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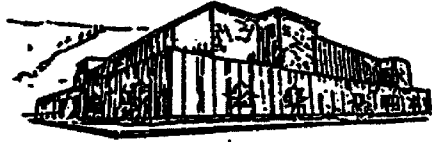
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Avian Community Composition and Nesting Productivity

Relative to Cattle Grazing in North-central Montana

By

Brian D. Logan

B.S., University of Arizona, 1993

Presented in partial fulfillment of the requirements

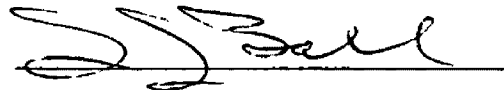
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Master of Science in Wildlife Biology

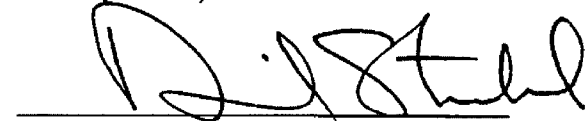
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Logan, Brian D. M.S., May 2001

Wildlife Biology

Avian Community Composition and Nesting Productivity Relative to Cattle Grazing in North-central Montana

Director: I. Joseph Ball



I examined avian community composition, nest density, and nest success relative to vegetation characteristics on grazed and ungrazed grassland habitats of north-central Montana. Grazed plots were characterized by higher cover of bare ground and shrubs, higher shrub density, and lower residual grass cover and vertical structure than ungrazed plots. Nest sites of each bird species differed between grazed and ungrazed sites. Additionally, nest sites of each ground-nesting species were more similar on grazed than on ungrazed sites. Lark bunting, Brewer's sparrow, and western meadowlark tended to nest at higher densities on ungrazed plots, but vesper sparrow nested at higher densities on grazed plots. On grazed plots, nest success was nominally lower for Brewer's sparrow, lark bunting, and western meadowlark in both 1998 and 1999, and for vesper sparrow in 1999. Vesper sparrow exhibited nominally higher nest success on grazed sites in 1998. Overall, productivity of the four focal species was significantly higher on ungrazed plots. Species diversity was somewhat higher on grazed sites, but evenness was higher on ungrazed sites due to higher densities of three of the four most common nesting species.

## ACKNOWLEDGEMENTS

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## INTRODUCTION

A combination of fire and grazing by free-ranging native herbivores once produced a shifting mosaic of grassland habitats in western North America, and prairie birds evolved with this plasticity. During the past 50 to 100 years, however, fire suppression and intensive grazing by domestic livestock have resulted in a relatively uniform and static environment (Knopf 1994, 1996). Livestock grazing is now the predominant land use in grasslands of the United States (Branson 1985). Grazing may cause substantial site-specific changes to habitats (Taylor 1986, Sedgwick and Knopf 1987, Knopf et al. 1988, Schulz and Leininger 1991, Saab et al. 1995, Ammon and Stacey 1997) and subsequently, to the attractiveness of those habitats to foraging and nesting birds. Changes in species composition and productivity of avifauna with increased grazing have been documented in several studies, though species responses have varied across studies and habitats (e.g., Kirsch and Higgins 1976, Saab et al. 1995). To develop habitat management plans that contribute to the conservation of local bird populations, information is needed on the effects of grazing on the breeding habitat of avian species in specific grassland habitat types.

Grazing can alter the species composition and structure of plant communities (Holechek et al. 1989, Hurlburt and Bedunah 1996). Heavy grazing in grassland habitats often leads to changes in the percentage cover of various cover types, namely increased amounts of shrub cover and bare ground and decreased residual and green grass cover (Branson 1985; Holechek et al. 1989). In grassland habitats, levels of structural heterogeneity generally decrease with grazing as unpalatable species (e.g., woody species)

become more predominant; eventually, homogeneous stands of a few unpalatable species may develop (Branson 1985).

Vegetation characteristics may partially explain the organization of bird communities and numerous studies have correlated presence, abundance, and breeding densities of bird species with structure and composition of vegetation (e.g., James 1971, Ambuel and Temple 1983, Lynch and Whigham 1984, Blake and Karr 1984; Martin 1988a, 1988b). Heavily grazed areas should be more attractive to those species with an affinity for areas with low ground cover and low structural heterogeneity. Conversely, species that prefer dense ground cover should decrease in abundance with heavy grazing. Furthermore, levels of structural heterogeneity may be an important factor in nesting and foraging sites. Prairie species associated with the high spatial heterogeneity of mixed shrub-grassland communities should decrease with the low heterogeneity found in shrub-dominated landscapes associated with heavy grazing in the northern mixed-grass prairie.

Factors that affect productivity may be the primary selective forces in structuring avian communities. Several recent hypotheses concerning the relationship between vegetation and nest success have been postulated to explain bird community structure, habitat selection, and life-history characteristics (Kelly 1993, Martin 1986, 1987, 1988a, 1988b). Indeed, several studies have found that the effects of vegetation structure and composition on nest success can produce significant impacts on avian communities (Holmes and Robinson 1981, Joern and Jackson 1983, Martin 1992, Kelly 1993). Grazing, by altering vegetative community composition and structure, may influence susceptibility to factors that affect nest success. Avian species may partition nesting habitat so that each species in

an area uses different substrates or structural characteristics for concealing and sheltering the nest. Martin (1988a, 1988b) suggested that nest site partitioning might allow co-occurring species to avoid predators that form search images for specific vegetation characters associated with nests. Because grazing can cause one or a few plant species to become dominant, reduced availability of suitable nesting sites may occur, and hence the probability of success for the species that nest there may decline. Additionally, vegetation may be important for concealing nests from predators and sheltering the nest from adverse weather conditions. Grazing, by altering the structural characteristics of existing vegetation, can reduce the suitability of available nest sites.

To investigate the effects of grazing on breeding prairie birds, I surveyed birds and located and monitored nests in north-central Montana in 1998 and 1999. My objectives were to compare grazed and ungrazed plots with respect to: (1) structural characteristics of vegetative communities, (2) structure of nest site vegetation, (3) nest densities, (4) nest success and mortality factors, (5) reproductive success of nesting birds, and (6) composition of breeding bird communities.

## STUDY AREA

The study was conducted on the U.L. Bend National Wildlife Refuge (ULB) and adjacent Bureau of Land Management (BLM) lands in north-central Montana. Soils of the area are primarily composed of varying densities of shale-derived clays, with many localized deposits of glacial till (Pan Spot range sites). Upland portions of the area are classified as the Northern Mixed Prairie (Holechek et al. 1989), represented here by Big

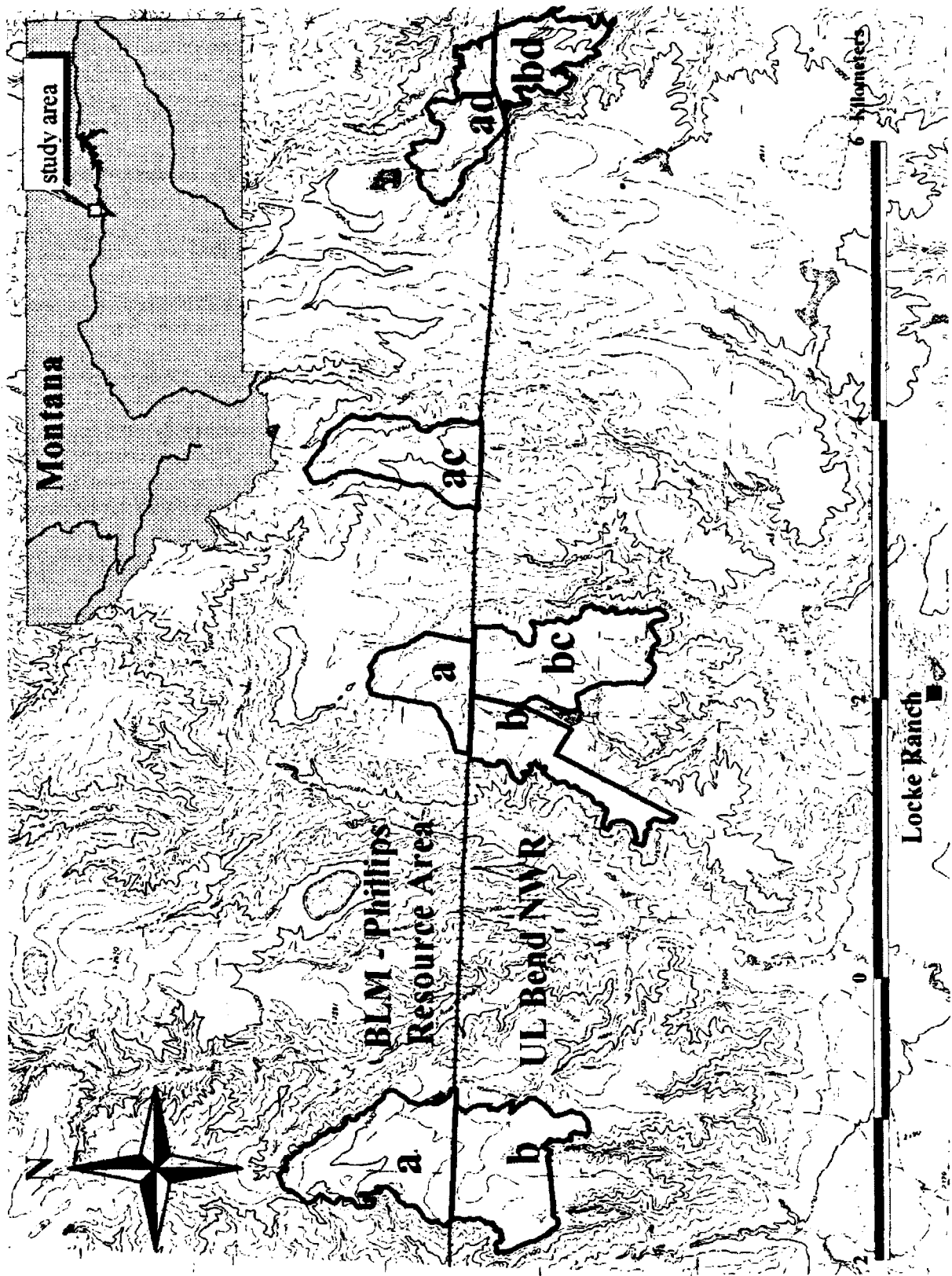
Sagebrush (*Artemisia tridentata*)/Western Wheatgrass (*Agropyron spicatum*)/Blue Grama (*Bouteloua gracilis*) associations (Knowles and Knowles 1994).

## METHODS

### Selection of Study Plots

Range site classifications (U. S. Soil Conservation Service 1977) indicated the vegetative potential of upland plots. In the absence of disturbance, and all other things being equal, vegetation present on any area in a given range site should be similar. Pan Spot range sites were the only range site that provided ungrazed areas with the potential to support vegetation communities that were reasonably representative of the study area, were present on comparable grazed plots, were relatively uniform in topography, and had similar moisture regimes. To isolate the effects of grazing, a matched-pair design was used to control for soil type, elevation, topography, and aspect. Each pair was a single range site polygon dissected by a fence, with cattle grazing on one side and no grazing on the other side (henceforth, grazed and ungrazed plots). Four sets of matched pairs (Fig. 1) were located using GIS databases. In 1998, I established three pairs of grazed and ungrazed plots on ULB and adjacent BLM lands. Two of the plots had been ungrazed since 1974 (W. Haglan, pers. commun.) and one had been ungrazed since 1996. The latter was part of a four-pasture rest-rotation system and was scheduled to be grazed in June of 1999. Therefore an alternate pair (grazed and rested) was selected to represent a pasture with two years of rest. BLM lands were grazed under a rest-rotation grazing system, and all study plots were grazed during 1998 and 1999.

Figure 1. Location of grazed and ungrazed study plots. a = grazed, b = ungrazed, c = plot used in 1998 only, d = plot used in 1999 only.



## Vegetation Measurements

I collected vegetation data as soon as possible after each nest either fledged or failed (1998:  $\bar{x}$  = 18.0 days,  $SD$  = 7.7 days; 1999:  $\bar{x}$  = 15.0 days,  $SD$  = 6.5 days), following modified BBird protocol (Martin et al. 1997) for grassland habitats. Circular plots of 5m radius were sampled, one centered on the nest (nest vegetation) and one at a point 35m in a random direction from each nest (random vegetation). Plots were divided into four equal quadrats with axes along the cardinal directions and delineated by a 5 m cord marked incrementally at 0.02 m, 0.25 m, 0.5 m, 1.0 m, 3.0 m, and 5.0 m from the nest. Height and density measurements (henceforth, HD; Robel et al. 1970), the height at which vegetation completely obscured a 2.5 cm diameter pole, were recorded at the nest center from each cardinal direction and at 1.0 m, 3.0 m, and 5.0 m along each axis. Leaf-contact measurements (Wiens and Rotenberry 1981) were recorded at all increments along each axis with type of contact recorded as green grass, residual grass, forb, or shrub. Depth of leaf litter was measured at 0.02 m, 1.0 m, 3.0 m, and 5.0 m along each axis. Ground cover in each quadrat was estimated for green grass, residual grass, forb, shrub, moss/lichen, cactus, leaf litter, brush, bare ground/gravel, and rock. Shrub density was measured by counting the number of shrubs of each species and height class (0-20 cm, 20-50 cm, 50-100 cm, and >100 cm) within each quadrat. The visibility of each nest was estimated from one meter in each cardinal direction and from one meter above the nest.

