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Nest density and nest success of ground-nesting grassland birds relative to grazing in western Montana

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NEST DENSITY AND NEST SUCCESS OF GROUND-NESTING GRASSLAND BIRDS RELATIVE TO GRAZING IN WESTERN MONTANA

By

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ABSTRACT

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I examined nest density and nest success of ground-nesting grassland birds on grazed and ungrazed plots in western Montana. Grazed plots had lower height and density (HD) of vegetation, lower litter depth, less litter cover, and greater forb and shrub cover than ungrazed plots. Nest density was correlated with HD of study plots for 11 of 13 common bird species. Species choosing high HD at nest sites occured in greatest densities on plots with high HD, and those choosing low HD at nest sites occurred in greatest density on plots with low HD. Although plot HD clearly was reduced by grazing, HD at nests did not differ between grazed and ungrazed plots for most species. This demonstrates that nest placement was not random with respect to HD, and supports the view that effects of grazing on bird communities reflects, at least in part, the effect of grazing on the availability of nest sites. Mayfield nest success did not differ significantly between grazed and ungrazed plots for Western Meadowlarks (*Sturnella neglecta*, 27% vs. 21%) or Gadwalls (*Anas strepera*, 34% vs. 32%), but was lower on grazed than on ungrazed plots for Savannah Sparrows (*Passerculus sandwichensis*, 7% vs. 20%) and Short-eared Owls (*Asio flammeous*, 14% vs. 66%). Among Savannah Sparrows, lower nest success on grazed plots resulted from increased trampling and increased parasitism by Brown-headed Cowbirds (*Molothrus ater*); among Short-eared Owls it resulted from increased predation. Birds chose vegetation features at the nest and adjacent to the nest (2.5 m radius of nest); most of features chosen were those associated with concealment. Nest parasitism was greater on grazed than on ungrazed plots for Western Meadowlarks and Savannah Sparrows, but I could not discriminate among several competing hypotheses about the factors responsible. Nest trampling was higher on plots with high stocking rates than on plots with low stocking rates, and nesting species varied in their vulnerability to trampling.

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INTRODUCTION

Population declines have occurred in many species of ground-nesting grassland birds including ducks (Johnson and Shaffer 1987) and nongame species (Robbins et al. 1986, Johnson and Schwartz 1993, Knopf 1994). However, the factors responsible for these trends are poorly understood (Clark and Nudds 1991, Knopf 1994). Livestock grazing is the primary land use of grasslands in the western United States (Lauenroth et al. 1994). Although prairie avifauna evolved in a grazed environment, the continually shifting mosaic of habitats created by fire and free-roaming native ungulates has been replaced by a spatially and temporally uniform landscape resulting from grazing by confined domestic livestock (Wells 1970, Knopf 1996a, 1996b). Grazing as currently practiced often results in simplified vegetation structure and changes in grassland floristics (Branson 1985, Vavra et al. 1994).

In summmarizing grazing effects on grassland birds, Kirsch et al. (1978) and Saab et al. (1995) concluded that density and species composition of avifauna change relative to grazing, but that species responses have varied across studies. Composition of grassland bird communities appear to be strongly influenced by vegetation structure (Cody 1968, Wiens 1969, Balda 1975), and this pattern may be largely explained by availability of nest sites (Martin 1988, 1993). Hence, the primary effect of grazing on grassland birds may result from changes to vegetation used for nesting (Kantrud and Kologiski 1982). If so, then one should be able to predict the response of species to grazing by examining the effects of grazing on the availability of nest sites.

Effects of grazing on grassland bird species have been judged largely based on bird abundance, which often is a poor indicator of habitat quality in comparison to direct measurements of fitness (Van Horne 1983). Impacts of grazing on vegetation might affect reproductive success by reducing density and structural heterogeneity of cover, which sometimes are correlated with nest success in a variety of grassland species (Wray and Whitmore 1979, Martin 1988, Johnson and Temple 1990, Clark and Nudds 1991, Riley et. al. 1992). Vegetation conditions at spatial scales broader than the immediate nest site itself often affect nest site selection and the probability of predation in birds of forests and shrublands (Martin and Roper 1988, Norment 1993, Badyaev 1995); however, issues of scale have seldom been examined in grasslands. Although Brown-headed Cowbirds (*Molothrus ater*) are associated with cattle (Robinson et al. 1995), factors affecting parasitism rates in grazed grasslands are largely undetermined. Grazing livestock also can directly affect nest success by nest trampling (Lanyon 1957, Ryder 1980, Shrubb 1990).

To examine the effects of grazing on grassland birds, I located nests and measured nest parameters of ground-nesting birds in western Montana in 1993 and 1994. My objectives were to measure and compare grazed and ungrazed plots with respect to: 1) vegetation structure and floristics, 2) breeding bird species composition and nest densities, 3) nest site vegetation, nest initiation, nest success, and mortality factors.

STUDY AREA

The study area was centered around the Ninepipe National Wildlife Refuge located on the Flathead Indian Reservation in the lower Flathead (Mission) Valley of west-central Montana. The local landscape was shaped by glaciation, resulting in high densities of wetlands. The refuge and surrounding lands were managed by state and federal wildlife agencies with planted cover and food for wildlife. Tribal and private lands beyond were used primarily for cattle pasture, hayland, and small grain farming. Grazed fields usually were idle in early spring, and $\geq$ 3 weeks of vegetation growth occurred before cattle were introduced in early to mid May; most fields were then grazed continuously throughout the breeding season. Most native vegetation has been replaced by plantings of tame grasses and legumes, and some areas were planted to trees and shrubs. Because of the numerous wetlands the breeding bird community was diverse, a mix of true grassland species and wetland species (Peterjohn and Sauer 1992).

METHODS

Plot Selection and Vegetation

I studied 9 plots in 1993 and 14 in 1994; 7 plots were studied in both years. Plot sizes ranged from 11 to 23 ha (grazed $\bar{x}$=16.4 ha; ungrazed $\bar{x}$=14.8 ha; t=1.53, 21 *df*, P=0.15). I selected plots subjectively to ensure homogeneity of vegetation cover within plots and to include a range of vegetation cover types among plots, to maximize dispersion of plots across the study area, and to maximize interspersion of grazed and ungrazed plots (Hurlbert 1984). Plot selection was severely constrained by availability of ungrazed areas, and all ungrazed plots had adjacent grazed areas. I considered a plot to be grazed if grazing by livestock occurred at any time during the nesting season. I calculated plot stocking rates in head/ha (hd/ha; Jenson et al. 1990). I classified each grazed field into one of two stocking rate categories: low (n=6) = 0.2-0.5 hd/ha and high (n=4) = 1.5-3.0 hd/ha.

Vegetation on plots was characterized by collecting data along a transect running diagonally across each plot three times during each breeding season. A cord marked at 20 m intervals was positioned between plot corners to locate sample points ($\geq$20) and to insure repeatability. In 1993, at each point along the transect I recorded vegetation height and density (HD) as modified from Robel et al. (1970) by Higgins and Barker (1982) and effective vegetation height (Kantrud and Higgins 1992). In 1994 I also measured litter depth and percent cover by vegetation type (% litter, % grass, % forb, % shrub). I used seven categories to estimate percent cover (after Mueller-Dombois and Ellenberg 1974): 0 = 0, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, and 6 = 96-100%. I calculated means of vegetation features for study plots and grazing status within years.

Nest Density and Success

Nests located per unit area (hereafter nest density) was used as an index to breeding bird density for each species. A bias could occur if nest detectability differed among cover types (Skinner 1975, Kantrud and Higgins 1992). To examine this potential bias I compared the average number of individuals detected on point counts with nest densities for several passerine species.

I used point counts of ten minute duration to census breeding songbirds between late May and early July, twice in 1993 and three times in 1994. Five points were systematically arranged within each plot, ≥100 m from fence or plot edge and ≥140 m between points. For Savannah Sparrows (*Passerculus sandwichensis*) count radii were fixed at 50 m. Western Meadowlarks (*Sturnella neglecta*) seemed wary of my presence; only 15% of sightings were within 50 m, and I noted a "fence effect" (Rotenberry and Knick 1995) in that 48% of all meadowlarks observed were on fences. Consequently, I used unlimited-radius counts for meadowlarks, scoring birds observed within plot boundaries as 1 and those on fences as 0.5. Meadowlark counts were then converted to density to account for varying plot areas. I recorded data and calculated totals according to Ralph et al. (1993), and averaged counts within years for analysis.

I searched study plots for nests three times each year, in 1993 on foot, dragging a rope with attached cans and chains (after Duebbert and Kantrud 1974) and in 1994 using 4-wheeled all-terrain cycles pulling a cable-chain drag (Higgins et al. 1969). Crews consisted of two drivers or rope-pullers and ≥ one observer. Nesting bird species were identified, and incubation stage (Westerkov 1950, Weller 1956) or approximate nestling age was determined. All nests were marked with an unflagged willow switch 5 m north of the nest. I revisited passerine nests at 4-6 day intervals and other nests at 7-12 day intervals. Nest fates and initiation dates were determined according to Klett et al. (1986) and Martin and Geupel (1993). Supplemental nesting data were obtained from a parallel study monitoring upland nesting birds within the study area but off of my study plots.

Nest Vegetation

When nests were located I recorded HD and effective vegetation height at the nest (0 m) for all study plot and supplemental nests in 1993 and 1994. I expanded both the number and scale of nest vegetation measurements for study plot nests and some supplemental nests in 1994. To avoid nest disturbance and to better measure conditions at the time of termination, these measurements were recorded within three days after nest fate was determined. Study plot nests were paired with a random point located within the same plot. Random points were plotted on aerial photos using a standardized grid and random numbers table; once the general location was reached on the ground, I threw a stick over my shoulder to obtain an exact location. At both nest and random point, and along two transects (one running north and one in a randomly chosen direction) at 2.5 m, 5 m, and 10 m, I recorded HD, litter depth, effective vegetation height, and percent cover by vegetation type. Values at corresponding distances along the two transects were then averaged for analysis. This resulted in two sets of nest vegetation data, a set including most nests, where two measurements were recorded when nests were located and a smaller, subset where more extensive nest vegetation measurements were recorded when nests terminated.

Statistical Analyses

All analyses were performed using SPSS (Norusis/SPSS Inc. 1993). Because this was an exploratory study of grazing effects, I wanted to reduce the risk of erroneously concluding grazing effects did not exist when they actually did (Type II error). Conversely, I needed to be cautious in interpreting the numerous multiple comparisons, especially those examining nest vegetation measurements. Therefore, I chose a Type I error rate of $\leq$5%, but did not otherwise correct for multiple comparisons. Seven of the 1994 plots (4 grazed and 3 ungrazed) had also been studied in 1993. I used Pearson correlations to test for between-year independence of nest densities by species, point counts, and plot HD. All comparisons appeared to be independent ($r<0.70$, $P>0.10$) both within treatments and for treatments pooled, so I considered the plots as independent points in analyses.

I used Mann-Whitney U-tests to compare nest initiation dates, nest densities, and species numbers between grazed and ungrazed plots because these data sets were not normally distributed. I used Spearman rank correlation to examine relationships between nest density and average point counts, daily survival rates, and parasitism rates. I used χ^2-tests to compare frequency of nest parasitism.

Effective vegetation height was correlated ($r>0.70$) with HD among plots, nests, and random points, so it was excluded from further analysis. I retained HD because it was less subjective and could be measured with greater precision than effective vegetation height. For percent cover measures, I used categories to calculate means and in univariate analysis. For univariate comparisons of vegetation data between nests and paired random points, I used paired t-tests for HD and litter depth, and Wilcoxon signed-rank tests for categorical variables (percent cover measures). For comparisons of vegetation between grazed and ungrazed plots, successful versus depredated nests, parasitized versus unparasitized nests, and nests in grazed plots versus nests in ungrazed plots, I used ANCOVA with date as a covariate for HD, t-tests for litter depth, and Mann-Whitney U-tests for categorical variables. I used ANCOVA for HD because HD often increased over the nesting season. In cases where slopes differed significantly between cells, I fit separate slopes for each cell.

I used regression analysis to examine the ability of vegetation measures and grazing regime to explain interplot variation in the density of individual species and the number of nesting species. Model selection began by examining scatter plots; next all variables were considered in forward step-wise selection ($P<0.1$ to enter) to select, and finally all variables were considered using curve estimation which included linear, logarithmic, inverse, and quadratic models. I used the 1994 data alone to select variables and models, and in cases where HD was selected I included 1993 data in calculating model statistics (because only HD data was collected in both 1993 and 1994).

Sample sizes of nests varied by analysis. Comparisons of vegetation variables at nest sites and random points included only study plot nests in 1994. Comparisons of nest sites in grazed and ungrazed plots also included the variable nest HD recorded when nests were located, which was measured at study plots and supplemental nests in 1993 and 1994. Comparisons of vegetation at successful versus depredated nests or parasitized nests included study plot and supplemental nests in 1994, and again included nest HD measured when nests were located. Daily nest survival and mortality rates were calculated using study plot and supplemental nests in 1993 and 1994.

A nest was considered successful if one egg hatched for ducks, if one young fledged for passerines, or if one young "branched" for owls. I calculated nest success using the Mayfield method (1975) as modified by Johnson (1979), and tested for differences in daily survival and daily mortality rates using the computer program "CONTRAST" (Hines and Sauer 1989). To examine specific causes of nest mortality, I followed Donovan et al. (1995) and broke total daily mortality into component parts (predation, parasitism, trampling, and other).

RESULTS

Plot Vegetation

Vegetation differed between grazed and ungrazed plots for most vegetation features (Table 1). HD, litter depth, and litter cover were reduced on grazed plots; forb and shrub cover were greater on grazed plots. However, ranges of all mean vegetation values on grazed and ungrazed plots overlapped.

Nest Density

Savannah Sparrow nest density was correlated with the average number of individuals detected on point counts (r_S=0.93, n=23, P<0.001); the correlation was weaker but still significant for Western Meadowlarks (r_S=0.62, n=23, P=0.002).

Nest density of the 13 most common species (hereafter common species) did not differ between years on grazed plots or ungrazed plots (U_1>6.0 and U_2>9.0, P>0.1). Consequently, nest densities were pooled across years. Most ducks, Ring-necked Pheasants (*Phasianus colchicus*), and raptors nested in densities 4-18 times higher on ungrazed than on grazed plots; Redheads (*Aythya americana*) and Northern Harriers (*Circus cyanus*) nested exclusively on ungrazed plots (Table 2). Gadwalls (*Anas strepera*) and Short-eared Owls (*Asio flammeous*) were unique among ducks and raptors; both nested in high densities on ungrazed plots (>10 nests/100 ha) but

Table 1. Mean, SD, and range of transect vegetation features on grazed and ungrazed study plots, 1993 and 1994.

Year	Vegetation Features	(unit)	Grazed n	$\bar{x}$	SD	range	Ungrazed n	$\bar{x}$	SD	range	Comparison[a] t	U	P
1993			4				5						
	HD	(dm)		0.57	0.10	0.48 - 0.67		1.80	0.28	1.44 - 2.10	9.1		0.001
1994			6				8						
	HD	(dm)		0.69	0.37	0.24 - 1.18		1.42	0.38	0.93 - 2.11	3.6		0.004
	Litter Depth	(cm)		1.29	0.52	0.85 - 2.26		4.11	1.35	1.60 - 5.77	4.8		0.001
	Litter Cover	(%)[b]		3.18	0.89	2.42 - 4.50		4.56	0.79	3.02 - 5.72		4.0	0.010
	Grass Cover	(%)		2.61	0.75	1.53 - 3.67		2.37	0.41	1.71 - 3.17		20.0	0.606
	Forb Cover	(%)		2.21	0.77	0.93 - 2.99		1.36	0.54	0.64 - 2.26		8.0	0.039
	Shrub Cover	(%)		0.04	0.09	0.00 - 0.23		0.00	0.00	0.00 - 0.00		12.0	0.031

[a] T-test used for HD and Litter Depth, and Mann-Whitney U-test for all others.

[b] Percent cover category: 0 = 0%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, and 6 = 96-100%.

Table 2. Mean (range) of nest densities (nests/100 ha) for the 13 most common species within grazed plots (n = 10) and ungrazed plots (n = 13) for 1993 and 1994.

Species	Grazed		Ungrazed		Mann-Whitney	
	x̄	range	x̄	range	*U*	*P*
Mallard (*Anas platyrhynchos*)	1.5	0.0 - 5.7	28.0	0.0 - 102.9	32.5	0.03
Northern Shoveler (*Anas clypeata*)	2.1	0.0 - 13.0	18.4	0.0 - 61.8	33.0	0.03
Cinnamon Teal (*Anas cyanoptera*) [a]	4.3	0.0 - 13.0	18.7	0.0 - 48.0	32.0	0.04
Redhead (*Aythya americana*)	0.0	-	5.4	0.0 - 27.4	45.0	0.06
American Wigeon (*Anas americana*)	0.5	0.0 - 4.8	3.4	0.0 - 13.7	44.0	0.09
Gadwall (*Anas strepera*)	11.3	0.0 - 34.5	19.8	0.0 - 115.8	52.5	0.43
Ring-necked Pheasant (*Phasianus colchicus*)	0.7	0.0 - 6.5	6.9	0.0 - 20.6	29.5	0.01
Northern Harrier (*Circus cyanus*)	0.0	-	3.8	0.0 - 27.4	50.0	0.11
Short-eared Owl (*Asio flammeous*)	7.7	0.0 - 20.6	12.1	0.0 - 41.2	50.5	0.36
Savannah Sparrow (*Passerculus sandwichensis*)	30.5	0.0 - 78.0	11.7	0.0 - 58.1	40.0	0.11
Western Meadowlark (*Sturnella neglecta*)	12.9	0.0 - 29.9	4.5	0.0 - 20.6	33.5	0.04
Common Snipe (*Gallinago gallinago*)	1.9	0.0 - 6.9	4.6	0.0 - 37.4	65.0	1.00
Killdeer (*Charadrius vociferus*)	3.3	0.0 - 13.7	0.3	0.0 - 3.8	49.0	0.13

[a] Includes approximately 20% Blue-winged Teal (*Anas discors*).

they also nested in relatively high densities on grazed plots (>7 nests/100 ha). Western Meadowlarks nested in densities 2.5 times higher on grazed than on ungrazed plots and Savannah Sparrows showed a similar pattern. All but two species were found on both grazed and ungrazed plots with overlapping ranges of nest density. Number of nesting species per plot tended to be lower on grazed (mean=4.9, range=4.0-6.0) than on ungrazed (mean=6.8, range=3.0-11.0) plots (U=35.5, P=0.06).

Despite these differences in nest densities between grazed and ungrazed plots, nest densities of all the common species were more strongly correlated with vegetation features than with grazing regime (Table 3). Nest density was positively correlated with plot HD for Ring-necked Pheasants, raptors, and for all duck species except Gadwalls. Savannah Sparrows appeared to nest in highest densities on plots with intermediate HD (ie. nest density decreased at both low and high plot HD). Nest density was negatively correlated with plot HD for Western Meadowlarks and Killdeers (*Charadrius vociferus*). Gadwall nest density was most strongly correlated (positively) with percent forb cover. Number of nesting species also was positively correlated with plot HD ($Y=5.9-3.5(HD)+2.4(HD)^2$, R^2=48.6, P=0.001).

Nest density seemed to be positively correlated with plot HD for species that chose nests with high HD. For

Table 3. Regression models and statistics using vegetation features of plots and grazing status as independant variables and nest densities of common bird species as dependant variables. Models were selected through visual inspection of scatter plots, step-wise regression, and curve estimation, and the model explaining the highest proportion of variation is reported.

Species	Plot Habitat Models[a]	R^2	P
Mallard	$Y = 19.4 - 57.1(HD) + 38.0(HD)^2$	75.4	0.000
Northern Shoveler	$Y = 24.0 - 61.5(HD) + 35.3(HD)^2$	89.1	0.000
Redhead	$Y = 3.8 - 12.6(HD) + 8.3(HD)^2$	44.2	0.003
Cinnamon Teal	$Y = 6.5 - 10.9(HD) + 11.1(HD)^2$	46.9	0.002
American Wigeon	$Y = -1.8 + 3.3(HD)$	24.1	0.017
Gadwall	Y = 5.6 + 10.6(%Forb Cover)	45.2	0.008
Ring-necked Pheasant	$Y = 4.3 - 10.8(HD) + 7.5(HD)^2$	58.3	0.000
Northen Harrier	$Y = 2.1 - 7.0(HD) + 4.0(HD)^2$	23.9	0.065
Short-eared Owl	$Y = 2.1 + 6.9(HD)$	14.7	0.071
Western Meadowlark	$Y = 34.7 - 43.3(HD) + 14.2(HD)^2$	48.1	0.001
Savannah Sparrow	$Y = -9.4 + 76.7(HD) - 35.9(HD)^2$	24.0	0.065
Common Snipe	Y = -15.1 +4.6 (%Litter Cover)	24.0	0.076
Killdeer	$Y = -1.9 + (2.9 / HD)$	39.2	0.001

[a] Other variables included: grazing status, litter depth, litter cover, and shrub cover; these did not significantly increase the amount of variation explained.

example HD at nests was high ($\bar{x}$=2.12-3.35 dm) in all eight species where nest density was positively correlated with HD of plots. Gadwalls were the only species with high nest HD ($\bar{x}$=3.06 dm) where nest density was not correlated with plot HD. Savannah Sparrows, which nested at highest densities on plots with intermediate HD, had an intermediate nest HD ($\bar{x}$=1.12 dm). Nest HDs were low for Killdeers ($\bar{x}$=0.00 dm) and intermediate for Western Meadowlarks ($\bar{x}$=1.12 dm), the two species where nest density was negatively correled with plot HD.

Nest Site Selection and Nest Initiation

I located adequate numbers of nests (>10) in both grazed and ungrazed plots to allow comparisons of nest parameters for four species: Western Meadowlarks, Savannah Sparrows, Short-eared Owls, and Gadwalls (hereafter abundant species). Western Meadowlarks chose nest sites with greater HD, litter depth, and litter cover than at random sites on grazed plots; on ungrazed plots they showed similar trends for litter depth and litter cover but not for HD (Table 4). Savannah Sparrows also chose nest sites with greater HD, litter depth, and litter cover than at random sites on grazed plots; on ungrazed plots they chose nest sites with greater forb cover. Gadwalls chose nest sites with greater HD, forb, and shrub cover than at random sites on grazed plots and greater HD on ungrazed plots. Short-eared Owls

Table 4. Mean (SD) of vegetation features at nests and paired random points in grazed and ungrazed plots for Western Meadowlarks, Savannah Sparows, Gadwalls, and Short-eared Owls. