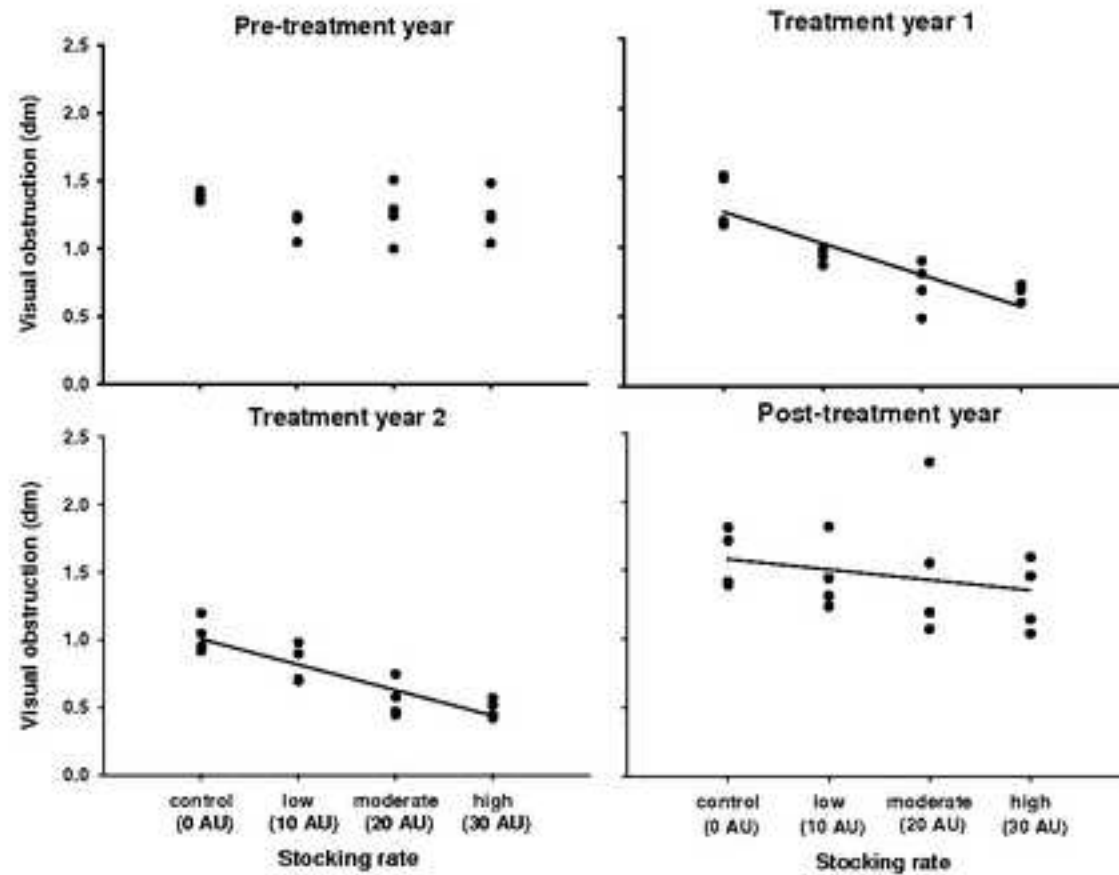
Variable	Correlation coefficient	
	Axis 1	Axis 2
Year	0.21	0.21
Stocking rate	-0.22	0.23
<i>Species</i>		
Savannah sparrow	0.66	-0.63
Vesper sparrow	-0.05	0.90
Western meadowlark	0.29	-0.26
Horned lark	0.26	0.87
Grasshopper sparrow	0.69	0.16
<i>Visual obstruction (VO)</i>		
Paddock-level VO	0.39	-0.27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

Figure
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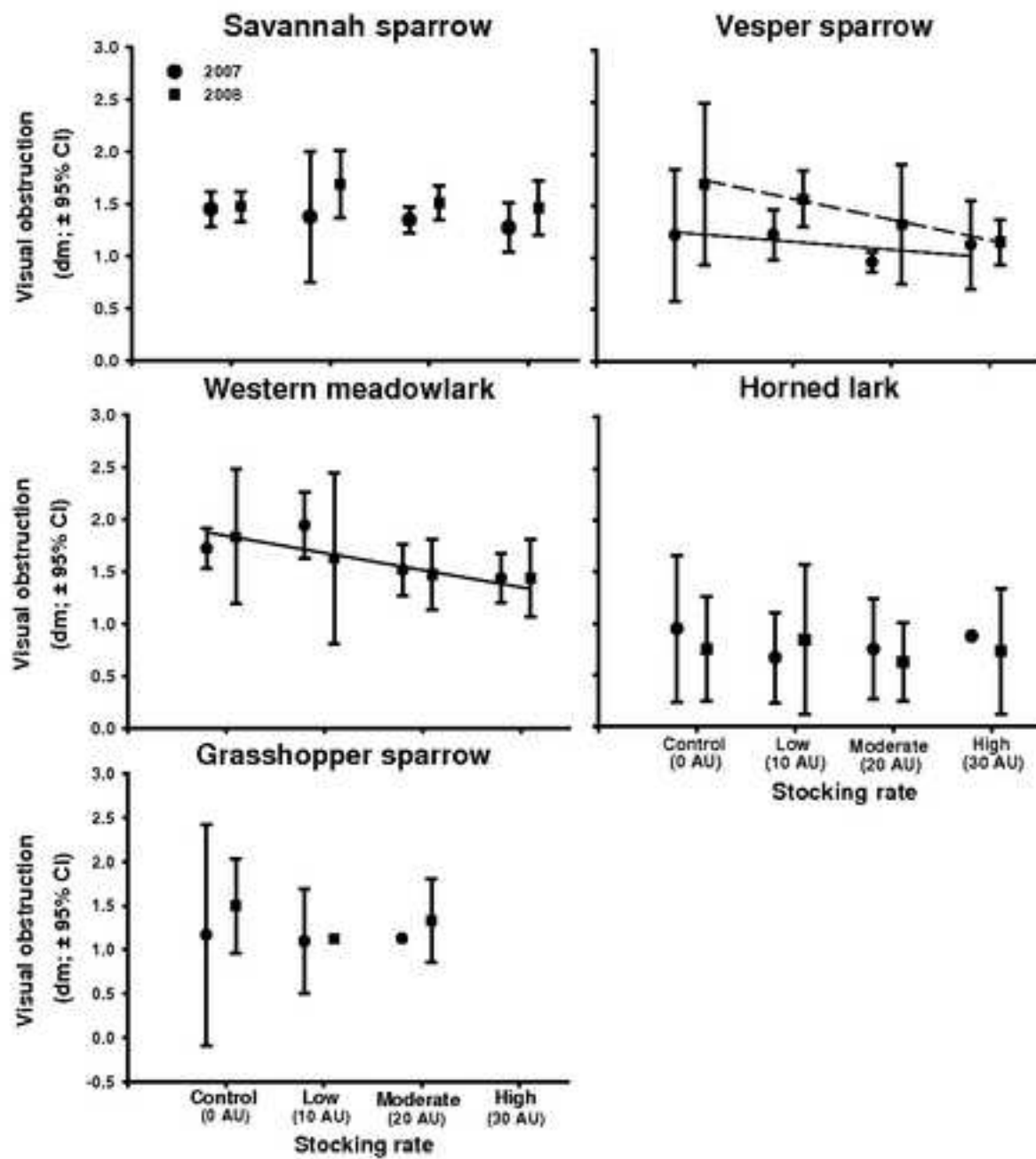
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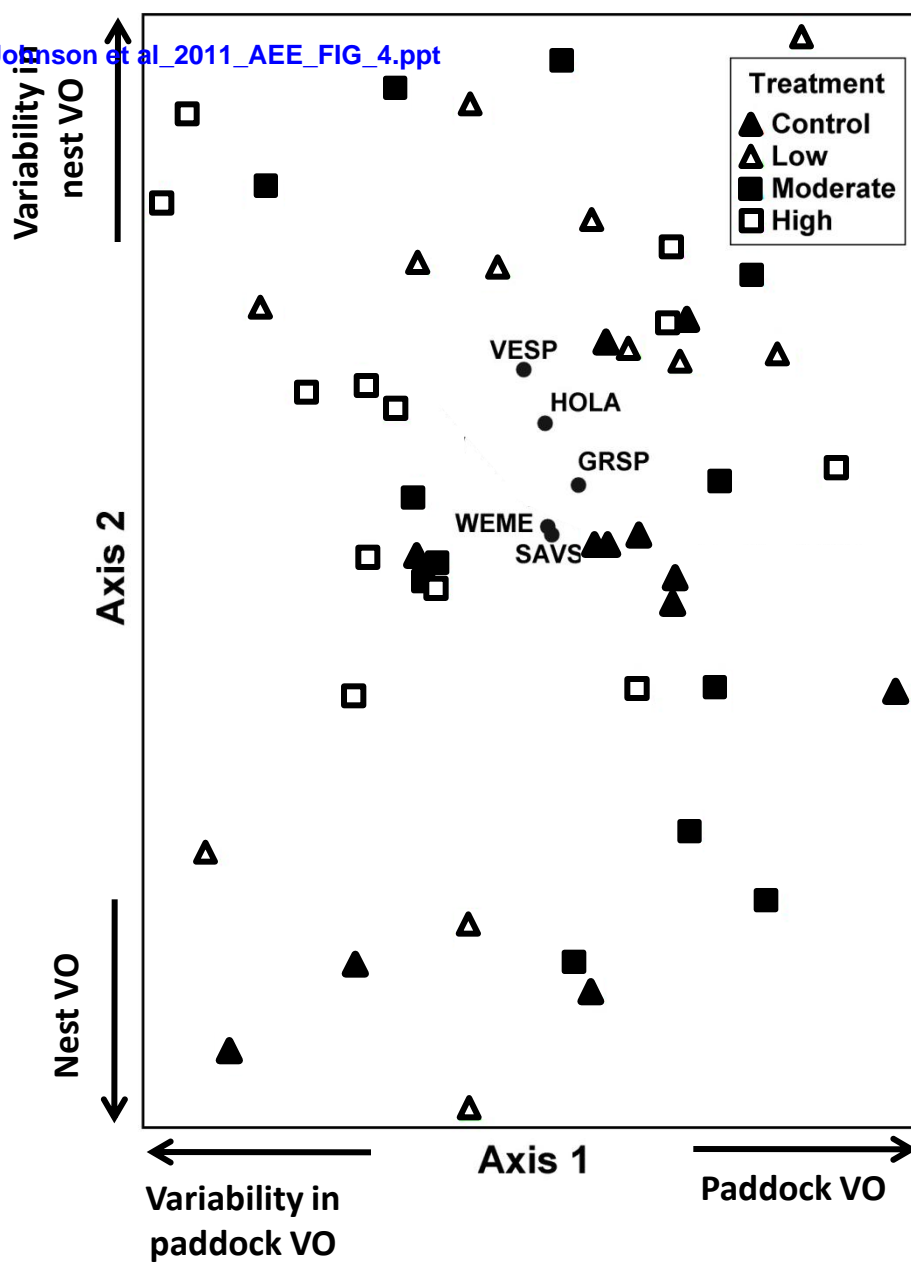
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Figure

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Appendix A. Mean population density (individuals per ha; estimated using Program Distance) and mean apparent nest density (nests per ha) of grassland songbirds in paddocks with four different cattle stocking rates ($n = 4$ replicates of each stocking rate) on the Zumwalt Prairie Preserve, northeastern Oregon, USA.

Species	Grazing intensity	Mean population density (95% CI) ^a				Mean apparent nest density (95% CI)	
		2006	2007	2008	2009	2007	2008
Savannah sparrow	<i>control</i>	1.26 (0.93,1.59)	0.86 (0.74,0.97)	0.62 (0.44,0.79)	1.04 (0.57,1.51)	0.10(0.07,0.13)	0.06(0.01,0.11)
	<i>low</i>	0.93 (0.70,1.16)	0.62 (0.28,0.96)	0.36 (0.24,0.48)	0.54 (0.30,0.80)	0.04(0.01,0.06)	0.06(0.02,0.11)
	<i>moderate</i>	0.86 (0.59,1.13)	1.06 (0.26,1.86)	0.60 (0.20,1.00)	0.76 (0.26,1.27)	0.11(0.03,0.19)	0.08(0.02,0.13)
	<i>high</i>	1.23 (0.52,1.93)	0.68 (0.40,0.97)	0.30 (0.21,0.39)	0.46 (0.15,0.76)	0.07(0.01,0.13)	0.06(0.04,0.09)
Vesper sparrow	<i>control</i>	0.09 (0.00,0.20)	0.04 (0.01,0.07)	0.07 (0.03,0.11)	0.05 (0.00,0.10)	0.03(0.00,0.05)	0.02(0.01,0.03)
	<i>low</i>	0.14 (0.02,0.26)	0.09 (0.01,0.17)	0.13 (0.00,0.26)	0.09 (0.03,0.16)	0.10(0.02,0.18)	0.09(0.02,0.17)
	<i>moderate</i>	0.09 (0.00,0.23)	0.07 (0.00,0.14)	0.07 (0.02,0.12)	0.08 (0.01,0.15)	0.07(0.01,0.12)	0.04(0.01,0.08)
	<i>high</i>	0.16 (0.00,0.34)	0.04 (0.01,0.08)	0.09 (0.05,0.14)	0.09 (0.04,0.14)	0.04(0.01,0.07)	0.09(0.01,0.17)
Western meadowlark	<i>control</i>	0.26 (0.12,0.39)	0.18 (0.06,0.29)	0.15 (0.10,0.20)	0.10 (0.06,0.14)	0.03(0.00,0.05)	0.03(0.00,0.05)
	<i>low</i>	0.14 (0.11,0.18)	0.15 (0.01,0.29)	0.19 (0.05,0.32)	0.11 (0.08,0.14)	0.04(0.01,0.07)	0.02(0.01,0.03)
	<i>moderate</i>	0.13 (0.03,0.22)	0.06 (0.03,0.08)	0.11 (0.05,0.16)	0.07 (0.03,0.11)	0.06(0.02,0.10)	0.03(0.02,0.04)
	<i>high</i>	0.16 (0.11,0.21)	0.19 (0.01,0.36)	0.13 (0.05,0.20)	0.07 (0.02,0.12)	0.07(0.03,0.11)	0.01(0.00,0.03)
Horned lark	<i>control</i>	0.31 (0.06,0.55)	0.26 (0.07,0.44)	0.23 (0.03,0.42)	0.20 (0.08,0.32)	0.05(0.03,0.07)	0.01(0.00,0.03)
	<i>low</i>	0.40 (0.07,0.73)	0.36 (0.12,0.61)	0.41 (0.14,0.67)	0.50 (0.18,0.82)	0.07(0.02,0.12)	0.03(0.00,0.05)
	<i>moderate</i>	0.42 (0.00,0.92)	0.19 (0.04,0.35)	0.36 (0.11,0.60)	0.41 (0.16,0.66)	0.04(0.02,0.07)	0.01(0.00,0.03)
	<i>high</i>	0.38 (0.00,0.75)	0.36 (0.01,0.72)	0.32 (0.21,0.43)	0.44 (0.27,0.60)	0.02(0.00,0.04)	0.04(0.01,0.08)
Grasshopper sparrow	<i>control</i>	0.13 (0.05,0.21)	0.08 (0.01,0.15)	0.13 (0.08,0.17)	0.26 (0.17,0.34)	0.03(0.00,0.05)	0.02(0.01,0.03)
	<i>low</i>	0.11 (0.03,0.19)	0.08 (0.04,0.12)	0.14 (0.02,0.27)	0.16 (0.12,0.21)	0.03(0.00,0.06)	0.01(0.00,0.02)
	<i>moderate</i>	0.13 (0.00,0.26)	0.09 (0.02,0.15)	0.16 (0.03,0.28)	0.22 (0.15,0.29)	0.02(0.00,0.04)	0.02(0.01,0.03)
	<i>high</i>	0.14 (0.05,0.24)	0.09 (0.04,0.14)	0.07 (0.00,0.14)	0.14 (0.09,0.18)	0.00	0.00

^a Confidence limits extending below zero were truncated at zero.