## Nest searches and monitoring

Nest searches on upland plots were conducted from 24 May to 30 June in 1998 and 17 May to 4 July in 1999. Initially, 5-6 people spent 40-48 person-hours on each plot



conducting a systematic grid search. Thereafter, two people searched each plot at three-day intervals. Search effort was approximately equal for grazed and ungrazed plots. Approximately 864 person-hours were spent searching for nests in 1998 and 1024 person-hours in 1999. Primary nest search techniques were systematic searches and observation of breeding behavior and movement of adults (Martin and Geupel 1993). Additionally, hand-held rope drags were used on a few small areas where a lack of shrubs allowed.

Nest locations were documented using a GPS unit. Nests were monitored every three days or when information on specific nesting stage was desired (Martin et al. 1997). Nests fledging at least one young were considered successful. Predation was assumed when the nest was disturbed, destroyed, or found empty after the first egg was laid. Nests that were found during building and abandoned before initiating egg laying were assumed to have been deserted due to observer influence (Martin et al. 1997) and were excluded from survival or density estimates.

#### Avian Community Composition

Relative bird abundance was sampled using 200 m radius (12.6 ha) point counts (Reynolds et al. 1980). Point count stations were visited at least twice during June of each year. Counts began at sunrise and ended three hours later; 10 minutes were spent at each count station. Both auditory detections and visual observations were recorded for avian species and potential nest predators.

## STATISTICAL ANALYSES

### Effects of grazing on plot vegetation

All analyses were performed using SPSS v10.05 unless otherwise noted (SPSS, Inc./Norrisus 1999). Correlation analyses, step-wise discriminant function (DFA), and univariate *t*-tests were used to investigate differences in vegetation within and between treatments (grazed and ungrazed). If grazing changed vegetation structure in consistent ways, given inherent variation among plots, I predicted that grazed plots would be more similar to each other than to the respective ungrazed pairs. Vegetation data collected at random locations were used for all comparisons and were subject to nearest neighbor analysis to investigate spatial independence of samples. Prior to univariate and discriminant analysis, log or natural log transformations were used to normalize data or to reduce statistical correlations between variables (Jongman et al. 1995). To test for a year effect on random vegetation, I conducted paired *t*-tests with data from study plots used in both 1998 and 1999 using vegetation variables I expected to be most influenced by annual variation in climate (i.e. grass structure and vegetation HD). For discriminant analysis, bivariate correlation matrices were constructed to identify variables that were highly correlated (Pearson's correlation coefficient  $\geq 0.5$ ). If strong positive intercorrelations among variables existed, one variable was chosen as a substitute to represent all correlated variables or variables were combined into a single compound variable. In all DFA's, covariance matrices were tested for homogeneity using Box's *M* criterion. Because many variable matrices exhibited significant heteroscedasticity ( $P < 0.0005$ ), separate group

covariance matrices were used for classification. Mahalanobis distance between group centroids was used to maximize discrete classification of plots in discriminant space. *F*-tests were conducted to determine the significance of discriminating functions. Structure correlation values for each variable were obtained to show the influence of each variable on the discriminating function. Classification rates of discriminating functions were presented as an index to effect size (Huberty 1994). To examine specific differences in vegetation between grazed and ungrazed plots, I included all variables, pooled within treatments, in univariate *t*-tests (Ott 1993).

#### Effects of grazing on nest site vegetation

Discriminant function analyses were used to examine whether grazing influenced patterns of nest site use among co-occurring species; I predicted that if grazing resulted in more homogeneous vegetation structure, species nesting on grazed plots would use sites more similar to each other than those nesting on ungrazed plots. Nests were classified according to species and treatment for inclusion in DFA's. To examine the effect of scale in determining whether patterns of nest site use could be identified, three scales relative to the nest were used: (1) nest micro-site (data collected 0.02 m, 0.25 m, and 0.50 m from the nest), (2) nest site (data collected 0.02 m, 0.25 m, and 0.50 m, and 1.00 m from the nest), and (3) nest patch (data collected at 1.00 m, 3.00 m, and 5.00 m of the nest). To test for a year effect, separate DFA's were conducted within each year. Univariate *t*-tests were also conducted between each year for each species nesting on grazed and ungrazed plots. Screening and selection of variables used in DFA's at all scales were done as

discussed in the preceding section covering the comparison of grazed and ungrazed random vegetation. Correct classification rates were used to identify the scale at which patterns of nest site use could best be distinguished. *F*-tests were used to determine whether species centroids differed statistically in ordinal space (Jongman et al. 1995).

To examine patterns of use among each species and potential relationships to successful or unsuccessful nesting attempts, DFA's were conducted as above, but with nests being classified according to species and fate within each treatment. Again, analyses were conducted at all scales relative to the nest. If birds nesting on grazed plots exhibit little separation among species in vegetation characteristics at nest sites, differences in vegetation between successful and unsuccessful nests should also be few. Conversely, relatively high heterogeneity on ungrazed plots may allow species to partition nest sites and greater variation in vegetation used by each species may allow certain nest site characteristics to be associated with successful nesting attempts. Additionally, if species increase the probability of success by partitioning nest sites, features that distinguish successful from unsuccessful nests should not be consistent across species. *F*-tests were conducted to assess statistical significance of discriminating functions and to determine if successful and unsuccessful nests were significantly different in Mahalanobis space (Jongman et al. 1995). Classification rates are provided as a measure of how well the discriminating functions classified the samples in the data set. Independent *t*-tests were also used to examine differences, within species, between nests on grazed and ungrazed plots (Ott 1993).

## Nest Density, Success, and Reproductive Parameters

I used nest densities as an index to treatment effects on the attractiveness of plots to nesting birds. Density estimates were calculated by dividing the total number of nests monitored on each plot by the area of search plots. Density and reproductive parameter estimates were not normally distributed, so I used Wilcoxon signed rank tests to compare grazed and ungrazed plots (Ott 1993).

Daily survival rates (DSR's) of nests were estimated using the Mayfield method (Mayfield 1975). Differences in DSR's between nests of each species on grazed and ungrazed plots were tested using program CONTRAST (Hines and Sauer 1989). I limited analyses to the those species for which adequate sample sizes were obtained ( $\geq 20$  nests/species/treatment/year) as estimates of nesting success based on fewer than 20 nests may not be reliable (Hensler and Nichols 1981). However, all nests found were monitored (Appendix A). Sample sizes were inadequate for testing for differences in DSR's between plots for each species during 1998 and 1999, so nests were pooled according to species, grazing status, and year in all tests. To assess the overall affect of grazing on nest success of all four of the most common species I used a Wilcoxon Signed Rank Test (Ott 1993).

## Avian Community Composition

Indices were constructed from point count survey data. Each survey location was treated independently within grazed and ungrazed plots. Average number of detections for each species was calculated for each point surveyed by dividing the total number of observations by number of survey visits. Additional calculations included the percent of

survey locations at which each species was detected, species richness, total number of species within grazed and ungrazed plots, diversity ( $H'$ ) (Shannon and Weaver 1949), and evenness ( $E$ ), using the modified Hill's ratio (Alatalo 1981). Data from point count surveys were not normally distributed, so Mann-Whitney  $U$  tests were used to test for differences between grazed and ungrazed plots (Ott 1993).

## RESULTS

### Effects of grazing on vegetation of plots

Vegetational differences attributable to grazing were significantly stronger than within-treatment differences between plots (Fig. 2). Grazed plots were characterized by increased bare ground and increased shrub cover (Fig. 2, Table 1). Ungrazed plots were characterized by increased residual grass cover and structure and increased H/D of vegetation (Fig. 2, Table 1). Ungrazed plots exhibited considerably more variation in the vegetation variables that distinguished them from grazed plots, and this variation encompassed essentially the entire range of samples from grazed plots (Fig. 2). DFA of vegetation on grazed and ungrazed plots generated 5 discriminating functions ( $\lambda=0.55$ ,  $\chi^2=338.4$ ,  $P\leq 0.001$ ; Box's  $M=475.9$ ,  $F=4.38$ ,  $P\leq 0.001$ ). The first two functions explained most of the variation in the data (function 1 = 45.9%; function 2 = 31.9%). Grazed and ungrazed plots were distinguished by the first discriminant function (eigenvalue 0.307, canonical correlation 0.484;  $\lambda = 0.81$ ,  $P \leq 0.0005$ ). Each matched pair of plots was distinguished from other matched pairs by the second function (eigenvalue 0.213, canonical correlation 0.419) (Fig. 2). Correct classification rates of the discriminating functions were more than twice as high for treatment effect (69.0%) than for plot effect (33.1%). Univariate *t*-tests of all variables, including those used in DFA, produced similar results: grazed plots had higher values for shrub variables and bare ground, and ungrazed plots had higher values for grass variables and HD (Table 2). Significant differences did exist within grazed and ungrazed plots between 1998 and 1999, but those differences were small (Table 3).

Figure 2. Ordination diagram showing group centroids of plots, with 95% CI based on sample scores, from discriminant function analysis of random vegetation on grazed and ungrazed plots. Corresponding symbols designate matched pairs of grazed (open symbols) and ungrazed (closed). Variables with a correlation value  $>0.5$  for each discriminating function are shown in parentheses on the axes. Area within ellipsoids represent spatial distribution for 95% of the samples based on euclidian distance from the mean.

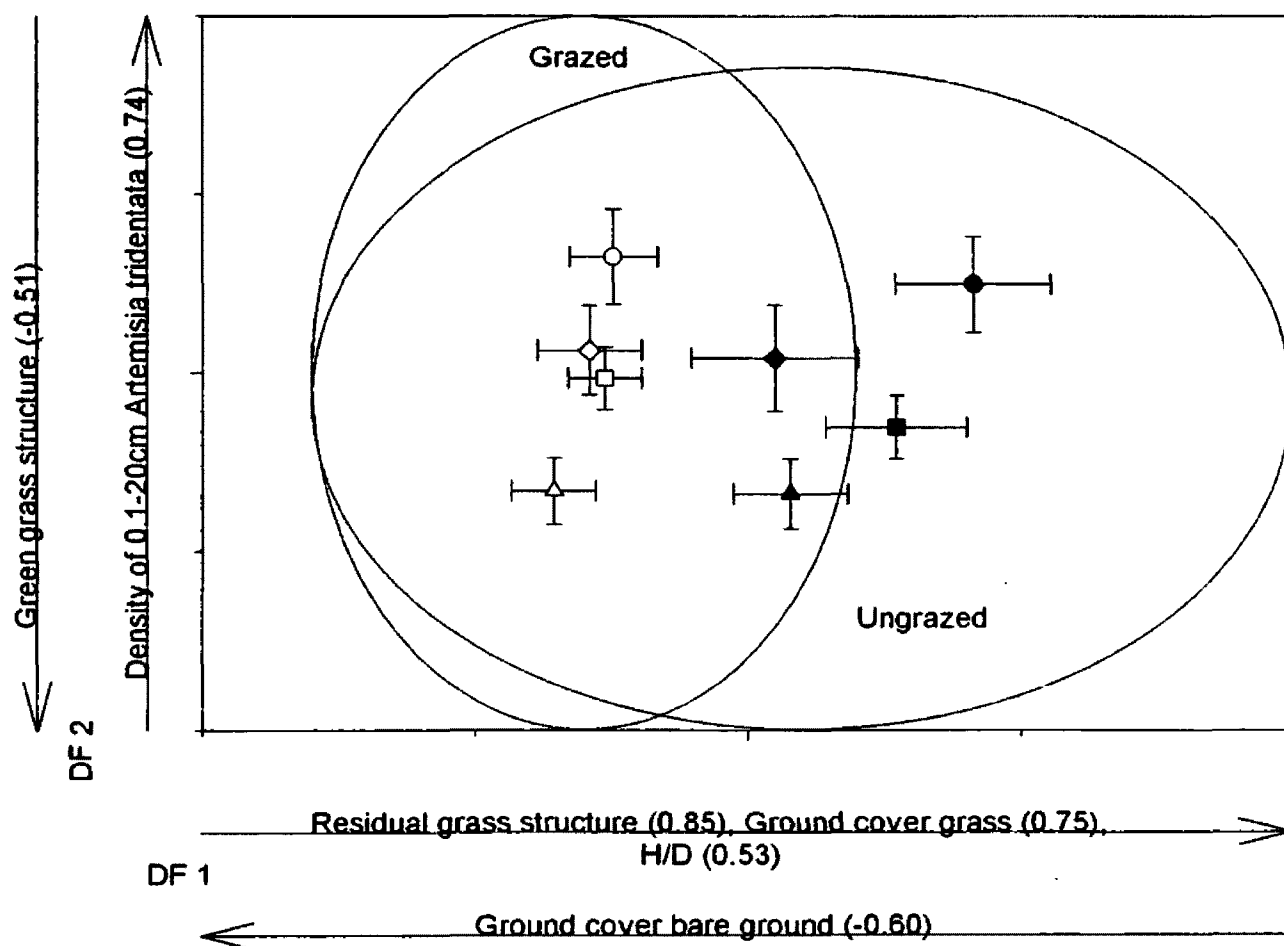




Table 1. Vegetation variables influencing ordination of plot centroids with structure correlations from DFA comparing grazed and ungrazed sites (n=8). Discriminant functions 1 (df1) and 2 (df2).

Variable	Correlation	
	df1	df2
<b>Ground cover</b>		
grass	0.75	-0.34 <sup>a</sup>
bare	-0.60	0.15
<b>Density of <i>A. tridentata</i></b>		
0-20cm	-0.36	0.21
<b>Vertical structure</b>		
green grass	0.29	-0.51
residual grass	0.85 <sup>a</sup>	0.02 <sup>a</sup>
shrub	-0.02	0.15
shrub heterogeneity	-0.01	0.21
<b>Height/density</b>	0.53	0.42

<sup>a</sup> Canonical coefficients of variables included in analysis:  
 Vertical structure residual grass df1=0.65, df2=0.27;  
 ground cover green grass df2=-0.18.

Table 2. Univariate comparison of vegetation on grazed and ungrazed plots.

Variable	Grazed	Ungrazed	P <sup>c</sup>
	$\bar{x} \pm SE$	$\bar{x} \pm SE$	
<b>Ground cover (%)</b>			
bare ground	56.75 ± 0.93	44.83 ± 1.02	<0.001
residual grass	9.24 ± 0.38	17.93 ± 0.55	<0.001
green grass	13.37 ± 0.41	17.70 ± 0.49	<0.001
shrub	10.73 ± 0.46	7.33 ± 0.35	<0.001
forb	2.82 ± 0.20	3.31 ± 0.23	0.110
cactus	2.62 ± 0.12	3.06 ± 0.11	0.005
<b>Litter depth (cm)</b>	0.39 ± 0.06	0.60 ± 0.06	0.140
<b>Density of <i>A. tridentata</i><sup>a</sup></b>			
0.1-20 cm	39.73 ± 1.63	27.74 ± 1.37	<0.001
20-50 cm	26.09 ± 1.32	15.89 ± 0.82	<0.001
50-100 cm	1.62 ± 0.31	1.81 ± 0.22	0.618
<b>Vertical structure<sup>b</sup></b>			
green grass	1.40 ± 0.05	1.74 ± 0.05	<0.001
residual grass	0.73 ± 0.06	1.41 ± 0.03	<0.001
shrub	0.49 ± 0.03	0.36 ± 0.02	0.002
shrub heterogeneity	0.14 ± 0.01	0.11 ± 0.01	0.001
<b>Height/density (cm)</b>	2.20 ± 2.10	3.40 ± 3.00	<0.001
<b>Grass height (cm)</b>			
green	12.40 ± 5.00	15.10 ± 6.40	<0.001
residual	5.70 ± 3.20	7.70 ± 4.00	<0.001

<sup>a</sup> Density of *A. tridentata* is number/78.5m<sup>2</sup>

<sup>b</sup> Vertical structure is recorded as number of contacts between 0-20cm for grass measures and 0-50cm for shrubs.

<sup>c</sup> P - values are from univariate t-tests.

Table 3. Results of paired *t*-test for year effect on grazed and ungrazed plots using vegetation measured at random points.

Variable	Year <sup>b</sup>	Grazed <sup>a</sup>		Ungrazed <sup>a</sup>	
		$\bar{x} \pm SD$	<i>P</i> <sup>c</sup>	$\bar{x} \pm SD$	<i>P</i> <sup>c</sup>
<b>Ground cover (%)</b>					
green grass	98	13.57 ± 7.38		20.61 ± 8.84	
	99	13.39 ± 5.89	1.000	14.83 ± 6.54	0.016
residual grass	98	10.09 ± 5.99		18.25 ± 9.42	
	99	8.55 ± 6.35	0.912	17.85 ± 9.99	1.000
forb	98	0.93 ± 0.96		1.27 ± 2.08	
	99	4.44 ± 3.37	0.016	5.03 ± 4.73	0.016
<b>H/D (cm)<sup>d</sup></b>					
	98	1.30 ± 1.44		2.16 ± 2.09	
	99	3.03 ± 2.20	0.016	4.43 ± 3.30	0.016
<b>Vertical Structure<sup>e</sup></b>					
green grass	98	1.61 ± 0.88		1.98 ± 0.96	
	99	1.24 ± 0.79	0.016	1.57 ± 0.84	0.016
residual grass	98	0.75 ± 0.63		1.49 ± 1.00	
	99	0.69 ± 0.50	1.000	1.47 ± 1.13	1.000
<b>Height<sup>f</sup> (cm)</b>					
green grass	98	11.94 ± 4.94		14.16 ± 5.65	
	99	13.23 ± 4.95	1.000	15.86 ± 6.72	0.576
residual grass	98	5.69 ± 3.85		8.51 ± 4.16	
	99	5.77 ± 2.57	1.000	7.25 ± 3.76	0.304

<sup>a</sup> Degrees of freedom: grazed = 123; ungrazed = 132.

<sup>b</sup> Plots used in one year only are excluded from analysis.

<sup>c</sup> *P*-values are for differences between years.

<sup>d</sup> Height and density of vegetation (Robel et al. 1970).

<sup>e</sup> Vertical structure is recorded as number of leaf contacts between 0-20 cm.

<sup>f</sup> Height of grass measured at height of tallest leaf blade within a distance of 10 cm.

## Effects of sites on vegetation of plots

Slope and aspect were nearly identical between grazed and ungrazed plots (% slope grazed: 3.7 (se 0.03); ungrazed: 3.4 (se 0.04),  $P = 0.58$ ; aspect grazed: 155°; ungrazed: 148°,  $P = 0.51$ ). Nearest neighbor analysis of nest spatial distributions showed nests to be randomly distributed on most plots each year and random vegetation was measured at random directions from nests.

## Effects of grazing on vegetation at nest sites

### *Patterns of nest site use among species*

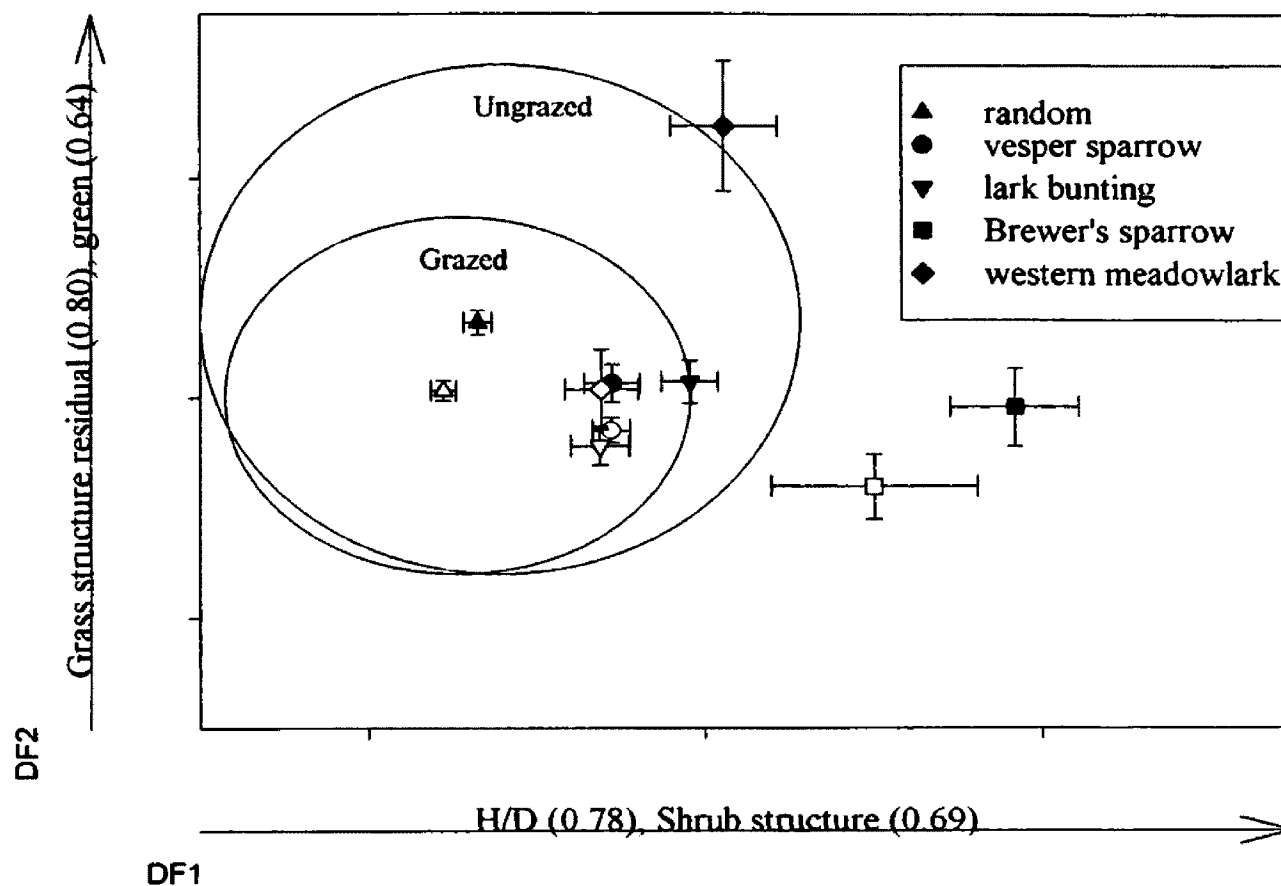
Samples were pooled across years because patterns of habitat use at nest sites among species were nearly identical across years ( $P \geq 0.05$ ) and I wanted to examine general patterns across years. DFA best distinguished patterns of use among species using vegetation at the nest micro-site (Table 4). Nest vegetation at the micro-site revealed fewer differences among species within grazed plots than in ungrazed plots (Fig. 3). Each species differed in nest site characteristics on grazed versus ungrazed plots primarily due to differences in residual and green grass structure, and these differences were generally consistent across species (Fig. 3). Five discriminating functions were generated at the micro-site scale ( $\lambda=0.37$ ,  $\chi^2=518.0$ ,  $P \leq 0.0005$ ). I focus on the first two functions because they explained 92.4% of the variation among nests of each species on grazed and ungrazed plots. On ungrazed plots only, the first discriminating function primarily distinguished among nest vegetation used by the four most common species (vesper sparrow [*Pooecetes gramineus*], lark bunting [*Calamospiza melanocorys*], Brewer's sparrow [*Spizella breweri*], and western meadowlark [*Sturnella neglecta*]) although no

Table 4. Correct classification rates for nests of the four most common species at three scales relative to the nest. Nests of all species, coded as grazed or ungrazed, were used in deriving discriminating functions.

Scale	Species <sup>a</sup>	% Correct Classification		
		Species and Treatment		Species
		Grazed	Ungrazed	
nest micro-site ( $\leq 0.5$ m)	vesper sparrow	79.4	15.6	77.8
	lark bunting	9.8	22.0	21.7
	Brewer's sparrow	20.5	51.8	51.0
	western meadowlark	16.0	74.3	51.7
	Overall	31.2	40.9	50.6
nest site ( $\leq 1.0$ m)	vesper sparrow	61.9	15.6	64.4
	lark bunting	34.4	24.0	55.9
	Brewer's sparrow	20.5	42.9	27.0
	western meadowlark	8.0	62.9	40.0
	Overall	31.2	36.4	46.8
nest patch (1-5 m)	vesper sparrow	73.0	17.8	72.2
	lark bunting	8.2	26.0	22.9
	Brewer's sparrow	15.9	21.4	24.0
	western meadowlark	0.0	48.6	28.3
	Overall	24.3	28.5	36.9

<sup>a</sup> Sample sizes for grazed and ungrazed: vesper sparrow 126, 90; lark bunting 61, 100; Brewer's sparrow 44, 56; western meadowlark 35, 25.

Figure 3. Partitioning of nest micro-sites (0.02-0.5 m from nest) by four common species nesting on grazed (open symbol) and ungrazed (closed symbol) plots. Centroids, with 95% CI, from DFA of vegetation within 0.5 m of nest. Area within ellipsoids contains 95% of random vegetation samples, based on euclidian distance from the mean, from grazed and ungrazed plots.



difference was detected between nest sites of vesper sparrow and lark bunting (Table 5). The first and second discriminating functions separated grazed from ungrazed nests within each species (Tables 5, 6). On grazed plots the first discriminating function was able to only distinguish the nests of Brewer's sparrow from those of vesper sparrow and lark bunting (Table 5). Correct classification rates were highest on ungrazed plots for lark bunting, Brewer's sparrow, and western meadowlark, reflecting their use of distinct nest sites. Vesper sparrow was the only species that had a higher correct classification rate on grazed plots. Within ungrazed plots, Brewer's sparrow exhibited strikingly different ( $P \leq 0.001$ ) patterns of use from the three other species, reflecting their use of shrubs as a nesting substrate. Within grazed plots, differences generally did not exist ( $P \geq 0.01$ ), between vesper sparrow, lark bunting, and western meadowlark, the three ground nesters. On ungrazed plots however, nests of western meadowlark were unique ( $P \leq 0.001$ ), driven primarily by residual grass structure (Fig. 3). Results of univariate t-tests mirrored those of DFA; differences between nests on grazed and ungrazed plots were primarily driven by grass structure, although significant differences also existed for shrub variables, bare ground, and nest concealment (Appendices B-E).

#### *Relationships between vegetation characteristics and nest success*

Within-species patterns between grazed and ungrazed plots were similar between years, so samples were pooled across years. Discriminant analysis of vegetation of successful and unsuccessful nests at the micro-site, site, and patch revealed inconsistent trends among species within grazed and ungrazed plots, so I present results for each species within grazed or ungrazed plots. Classification rates also varied by species, scale,

Table 5. Pairwise group comparisons on discriminant function 1 from DFA of four common species nesting on ungrazed and grazed plots.

Treatment	Species	Ungrazed				Grazed			
		vesper sparrow	lark bunting	Brewer's sparrow	western meadowlark	vesper sparrow	lark bunting	Brewer's sparrow	western meadowlark
Ungrazed	vesper sparrow	<i>F</i>	1.006	23.975	41.443	0.648	1.853	11.845	6.085
		<i>P</i>	0.316	0.001	0.001	0.421	0.174	0.001	0.014
	lark bunting	<i>F</i>	1.006	17.018	53.013	0.066	0.246	7.237	3.414
		<i>P</i>	0.316	0.001	0.001	0.797	0.620	0.007	0.065
	Brewer's sparrow	<i>F</i>	23.975	17.018	96.607	20.220	10.746	1.079	1.287
		<i>P</i>	0.001	0.001	0.001	0.001	0.001	0.299	0.257
	western meadowlark	<i>F</i>	41.443	53.013	96.607	53.315	50.457	72.006	48.967
		<i>P</i>	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Grazed	vesper sparrow	<i>F</i>	0.648	20.220	53.315	0.543	8.867	4.170	
		<i>P</i>	0.421	0.001	0.001	0.462	0.003	0.042	
	lark bunting	<i>F</i>	1.853	10.746	50.457	0.543	4.163	1.961	
		<i>P</i>	0.174	0.001	0.001	0.462	0.042	0.162	
	Brewer's sparrow	<i>F</i>	11.845	1.079	72.006	8.867	4.163	0.071	
		<i>P</i>	0.001	0.299	0.001	0.003	0.042	0.791	
	western meadowlark	<i>F</i>	6.085	1.287	48.967	4.170	1.961	0.071	
		<i>P</i>	0.014	0.257	0.001	0.042	0.162	0.791	



Table 6. Pairwise group comparisons on discriminant function 2 from DFA of four common species nesting on ungrazed and grazed plots.

Treatment	Species	Ungrazed				Grazed			
		vesper sparrow	lark bunting	Brewer's sparrow	western meadowlark	vesper sparrow	lark bunting	Brewer's sparrow	western meadowlark
Ungrazed	vesper sparrow	<i>F</i>	0.502	51.417	22.344	3.147	7.585	10.786	4.825
		<i>P</i>	0.606	0.001	0.001	0.044	0.001	0.001	0.008
	lark bunting	<i>F</i>	0.502	49.450	28.153	3.065	7.105	8.629	3.546
		<i>P</i>	0.606	0.001	0.001	0.047	0.001	0.001	0.030
	Brewer's sparrow	<i>F</i>	51.417	49.450	62.771	75.514	70.505	11.688	32.919
		<i>P</i>	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	western meadowlark	<i>F</i>	22.344	28.153	62.771	33.210	35.698	36.372	28.992
		<i>P</i>	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Grazed	vesper sparrow	<i>F</i>	3.147	3.065	75.514	33.210	1.860	17.793	2.189
		<i>P</i>	0.044	0.047	0.001	0.001	0.157	0.001	0.113
	lark bunting	<i>F</i>	7.585	7.105	70.505	35.698	1.860	19.941	1.250
		<i>P</i>	0.001	0.001	0.001	0.001	0.157	0.001	0.287
	Brewer's sparrow	<i>F</i>	10.786	8.629	11.688	36.372	17.793	19.941	7.988
		<i>P</i>	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	western meadowlark	<i>F</i>	4.825	3.546	32.919	28.992	2.189	1.250	7.988
		<i>P</i>	0.008	0.030	0.001	0.001	0.113	0.287	0.001

and successful or unsuccessful nests (Table 7). Generally, vesper sparrow were correctly classified to species at higher rates on grazed plots but lark bunting, Brewer's sparrow, and western meadowlark were correctly classified to species at higher rates on ungrazed plots.

On grazed plots and ungrazed plots, successful and unsuccessful nests of all species did not clearly differ (Figs. 4, 5). However, decreased residual grass structure was associated with successful nests of vesper sparrow (site:  $F = 2.41$ ,  $P \leq 0.10$ ), lark bunting (site:  $F = 3.51$ ,  $P \leq 0.05$ ), and Brewer's sparrow (micro-site:  $F = 2.41$ ,  $P \leq 0.10$ ) on ungrazed plots. On grazed plots successful nests of western meadowlark were characterized by increased shrub structure at the patch scale ( $F = 2.41$ ,  $P = 0.001$ ).

#### Nest Density, Reproductive Parameters, & Nest Success Relative to Grazing

Nesting densities did not differ between grazed and ungrazed paired plots for any species (Fig. 6). The four focal species did exhibit varied responses to grazing in mean number fledged per attempt, mean number fledged per successful nest, and mean number fledged per hectare (Table 8). Clutch size did not differ between treatments for any of the four species. Total number fledged was nominally higher for all species on ungrazed plots except for vesper sparrow on grazed plots in 1998. Mean number fledged per attempt was nominally higher for all species on ungrazed plots in both 1998 and 1999 and these differences were significant in 50% of the cases. The mean number fledged per successful nest did not differ between treatments for any species except vesper sparrow in 1999. The

Table 7. Correct classification rates from DFA of nest vegetation at three scales. Original groupings used in DFA are species/treatment/fate.

Scale	species <sup>a</sup>	treatment	% correct species	% correct successful	% correct failed
<b>nest micro-site</b>	VESP	grazed	67.1	36.0	60.0
		ungrazed	35.1	22.2	28.6
	LARB	grazed	10.3	0.0	13.3
		ungrazed	41.3	39.5	50.0
	BRSP	grazed	24.2	27.3	33.3
		ungrazed	64.1	65.5	60.0
	WEME	grazed	100.0	83.3	100.0
		ungrazed	90.0	33.3	85.7
<b>Overall</b>			49.5	45.0	
<b>nest site</b>	VESP	grazed	58.6	48.0	31.1
		ungrazed	22.8	11.1	14.3
	LARB	grazed	41.2	50.0	13.3
		ungrazed	30.4	28.9	25.0
	BRSP	grazed	12.1	9.1	25.0
		ungrazed	71.8	72.4	60.0
	WEME	grazed	85.6	100.0	75.0
		ungrazed	20.0	78.6	83.3
<b>Overall</b>			41.1	38.3	
<b>nest patch</b>	VESP	grazed	60.0	44.0	44.4
		ungrazed	35.1	30.6	28.6
	LARB	grazed	48.3	21.1	75.0
		ungrazed	39.1	35.7	46.7
	BRSP	grazed	21.2	27.3	33.3
		ungrazed	33.3	31.0	21.0
	WEME	grazed	85.7	66.7	100.0
		ungrazed	60.0	57.1	66.7
<b>Overall</b>			44.4	38.9	

<sup>a</sup> Sample size for grazed, ungrazed: VESP 70, 57; LARB 29, 46; BRSP 33, 39; WEME 14, 20

Figure 4. Vegetation characteristics of successful (open symbols) and unsuccessful (symbols with crosshairs) nests of four common species on grazed plots. Centroids with 95% CI of sample scores for each nest type are from DFA of vegetation at the micro-site (0.02-0.5 m from nest) and patch (1.0-5.0 m from the nest) scales.

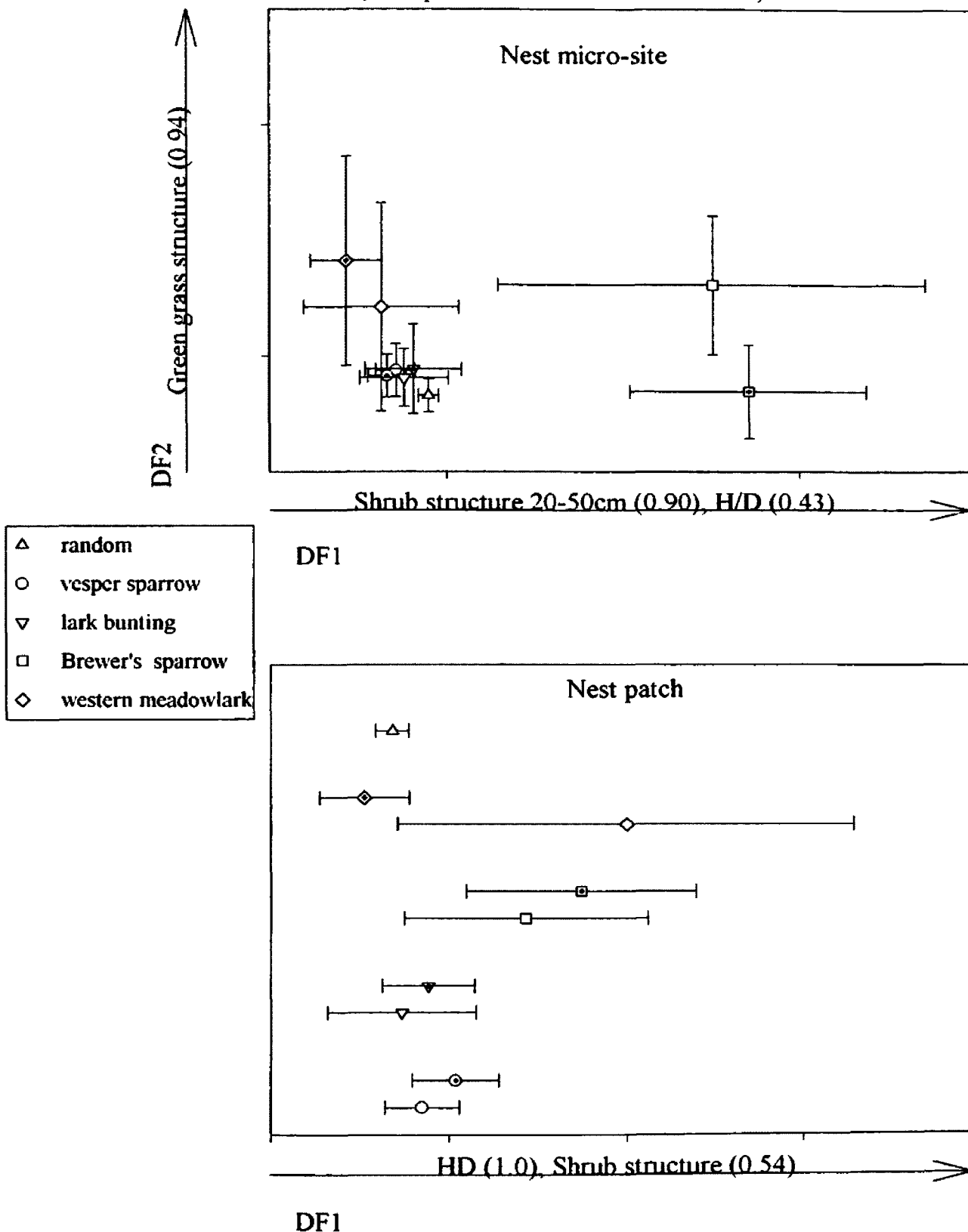


Figure 5. Vegetation characteristics of successful (closed symbol) and unsuccessful (symbols with crosshairs) nests of four common species on ungrazed plots. Centroids with 95% CI of sample scores for each nest type are from DFA of vegetation at the micro-site (0.02-0.5 m from the nest) and patch (1.0-5.0 m from the nest) scales.

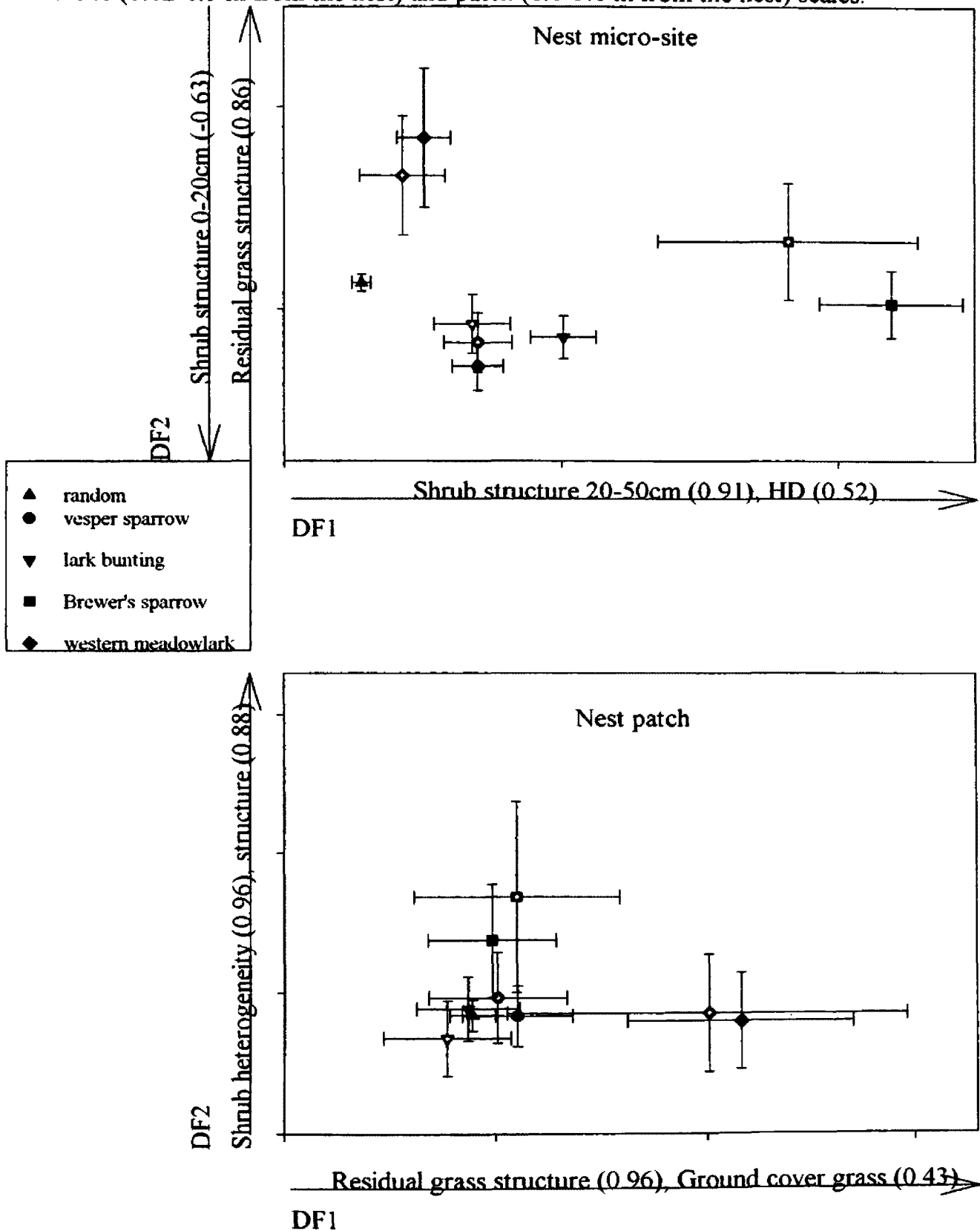
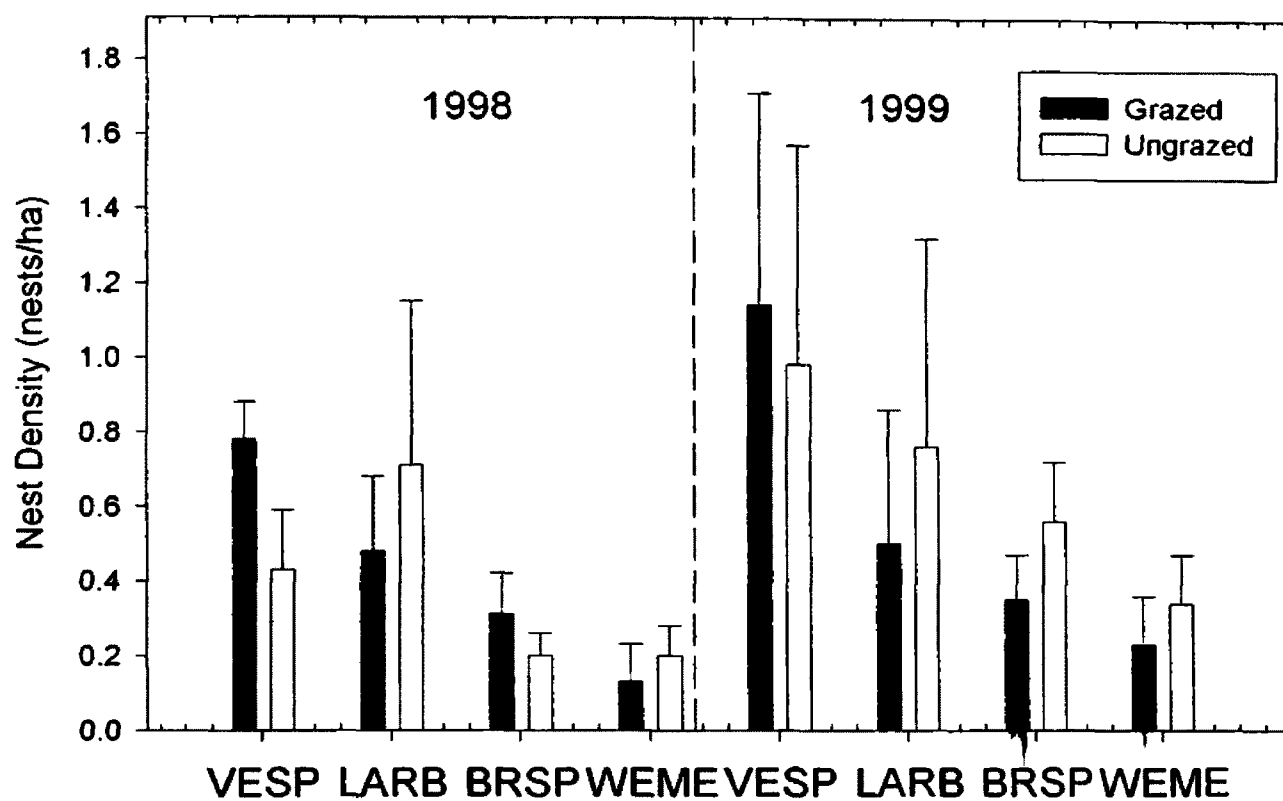


Figure 6. Nesting densities of vesper sparrow (VESP), lark bunting (LARB), Brewer's sparrow (BRSP), and western meadowlark (WEME) on grazed and ungrazed plots in 1998 and 1999.



**Table 8.** Estimated reproductive parameters for vesper sparrow, lark bunting, Brewer's sparrow, and western meadowlark on grazed and ungrazed plots.

Species	Treatment	Year	Clutch size	# Fledged	# Fledged/attempt	# Fledged/successful	# Fledged/ha
			$\bar{x} \pm 2 \text{ SE}$		$\bar{x} \pm 2 \text{ SE}$	$\bar{x} \pm 2 \text{ SE}$	
vesper sparrow	grazed	98	4.21 ± 0.16	118	2.14 ± 0.54	3.93 ± 0.18	0.80
	ungrazed	98	4.28 ± 0.24	73	2.21 ± 0.72	4.06 ± 0.50	0.45
	grazed	99	3.95 ± 0.14	86	1.32 ± 0.44 <sup>c</sup>	3.44 ± 0.40 <sup>a</sup>	0.59
	ungrazed	99	4.15 ± 0.15	128	2.33 ± 0.54 <sup>c</sup>	3.88 ± 0.26 <sup>a</sup>	0.97
lark bunting	grazed	98	4.97 ± 0.19	73	2.21 ± 0.82	4.29 ± 0.66	0.50
	ungrazed	98	4.96 ± 0.26	161	2.98 ± 0.68	4.74 ± 0.38	0.99
	grazed	99	4.57 ± 0.40	66	2.28 ± 0.38 <sup>c</sup>	4.13 ± 0.44	0.45
	ungrazed	99	4.85 ± 0.26	175	3.72 ± 0.58 <sup>c</sup>	4.37 ± 0.40	1.32
Brewer's sparrow	grazed	98	3.77 ± 0.19	33	1.50 ± 0.80	3.67 ± 0.34	0.22
	ungrazed	98	3.82 ± 0.26	35	2.06 ± 0.92	3.50 ± 0.54	0.22
	grazed	99	3.68 ± 0.24	39	1.77 ± 0.79 <sup>b</sup>	3.55 ± 0.42	0.27
	ungrazed	99	3.89 ± 0.16	100	2.78 ± 0.58 <sup>b</sup>	3.57 ± 0.36	0.75
western meadowlark	grazed	98	5.09 ± 0.42	6	0.55 ± 1.10 <sup>b</sup>	6.00 ± 0.00	0.04
	ungrazed	98	5.33 ± 0.38	50	3.13 ± 1.28 <sup>b</sup>	4.93 ± 0.26	0.31
	grazed	99	5.36 ± 0.34	28	2.15 ± 1.10	4.67 ± 1.12	0.19
	ungrazed	99	5.20 ± 0.24	69	3.45 ± 1.28	4.93 ± 0.26	0.52

<sup>a</sup>  $p < 0.10$  grazed vs. ungrazed plots, Wilcoxon signed-rank test.

<sup>b</sup>  $p < 0.05$  grazed vs. ungrazed plots, Wilcoxon signed-rank test.

<sup>c</sup>  $p < 0.002$  grazed vs. ungrazed plots, Wilcoxon signed-rank test.

mean number fledged per hectare was nominally higher on ungrazed plots for 75% of the cases.

Evaluation of nest success during the 1998 breeding season showed a mixed response to grazing across species (Table 9). Three (lark bunting, Brewer's sparrow, and western meadowlark) of the four most common nesters exhibited nominally higher nest success on ungrazed plots. Only vesper sparrow had a higher nest success on grazed plots. During the 1999 breeding season all four species exhibited higher daily survival rates for the nestling period and nominally higher overall nest success on ungrazed plots. Overall, seven out of eight comparisons of nest success between grazed and ungrazed plots revealed higher success on ungrazed plots ( $Z = -2.38$ ,  $P = 0.017$ ).

Incidental observations of predators were higher on grazed plots for all taxa. Snakes were observed more frequently on grazed plots (1998: grazed = 21 vs. ungrazed = 6; 1999: grazed = 30 vs. ungrazed = 24). The majority of snake observations were of bull snake (*Pituophis melanoleucus*), racer (*Coluber constrictor*), and prairie rattlesnake (*Crotalus viridis viridis*). All snakes were observed more frequently on grazed plots but rattlesnakes were encountered infrequently on ungrazed plots (one in 1998 and none in 1999). Observations of mammalian nest predators were also higher on grazed plots (1998: grazed = 17 vs. ungrazed = 2; 1999: grazed = 9 vs. ungrazed = 8). Finally, avian predators were observed more frequently on grazed plots (1998: grazed = 8 vs. ungrazed = 4; 1999: grazed = 18 vs. ungrazed = 12).



Table 9. Estimates of daily survival rates (DSR) and percent success for nests of vesper sparrow, lark bunting, Brewer's sparrow, and western meadowlark. All *P* values are from comparisons between nests on grazed and ungrazed plots within each species and year.

Species	Treatment	Year	<i>n</i>	Laying & Incubation		Nestling		Overall
				DSR (se)	Success (95%CI)	DSR (se)	Success (95%CI)	Success (95%CI)
vesper sparrow	grazed	98	57	0.962 (.010)	55.8 (41.0-75.5)	0.965 (.010)	72.4 (60.7-86.2)	40.5 (24.9-65.1)
	ungrazed	98	34	0.970 (.012)	63.8 (44.3-91.0)	0.949 (.016)	62.1 (46.3-82.5)	39.6 (20.5-75.1)
	grazed	99	71	0.934 (.012)	36.0 (24.7-51.9)	0.949 (.011) <sup>b</sup>	62.3 (51.1-75.6)	22.4 (12.6-39.2)
	ungrazed	99	55	0.953 (.012)	48.9 (33.9-69.9)	0.981 (.008) <sup>b</sup>	83.9 (73.0-96.2)	41.0 (24.7-67.3)
lark bunting	grazed	98	33	0.983 (.008)	75.7 (59.2- 96.4)	0.958 (.016) <sup>a</sup>	63.3 (49.8-80.0)	47.9 (29.5-77.1)
	ungrazed	98	54	0.974 (.008)	65.4 (50.7-83.9)	0.975 (.008) <sup>a</sup>	79.7 (69.3-91.3)	52.1 (35.2-76.6)
	grazed	99	30	0.941 (.019) <sup>a</sup>	37.9 (19.9-70.6)	0.958 (.016) <sup>a</sup>	68.1 (50.3-91.3)	25.8 (10.0-64.4)
	ungrazed	99	48	0.981 (.009) <sup>a</sup>	73.3 (55.8-96.0)	0.990 (.006) <sup>a</sup>	91.2 (81.5-100)	66.9 (45.4-97.8)
Brewer's sparrow	grazed	98	22	0.958 (.017)	52.6 (31.1-87.2)	0.952 (.018)	64.4 (45.9-89.0)	33.8 (33.8-54.3)
	ungrazed	98	17	0.984 (.011)	78.7 (56.2-100.0)	0.951 (.019)	63.8 (44.3-90.4)	50.2 (24.9-98.8)
	grazed	99	23	0.964 (.021)	57.7 (30.4-100.0)	0.933 (.028) <sup>b</sup>	53.3 (31.2-88.5)	30.7 (9.5-93.9)
	ungrazed	99	39	0.960 (.014)	54.6 (35.7-82.6)	0.991 (.007) <sup>b</sup>	92.5 (82.3-10.0)	50.5 (29.4-85.7)
western meadowlark	grazed	98	11	0.919 (.032) <sup>a</sup>	21.8 (6.2-70.9)	0.917 (.032) <sup>a</sup>	32.3 (12.6-76.5)	7.0 (0.8-54.3)
	ungrazed	98	26	0.974 (.015) <sup>a</sup>	61.7 (35.5-100.0)	0.975 (.015) <sup>a</sup>	72.0 (48.8-100.0)	44.4 (17.3-100.0)
	grazed	99	14	0.991 (.009)	85.1 (61.8-100.0)	0.934 (.024) <sup>b</sup>	41.0 (21.2-76.6)	34.9 (13.1-89.2)
	ungrazed	99	20	0.954 (.020)	42.6 (19.8-88.7)	0.993 (.008) <sup>b</sup>	90.9 (73.6-100.0)	38.7 (14.6-99.3)

<sup>a</sup> *p* < 0.10

<sup>b</sup> *p* < 0.05

## Avian Community Composition

During the 1998 field season 18 species were detected during point counts on upland plots (Table 10). Overall species richness was nominally higher on ungrazed plots than on grazed plots (16 vs. 13). Diversity and evenness, adjusted for sample sizes, were however nominally lower on ungrazed plots than on grazed plots ( $H' = 1.96$  vs.  $2.17$ ;  $E = 0.37$  vs.  $0.39$ ). In 1999, 14 upland species were detected and overall species richness was equal between ungrazed and grazed plots (10 vs. 10). Species diversity was again lower on ungrazed plots, however evenness was nominally higher ( $H' = 1.63$  vs.  $1.84$ ;  $E = 0.61$  vs.  $0.50$ ). During the 1998 season, 6 species were detected at more survey points on ungrazed plots and 3 were present at more points on grazed plots. In 1999, 2 species occurred at more points on ungrazed and 1 occurred at more points on grazed plots (Table 10). Relative densities for 7 species were higher ( $P < 0.10$ ) on ungrazed plots in 1998 and 2 were higher on grazed plots. Two species exhibited higher densities on ungrazed plots in 1999 and 1 species was present at higher densities on grazed plots.

Table 10. Point count survey data on grazed and ungrazed sites 1998 and 1999.

Species	Treatment	1998	1999	$\bar{x} \pm SD$	
				1998	1999
sage grouse ( <i>Centrocercus urophasianus</i> )	grazed	0	0	0.00 <sup>a</sup>	0.00
	ungrazed	30	8	1.45 $\pm$ 2.58 <sup>a</sup>	0.08 $\pm$ 0.29
killdeer ( <i>Charadrius vociferus</i> )	grazed	30	0	0.44 $\pm$ 0.66 <sup>b</sup>	0.00
	ungrazed	0	0	0.00 <sup>b</sup>	0.00
willet ( <i>Catoptrophorus semipalmatus</i> )	grazed	10	33	0.22 $\pm$ 0.63	0.33 $\pm$ 0.49
	ungrazed	40	25	0.64 $\pm$ 0.92	0.25 $\pm$ 0.45
upland sandpiper ( <i>Bartramia longicauda</i> )	grazed	0	33	0.00 <sup>a</sup>	0.33 $\pm$ 0.49 <sup>b</sup>
	ungrazed	30	0	0.36 $\pm$ 0.67 <sup>a</sup>	0.00 <sup>b</sup>
mourning dove ( <i>Zenaida macroura</i> )	grazed	20	42	0.12 $\pm$ 0.32	0.67 $\pm$ 0.67
	ungrazed	30	50	0.45 $\pm$ 0.69	0.50 $\pm$ 0.52
common nighthawk ( <i>Chordeiles minor</i> )	grazed	30	0	0.23 $\pm$ 0.42	0.00
	ungrazed	20	0	0.27 $\pm$ 0.47	0.00
eastern kingbird ( <i>Tyrannus tyrannus</i> )	grazed	10	0	0.11 $\pm$ 0.31	0.00
	ungrazed	20	0	0.27 $\pm$ 0.65	0.00
horned lark ( <i>Eremophila alpestris</i> )	grazed	60	17	0.10 $\pm$ 0.79 <sup>a</sup>	0.17 $\pm$ 0.39
	ungrazed	10	0	0.27 $\pm$ 0.65 <sup>a</sup>	0.00
loggerhead shrike ( <i>Lanius ludovicianus</i> )	grazed	10	8	0.11 $\pm$ 0.31	0.08 $\pm$ 0.29
	ungrazed	40	0	0.70 $\pm$ 1.06	0.00
western meadowlark ( <i>Sturnella neglecta</i> )	grazed	70	100	3.19 $\pm$ 2.44 <sup>b</sup>	3.33 $\pm$ 1.23 <sup>b</sup>
	ungrazed	100	100	5.55 $\pm$ 2.46 <sup>b</sup>	4.50 $\pm$ 1.45 <sup>b</sup>
brown-headed cowbird ( <i>Molothrus ater</i> )	grazed	30	17	0.55 $\pm$ 0.83	0.17 $\pm$ 0.39
	ungrazed	20	0	0.45 $\pm$ 1.21	0.00
lark bunting ( <i>Calamospiza melanocorys</i> )	grazed	80	92	3.53 $\pm$ 2.36 <sup>b</sup>	5.50 $\pm$ 2.71
	ungrazed	100	100	6.55 $\pm$ 3.61 <sup>b</sup>	7.25 $\pm$ 3.60
grasshopper sparrow ( <i>Ammodramus savannarum</i> )	grazed	0	0	0.00 <sup>b</sup>	0.00 <sup>c</sup>
	ungrazed	40	42	0.73 $\pm$ 1.27 <sup>b</sup>	0.67 $\pm$ 0.89 <sup>c</sup>
vesper sparrow ( <i>Pooecetes gramineus</i> )	grazed	100	92	3.32 $\pm$ 1.33	2.83 $\pm$ 2.86
	ungrazed	100	75	3.36 $\pm$ 0.92	1.67 $\pm$ 1.78
lark sparrow ( <i>Chondestes grammacus</i> )	grazed	20	0	0.12 $\pm$ 0.32	0.00
	ungrazed	0	0	0.09 $\pm$ 0.30	0.00
field sparrow ( <i>Spizella pusilla</i> )	grazed	0	0	0.00 <sup>b</sup>	0.00
	ungrazed	40	17	0.36 $\pm$ 0.50 <sup>b</sup>	0.17 $\pm$ 0.39
Brewer's sparrow ( <i>Spizella breweri</i> )	grazed	100	92	2.32 $\pm$ 0.82 <sup>c</sup>	2.42 $\pm$ 1.44
	ungrazed	50	100	1.00 $\pm$ 1.18 <sup>c</sup>	3.00 $\pm$ 1.35
Baird's sparrow ( <i>Ammodramus bairdii</i> )	grazed	0	0	0.00	0.00
	ungrazed	10	0	0.10 $\pm$ 0.30	0.00
chestnut-collared longspur ( <i>Calcarius ornatus</i> )	grazed	0	0	0.00	0.00
	ungrazed	0	8	0.00	0.08 $\pm$ 0.29

<sup>a</sup>  $p < 0.10$ , Mann-Whitney  $U$  test, grazed vs. ungrazed within each year.

<sup>b</sup>  $p < 0.05$ , Mann-Whitney  $U$  test, grazed vs. ungrazed within each year.

<sup>c</sup>  $p < 0.02$ , Mann-Whitney  $U$  test, grazed vs. ungrazed within each year.

## DISCUSSION

## Effects of grazing on vegetation

*Treatment effect versus plot effect*

Grazing clearly affected structure of vegetation of plots, causing increased coverage by bare ground and reduced residual grass structure, reduced ground cover of grass, and reduced HD. Structural changes associated with grazing were reductions in vertical heterogeneity, cover and height of green and residual grass, vertical structure of green grass, and cover of cactus. Grazed plots were much more homogeneous, and the range of values for grazed plots was almost completely contained within the range of the more heterogeneous ungrazed plots. Reduced grass structure and cover, and reduced structural heterogeneity in response to grazing have also been observed in numerous other studies (e.g., Turner 1971, Holechek and Stephenson 1983, Medin and Clary 1990, Bock et al. 1992).

Grazing also caused an increase in cover, density, and structure of big sagebrush. Ryder (1980), Branson (1985), and Holechek et al. (1989) confirm that big sagebrush typically increases under heavy grazing. Sagebrush grasslands generally recover slowly from overgrazing (Holechek and Stephenson 1983). Densities of large (>50 cm) sagebrush plants did not differ between grazed and ungrazed plots, presumably reflecting historic heavy grazing on all plots used in this study, but densities of small (<50 cm) sagebrush were nearly twice as high on grazed plots as on ungrazed plots. Angell (1997) also observed increased survival of sagebrush seedlings on continuously grazed plots, but no difference in densities of larger plants. Where relatively productive sites extended

across the fence separating plots, vigorous sagebrush plants typically existed on the grazed side but most plants on the ungrazed were dead or dying. Based on this observation and on the relative scarcity of sagebrush recruitment on ungrazed plots, I suspect that the ungrazed plots were still in an intermediate stage of recovery from past heavy grazing. Smith and Schmutz (1975) observed similar patterns in their study of ungrazed versus continuously grazed grasslands in Arizona.

This study can best be described as a natural snapshot experiment (Diamond 1986); I had no control over how cattle had been grazed on the landscape nor could I randomly select sites. A matched-pair design was used to address the preceding problems, although many confounding factors may still be present. Although some variation existed among grazed and ungrazed pairs, vegetative conditions were similar among plots within each treatment suggesting that each site responded similarly to the presence or lack of grazing. The design was chosen to isolate the effects of grazing, but independence within the paired plots is of concern. I assumed that any influences of interdependent factors were equalized between grazed and ungrazed plots and therefore that any observed differences could be attributed to grazing.

Annual weather patterns can influence vegetation structure in grassland habitats (Branson 1985, Smoliak 1986, Holechek et al. 1989), and yearly differences existed on the plots used in this study. However, vegetative trends were similar within grazed and ungrazed plots over the two years, and differences between grazed and ungrazed plots were nearly identical within each year. Although significant differences in grass height existed between 1998 and 1999 within grazed and ungrazed plots, these differences were

most consistent with slightly higher precipitation in 1999. Both years however, had higher than normal precipitation during the breeding season. Initially, all analyses were conducted within years. Patterns across years were similar within and between grazed and ungrazed plots. Year effects were generally small overall, and I judged them to be of minimal biological relevance.

### *Characteristics of nest vegetation*

#### Nest site use among species within grazed and ungrazed plots

Nest sites were similar among the four most common species on grazed plots, but the same species appeared to partition nest sites on ungrazed plots. Vesper sparrow, lark bunting, and western meadowlark, all ground nesters, nested in similar vegetation on grazed plots where the vegetation was fairly homogeneous. On the relatively heterogeneous ungrazed plots, these same species used somewhat different vegetation from one another for nesting. If co-occurring species partition nest sites to increase the probability of success (Martin 1988b, 1993; but note Reitsma and Whelan 2000) and availability of suitable nest sites is limited, birds may use sites more similar to one another and exhibit lower success rates or densities. This study and others (e.g., Martin 1988b, 1993) generally support this prediction, although trends among species were not totally consistent between grazed and ungrazed plots.

On ungrazed plots a strong preference for residual and green grass by meadowlark distinguished nests of this species from those of vesper sparrow and lark bunting, the two other common ground nesters. On grazed plots, where the availability of grass was

greatly reduced, I was unable to distinguish among nests of meadowlark versus vesper sparrow and lark bunting. Meadowlarks build domed nests of interwoven grass blades and nests sites usually are characterized by increased grass or decreased shrub cover and structure (e.g., Niven 1973, Ryder 1980, Wiens and Rotenberry 1981, Knick and Rotenberry 1995). Knick and Rotenberry (1995) found that meadowlark density was correlated with grass cover and scattered low shrubs, the latter being used as song perches. Although sagebrush may compete with grass for water and nutrients (Caldwell et al. 1985, 1987; Holechek et al. 1989), relatively dense clumps of grass on my grazed plots occurred primarily beneath sagebrush plants where cattle grazing tended to be reduced. As a result, meadowlark nested mainly in grass under sagebrush on my grazed plots. Other studies have reported the formation of herbivory-induced refuges for palatable plants within those plants that were unpalatable (Rausher 1981, Lubchenco 1983, Pfister and Hay 1988).

On my study area, vesper sparrow and lark bunting nested under sagebrush almost exclusively, and nests of these two species were indistinguishable on grazed plots; whereas on ungrazed plots, lark bunting exhibited a greater preference for HD and shrub structure, although differences were generally small. Vesper sparrow twice nested in the old nest bowl of a lark bunting; both nests had been abandoned, one the year before, and one the same year by the lark bunting. Vesper sparrow inhabit a variety of habitats, including grassland, prairie, savanna, old-field, arid scrub, and woodland clearings (Ehrlich et al. 1988) and are likely to be habitat generalists on my study area.

The nests of Brewer's sparrow in my study were distinguished from all others, on both grazed and ungrazed plots, by increased HD and shrub structure. Although HD was correlated with shrub cover on grazed plots, the relationship was weaker on ungrazed plots where the role of grass in contributing to HD was more pronounced. Wiens and Rotenberry (1981) demonstrated an association of Brewer's sparrow with shrub cover and both vertical and horizontal heterogeneity.

Generally, the characteristics that distinguished between grazed and ungrazed plots, namely grass variables, also characterized intraspecific differences between nests on grazed and ungrazed plots: this relationship was especially strong for meadowlark.

#### Relationships between vegetation characteristics and nest success

Patterns of vegetation characteristics between successful and unsuccessful nests generally were inconsistent across all species, and were often reversed between grazed and ungrazed plots. On grazed plots, successful nests of vesper sparrow, lark bunting, and Brewer's sparrow were typically situated in areas with decreased HD, reduced shrub structure, and reduced shrub vertical heterogeneity. Interestingly, when not considering fate, the species mentioned above preferred patches with higher HD and that were shrubbier than random vegetation on grazed plots. On ungrazed plots, successful nests of vesper and Brewer's sparrow were generally associated with reduced residual grass structure and increased shrub cover at the patch scale surrounding the nest. Seemingly, as birds nested in or under shrubs that were situated in patches with low shrub density, the probability of failure increased. It may be more difficult for predators to find nests that are



situated in areas with relatively high densities of the preferred nesting substrate (Martin and Roper 1988). Lark bunting seemed to benefit from the same relationship, but different vegetative characteristics were involved; successful nests were associated with relatively little residual grass structure in the microhabitat immediately around the nest. However, successful bunting nests were situated in patches of high residual grass structure, relative to both the nest microhabitat and random vegetation. The importance of residual grass at the patch scale to successful nesting by lark bunting may be related to the concealment it provides. In a study of the use of space around cover, Lima (1990) found that lark bunting would forage near available cover but not in it; they also did not use cover for escape, but may have benefited from the visual obstruction it afforded.

Although meadowlarks generally prefer grass habitats (Niven 1973, Ryder 1980, Wiens and Rotenberry 1981, Knick and Rotenberry 1995), successful meadowlark nests on grazed plots were associated with increased HD, shrub structure and shrub heterogeneity at the patch scale. Unsuccessful nests of meadowlark tended to be situated in patches with increased bare ground. Successful nests of meadowlark on grazed plots were also associated with increased vertical grass structure within one meter around the nest. Perhaps denser stands of sagebrush provided concealment not of the nest itself but of the preferred microhabitat of meadowlark, making small dense patches of grass less obvious than those surrounded by higher levels of bare ground.

On ungrazed plots, successful nests of meadowlark were associated with higher residual grass structure at all scales, reflecting the preferences of this species observed in similar studies (Ryder 1980, Wiens and Rotenberry 1981, Knick and Rotenberry 1995).

Ungrazed plots tended to have higher coverage and structure of residual grass, and the dense grassy areas preferred by meadowlark may have been less obvious relative to the surroundings (see Martin and Roper 1988).

My results suggest that if species partition nest sites to increase the probability of success, those factors contributing to success may be inconsistent across species. Additionally, any factors that contribute to success may also vary according to the vegetational context in which a nest is situated (Martin and Roper 1988).

## Productivity

### *Nest Density*

Grazing negatively affected nesting densities of three of the four most common nesting birds, but densities of vesper sparrow apparently responded positively to grazing. Nest density estimates of vesper sparrow were higher, by 45% in 1998 and 14% in 1999, on grazed plots; point count surveys revealed similar trends. In a review of studies examining the effect of livestock grazing on birds, Saab et al. (1995) reported mixed responses to grazing by vesper sparrow. Contrary to my results, Kantrud and Kologiski (1983) estimated that grazing reduced vesper sparrow populations 44% in both the transition (region of intergradation between the northern and shrub-steppe regions) and shrub steppe regions of the Northern Great Plains.

Lark bunting and western meadowlark may decrease with grazing pressure (Niven 1973, Ryder 1980, Kantrud and Kologiski 1983, but also see Saab et. al., 1995). During both years of my study, lark bunting and western meadowlark nested at lower densities on

grazed plots. My grazed plots had 36% fewer meadowlark nests in 1998 and 32% fewer nests in 1999. These differences in nest density were consistent with Kantrud and Kologiski (1983) who reported a 59% and 63% decline of meadowlark between lightly grazed and heavily grazed sites, within the transition and shrub steppe regions, respectively. In the shortgrass prairie of Saskatchewan, Maher (1979) reported a 73% decline in meadowlark densities on grazed sites as compared to ungrazed sites.

Similar to meadowlark, lower nesting densities of lark bunting were observed on grazed versus ungrazed plots both years. Kantrud and Kologiski (1983) also observed a 58% decrease in densities, relative to grazing, in the shrub steppe region. For meadowlark and lark bunting, differences in nest density were not statistically significant but density estimates from point count surveys did reveal significant differences of similar magnitude and direction. The higher observed densities of lark bunting and meadowlark on ungrazed plots may reflect the nest site preferences, and vegetative characters associated with successful nest attempts, namely residual grass, of each species on ungrazed plots.

Nesting densities of Brewer's sparrow were 35% higher on grazed plots in 1998 and 37% higher on ungrazed plots in 1999. Density estimates from point count data reveal similar trends. The mixed reaction of Brewer's sparrow to grazing may be explained by annual variation in settling patterns. However, the minimal year effects observed in nest site use, on both grazed and ungrazed sites, could not explain this. Knick and Rotenberry (1995) also reported large annual variation in densities of Brewer's sparrow. Kantrud and Kologiski (1983) reported Brewer's sparrow densities that were 48% lower on heavily grazed sites.

Low availability of ungrazed areas limited my study to three paired plots each year which reduced my ability to detect significant differences in densities between grazed and ungrazed plots.

In the absence of productivity estimates, densities of breeding birds may be a poor indicator of habitat quality (Van Horne 1983, Maurer 1986, Purcell and Verner 1997). However, I present nest density estimates based on nests found in combination with nest success rates. Little information on nesting densities is available in the literature, so direct comparisons of nesting densities to other studies and regions were not possible. I use estimates of nest densities as an index to the effects of grazing. I did not mark birds or otherwise identify re-nesting attempts. Density estimates may be biased high, however those nests not located may help offset this bias. Search effort was kept as equal as possible between grazed and ungrazed plots to address some of the inherent biases associated with using nests found, and to validate the use of density estimates as an index for assessing the effects of grazing.

### *Nest Success*

Grazing tended to reduce nest success and overall productivity of three of the four most common species both years of my study. Although individual differences were not statistically significant, the overall trend was toward lower nest success and reproductive output on grazed plots. Vesper sparrow occurred in higher densities on grazed plots both years, yet nest success was twice as high on ungrazed plots as on grazed plots in 1999. Brewer's sparrow nested in higher densities on grazed plots in 1998, yet had higher nest success on ungrazed plots both years. Lark bunting and western meadowlark exhibited

higher nest success and nesting densities on ungrazed plots both years. Overall, more individuals were produced of each species on ungrazed plots. Productivity ranged from two to nine and a half times higher on ungrazed plots than on grazed plots for lark bunting, Brewer's sparrow, and western meadowlark. Vesper sparrow again was the exception, producing twice as many individuals on grazed plots in 1998; however, the opposite occurred in 1999.

Small differences in nest success can have serious consequences for recruitment and demographic performance of bird populations. I used the mean number of females fledged per attempt, estimated adult annual survival for ground nesting or shrub nesting birds (Martin 1995), and estimated juvenile female survival during the first year (Budnik, et al. 2000) to approximate relative differences between grazed and ungrazed plots in the infinite rate of increase ( $\lambda$ ) for my study populations. In all cases  $\lambda$  was higher on ungrazed plots than on grazed plots (differences in  $\lambda$ : vesper sparrow + 0.12; lark bunting + 0.24; Brewer's sparrow + 0.17; meadowlark + 0.41) when averaged over the two years of the study. The number fledged per attempt reflects differences in nest success between grazed and ungrazed plots but does not correct for multiple nest attempts which could change the magnitude of estimated differences in population growth between grazed and ungrazed plots. There should be no bias associated with the relative differences between grazed and ungrazed plots given the assumption that the data was from a random sample of the populations.

Predation was the primary source of mortality for all species on grazed and ungrazed plots, accounting for 95-99% of nest loss. Other studies reported similar levels of nesting

mortality resulting from predation (e.g., Martin and Roper 1988, Martin 1992). Rates of nest predation often are highest during the nestling stage (Lack 1947, 1948, 1949; Skutch 1949, 1966, 1985; Bosque and Bosque 1995; but see also Roper and Goldstein 1997). However, success rates during the nestling period were higher in 69% of the cases over both years in my study (grazed: 38% in 1998 and 50% in 1999; ungrazed: 50% in 1998 and 100% in 1999). Although nest success rates were higher during the nestling period on both grazed and ungrazed plots, higher nest success rates by all species on ungrazed plots were generally driven by differences in survival during the nestling stage, especially in 1999.

Differences in nest success observed between grazed and ungrazed plots can be used to estimate the effect of grazing on the focal species, only in the study area or nearby areas with similar vegetative potential. Although this study was not designed to estimate predator densities, incidental observations of all classes of predators were higher on grazed plots. Higher observation rates of snakes on grazed plots may be explained by an increase in detectability due to more open ground conditions, although this could not account for increased observations of avian and mammalian predators. Bull snakes and racers are known to consume eggs and nestlings, and were observed doing so over the course of this study. Rattlesnakes however, are reported to consume eggs only infrequently (Klauber 1972, Stebbins 1985), but readily prey upon nestlings, fledglings, or adult birds. The apparent scarcity of rattlesnakes on ungrazed plots could help explain the differences in nestling survival between grazed and ungrazed plots.

Nest parasitism by brown-headed cowbird (*Molothrus ater*) can also be a significant source of mortality for grassland birds (Sealy-Spencer 1999), and frequency of parasitism is often greatest near concentrations of cattle (Verner and Ritter 1983, Robinson et al. 1995); however only one nest (a lark bunting on a grazed plot) was parasitized over the course of this study. Robinson et al. (1995) lists the northern Great Plains as being an area of high cowbird parasitism, and parasitism rates have been tied to host densities (Robinson and Wilcove 1994). In a concurrent study of the effects of cattle grazing on riparian birds, conducted along the nearby Missouri River where host densities were substantially higher, parasitism rates as high as 50% were observed (Logan unpublished data). Cowbirds on the upland study area were observed to congregate on blacktail prairie dog (*Cynomys ludovicianus*) towns (whether occupied by cattle or not) whereas all observations of cowbirds on the study plots were of birds flying over.

#### Avian Community Composition

Significant differences existed in avian community composition between grazed and ungrazed plots. Clear trends did not exist across all species; some occurred at higher densities on grazed plots while others were present at higher densities on ungrazed plots. However, some of the species occurring at lower densities on grazed plots (i.e., meadowlark, lark bunting, and grasshopper sparrow [*Calamospiza melanocorys*]) were those generally associated with the vegetative characteristics typical of ungrazed plots. Similarly, those species that occurred at higher densities on grazed plots were those associated with bare ground (i.e., killdeer [*Charadrius vociferus*]) although the pattern was inconsistent. In a review of studies regarding the effects of grazing on bird

communities in western North America, Saab et al. (1995) reported similar responses to grazing by many of the same species present on study plots, although responses varied by habitat. More species that were relatively uncommon on my study plots occurred on ungrazed plots and more common species occurred on grazed plots. Higher densities of three of the four most common species contributed to higher species evenness on ungrazed plots. Diversity indices are sensitive to species evenness (Ludwig and Reynolds 1988) and, although more rare species generally occurred on ungrazed plots, higher species evenness reduced diversity indices within ungrazed plots relative to grazed plots.

Point count surveys are inherently subject to numerous biases (i.e., observer, time of day or season, weather conditions, etc.). Standardized protocols and equalized sampling effort were used to reduce bias, although complete elimination of biases probably cannot be expected. Therefore, survey data are provided as an index to the effects of livestock grazing.

#### Management and Research Implications

Livestock grazing is the predominant use of grasslands in western North America (Holechek et al., 1989). In order to conserve grassland bird populations, grazing practices need to be designed and implemented that favor creation or maintenance of suitable habitat conditions for a variety of species. Vegetation structure is a useful indicator of whether grazing is changing the suitability of the habitat for breeding birds (Wiens 1969, Kantrud and Higgins 1992). Vegetative heterogeneity and residual grass cover were important to successful breeding for most of the species studied.



Grazing influenced the vegetation structure on my grazed study plots, whereas less forage was allocated to cattle on rested pastures when in use and the vegetation was relatively unaffected. Additionally, rested pastures were generally rested for longer periods of time than those used as grazed plots (W. Haglan personal comm.). Rested pastures on ULB were similar, in both vegetation structure and avian productivity, to those that had been ungrazed for nearly 30 years. This similarity may reflect management that favors the maintenance of suitable nesting habitat for the birds breeding there. Another explanation may be that recovery from past grazing is very slow in the unproductive, dense clay soil types of the northern mixed prairie, and current vegetative conditions reflect an intermediate stage of recovery.

Higher intensity grazing over a longer period on grazed plots created a more homogeneous landscape that was dominated by shrubs and appeared less suitable for a number of declining species (DeSante and Luke 1994, Igl 1997). Some species did respond positively to grazing or show no significant effect, however. Disturbance from grazing and fire can create suitable habitat for many grassland species (Kantrud 1981, Johnson and Temple 1990, Kantrud and Higgins 1992, Knopf 1996). Furthermore, even those species associated with dense grass cover can be negatively affected by excessive accumulations of residual vegetation (Kirsch et al. 1978), and periodic disturbance by grazing or fire can maintain plant vigor over time (Holechek et al. 1989).

To conserve prairie birds, managers should consider the habitat requirements for maintaining stable populations of all species and manage lands with these diverse requirements in mind. Grazing may have less of an effect on breeding birds if a grazing

system is used to minimize changes in vegetation structure. Grazing during the nesting season coincides with the growing season of the vegetation and hence has the most potential to influence vegetation structure over time. Grazing systems can be utilized that include grazing during the non-growing season of the vegetation (Holechek et al. 1989, Hansen et al. 1995) or rest-rotation grazing systems that incorporate periods of rest during growing seasons, encouraging the maintenance of standing residual vegetation and vigor of grasses (Holechek et al. 1989, Packard and Mutel 1997).

Knowledge of the effects of grazing on avian community composition and nesting productivity are presently limited. Grazing can directly influence vegetation structure and indirectly influence nest density, nest site use and availability, cowbird parasitism (Robinson et al. 1995), and predator community (Szaro and Jakle 1985). All of these factors can consequently influence the maintenance of breeding bird populations (Martin 1988b, Clark and Nudds 1991). Additional research is needed on the influence of grazing on these factors, the interactions among them, and how grazing can be managed to maintain or create suitable breeding habitat for a variety of grassland birds.

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Appendix A. Nests Monitored in Upland Habitat - Field Season 1998 & 1999.  
 All monitoring and vegetation data for these nests are available from the BBIRD  
 database, Montana Cooperative Wildlife Research Unit, University of Montana,  
 Missoula, MT 59812.

Species	# of nests				
	Grazed		Ungrazed		Total
	98	99	98	99	98 & 99
Vesper Sparrow	58	59	39	87	243
Lark Bunting	35	44	60	48	187
Brewer's Sparrow	25	26	17	30	98
Western Meadowlark	11	22	22	24	79
Sage Grouse	1	6	8	4	19
Mallard	0	5	3	4	12
Common Nighthawk	3	2	1	1	7
Grasshopper Sparrow	0	0	2	2	4
Golden Eagle	0	0	1	1	2
Lark Sparrow	0	1	1	0	2
Northern Harrier	0	0	1	0	1
Sharp-tailed Grouse	0	0	0	1	1
Blue-winged Teal	0	0	0	1	1
Willet	0	1	0	0	1
Upland Sandpiper	0	1	0	0	1
	133	167	155	203	658

Appendix B. Vegetation measured at the nests of vesper sparrow. Univariate *t*- tests used to compare nests on grazed and ungrazed plots from 1998 and 1999.

	Grazed			Ungrazed			P
	N	Mean	SD	N	Mean	SD	
<b>Micro-site (&lt;0.5 m)</b>							
side cover (%)	123	65.54	18.28	88	72.21	16.73	0.007
overhead cover (%)	123	65.53	27.68	88	68.51	24.75	0.417
<b>grass height (cm)</b>							
green	123	21.48	11.28	88	21.13	10.93	0.819
residual	123	10.87	7.87	88	12.11	7.87	0.260
HD (cm)	123	8.43	4.18	88	10.28	4.82	0.004
<b>vertical structure</b>							
green grass	123	1.31	0.70	88	1.77	1.02	0.001
residual grass	123	0.90	0.74	88	1.42	1.14	0.001
shrub 0-20cm	123	1.15	0.54	88	1.20	0.73	0.637
shrub 20-50cm	123	0.21	0.29	88	0.32	0.42	0.041
shrub heterogeneity	123	0.20	0.08	88	0.20	0.09	0.476
<b>Site (&lt;1.0 m)</b>							
<b>grass height (cm)</b>							
green	123	14.60	6.59	88	16.89	7.32	0.021
residual	123	6.40	3.89	88	9.03	4.49	0.001
HD (cm)	123	5.69	3.20	88	7.16	3.64	0.003
<b>vertical structure</b>							
green	123	0.90	0.72	88	1.24	0.89	0.003
residual	123	0.56	0.47	88	0.95	0.83	0.001
shrub 0-50cm	123	1.13	0.53	88	1.21	0.84	0.437
shrub heterogeneity	123	0.19	0.76	88	0.17	0.09	0.206
<b>Patch (1-5 m)</b>							
<b>grass height (cm)</b>							
green	123	13.73	5.76	88	15.99	6.21	0.001
residual	123	5.91	3.27	88	9.05	6.18	0.001
HD (cm)	123	2.89	2.56	88	3.88	2.80	0.004
<b>vertical structure</b>							
green grass	123	1.22	0.72	88	1.57	0.73	0.001
residual grass	123	0.67	0.53	88	1.29	0.97	0.001
shrub 0-50cm	123	0.50	0.50	88	0.37	0.46	0.056
shrub heterogeneity	123	0.14	0.10	88	0.11	0.10	0.056
<b>ground cover (%)</b>							
green grass	123	13.54	6.71	88	17.25	7.73	0.008
residual grass	123	9.46	6.14	88	17.97	8.48	0.000
shrub	123	10.85	6.36	88	8.00	4.95	0.001
cactus	123	2.39	1.45	88	2.69	1.40	0.129
bare	123	56.29	14.61	88	41.67	18.17	0.001
<b>shrub density (#)</b>							
0-20cm	123	40.76	27.17	88	28.93	22.15	0.001
20-50cm	123	29.69	20.30	88	19.57	16.13	0.001
50-100cm	123	2.63	5.36	88	3.25	6.67	0.475

Appendix C. Vegetation measured at the nests of lark bunting. Univariate *t*- tests used to compare nests on grazed and ungrazed plots from 1998 and 1999.

	Grazed			Ungrazed			P
	N	Mean	SD	N	Mean	SD	
<b>Micro-site (<math>\leq 0.5</math> m)</b>							
side cover (%)	59	61.64	16.44	98	68.78	17.70	0.012
overhead cover (%)	59	70.65	24.61	96	68.48	28.07	0.613
<b>grass height (cm)</b>							
green	59	19.15	12.17	98	25.82	12.80	0.001
residual	59	10.05	7.55	98	12.72	8.90	0.046
HD (cm)	59	6.92	5.00	98	10.48	5.90	0.001
<b>vertical structure</b>							
green grass	59	1.24	0.75	98	1.78	0.87	0.001
residual grass	59	0.89	0.71	98	1.62	1.31	0.001
shrub 0-20cm	59	1.21	0.54	98	1.01	0.46	0.024
shrub 20-50cm	59	0.33	0.47	98	0.56	0.64	0.014
shrub heterogeneity	59	0.21	0.08	98	0.21	0.08	0.633
<b>Site (<math>\leq 1.0</math> m)</b>							
<b>grass height (cm)</b>							
green	59	27.75	10.49	98	18.66	7.17	0.506
residual	59	7.32	6.91	98	9.47	5.04	0.038
HD (cm)	59	4.68	3.43	98	7.47	4.55	0.001
<b>vertical structure</b>							
green	59	0.69	0.51	98	1.00	0.72	0.002
residual	59	0.41	0.32	98	0.77	0.58	0.001
shrub 0-50cm	59	1.27	0.65	98	1.23	0.67	0.696
shrub heterogeneity	59	0.20	0.09	98	0.18	0.08	0.128
<b>Patch (1-5 m)</b>							
<b>grass height (cm)</b>							
green	59	19.98	4.75	98	17.60	6.35	0.702
residual	59	0.07	0.03	98	0.09	0.04	0.001
HD (cm)	59	2.55	2.60	98	4.31	3.42	0.001
<b>vertical structure</b>							
green grass	59	1.33	0.60	98	1.67	0.85	0.004
residual grass	59	0.68	0.43	98	1.35	1.08	0.001
shrub 0-50cm	59	0.47	0.42	98	0.35	0.37	0.088
shrub heterogeneity	59	0.14	0.09	98	0.11	0.09	0.025
<b>ground cover (%)</b>							
green grass	59	14.70	7.03	98	19.38	7.60	0.001
residual grass	59	10.14	6.05	98	17.42	8.71	0.001
shrub	59	10.63	7.42	98	8.32	7.16	0.056
cactus	59	2.37	1.47	98	2.73	1.52	0.135
bare	59	55.17	16.54	98	42.87	17.97	0.001
<b>shrub density (#)</b>							
0-20cm	59	39.83	27.75	98	22.22	20.79	0.001
20-50cm	59	25.59	17.27	98	17.18	12.01	0.001
50-100cm	59	1.36	3.59	98	2.89	6.18	0.051

Appendix D. Vegetation measured at the nest of Brewer's sparrow. Univariate *t*-tests used to compare nests on grazed and ungrazed plots from 1998 and 1999.

	Grazed			Ungrazed			P
	N	Mean	SD	N	Mean	SD	
<b>Micro-site (<math>\leq 0.5</math> m)</b>							
side cover (%)	44	65.88	22.10	50	72.72	14.43	0.087
overhead cover (%)	44	69.44	25.43	52	64.50	31.00	0.395
<b>grass height (cm)</b>							
green	44	27.57	15.57	54	30.07	14.70	0.419
residual	44	15.79	10.87	54	16.91	10.28	0.608
HD (cm)	44	14.58	9.06	54	20.63	10.85	0.003
<b>vertical structure</b>							
green grass	44	1.25	0.78	54	1.47	0.98	0.224
residual grass	44	1.19	0.84	54	2.33	1.80	0.001
shrub 0-20cm	44	1.55	1.36	54	1.26	0.66	0.211
shrub 20-50cm	44	1.82	1.93	54	2.02	1.14	0.548
shrub heterogeneity	44	0.25	0.07	56	0.26	0.09	0.658
<b>Site (<math>\leq 1.0</math> m)</b>							
<b>grass height (cm)</b>							
green	44	17.24	7.69	54	23.14	7.05	0.001
residual	44	8.49	5.29	54	12.36	5.67	0.001
HD (cm)	44	9.93	6.25	54	14.21	7.68	0.003
<b>vertical structure</b>							
green	44	0.82	0.66	54	1.10	0.70	0.048
residual	44	0.60	0.54	54	1.56	1.41	0.001
shrub 0-50cm	44	2.70	2.45	54	2.65	1.12	0.899
shrub heterogeneity	44	0.23	0.08	56	0.24	0.09	0.509
<b>Patch (1-5 m)</b>							
<b>grass height (cm)</b>							
green	44	15.29	6.35	54	20.44	5.66	0.001
residual	44	7.30	4.15	54	10.57	3.97	0.001
HD (cm)	44	4.76	4.11	54	6.64	4.75	0.038
<b>vertical structure</b>							
green grass	44	1.39	0.84	54	1.71	0.76	0.054
residual grass	44	0.69	0.61	54	1.74	1.05	0.001
shrub 0-50cm	44	0.65	0.78	54	0.66	0.63	0.953
shrub heterogeneity	44	0.17	0.11	56	0.16	0.12	0.803
<b>ground cover (%)</b>							
green grass	44	12.61	7.09	54	17.39	7.38	0.002
residual grass	44	7.05	5.62	54	19.69	10.06	0.001
shrub	44	13.36	8.69	54	11.87	8.42	0.393
cactus	44	1.93	1.42	54	2.93	1.76	0.003
bare	44	55.98	14.38	54	38.33	16.93	0.001
<b>shrub density (#)</b>							
0-20cm	44	38.93	25.40	54	22.30	17.65	0.001
20-50cm	44	31.09	17.32	54	21.87	12.55	0.004
50-100cm	44	6.02	10.56	54	8.63	12.20	0.260

Appendix E. Vegetation measured at the nest of western meadowlark. Univariate *t*-tests used to compare nests on grazed and ungrazed plots from 1998 and 1999.

	Grazed			Ungrazed			P
	N	Mean	SD	N	Mean	SD	
<b>Micro-site (<math>\leq 0.5</math> m)</b>							
side cover (%)	24	66.71	24.53	35	77.89	16.56	0.060
overhead cover (%)	24	71.13	30.49	35	77.38	28.99	0.436
<b>grass height (cm)</b>							
green	24	23.08	12.29	35	22.71	10.43	0.905
residual	24	13.38	7.48	35	13.34	8.11	0.988
<b>HD (cm)</b>	24	8.40	3.98	35	10.81	3.67	0.020
<b>vertical structure</b>							
green grass	24	2.07	1.39	35	2.98	1.25	0.013
residual grass	24	1.33	0.93	35	4.12	2.55	0.001
shrub 0-20cm	24	0.95	0.42	35	0.27	0.37	0.001
shrub 20-50cm	24	0.19	0.21	35	0.05	0.11	0.005
shrub heterogeneity	24	0.24	0.08	35	0.09	0.10	0.001
<b>Site (<math>\leq 1.0</math> m)</b>							
<b>grass height (cm)</b>							
green	24	17.23	6.93	35	20.94	6.27	0.042
residual	24	7.24	2.88	35	10.53	4.16	0.001
<b>HD (cm)</b>	24	5.78	2.98	35	8.54	3.61	0.002
<b>vertical structure</b>							
green	24	1.18	0.68	35	1.96	1.34	0.005
residual	24	0.73	0.58	35	2.48	1.95	0.001
shrub 0-50cm	24	0.93	0.39	35	0.28	0.37	0.001
shrub heterogeneity	24	0.20	0.07	35	0.08	0.09	0.001
<b>Patch (1-5 m)</b>							
<b>grass height (cm)</b>							
green	24	15.83	5.90	35	20.38	6.22	0.006
residual	24	7.14	2.90	35	10.57	3.99	0.001
<b>HD (cm)</b>	24	2.91	2.97	35	5.40	3.63	0.006
<b>vertical structure</b>							
green grass	24	1.33	0.64	35	2.12	0.76	0.001
residual grass	24	0.70	0.48	35	2.68	1.44	0.001
shrub 0-50cm	24	0.44	0.55	35	0.24	0.26	0.056
shrub heterogeneity	24	0.12	0.11	35	0.07	0.07	0.043
<b>ground cover (%)</b>							
green grass	24	13.96	5.54	35	24.51	10.00	0.001
residual grass	24	10.25	4.76	35	27.26	11.87	0.001
shrub	24	12.92	7.73	35	6.17	6.37	0.001
cactus	24	2.67	1.55	35	2.43	1.60	0.570
bare	24	53.46	10.70	35	31.00	16.65	0.001
<b>shrub density (#)</b>							
0-20cm	24	62.25	57.97	35	13.57	20.55	0.001
20-50cm	24	33.58	21.83	35	12.91	12.18	0.001
50-100cm	24	1.96	5.32	35	1.69	3.31	0.825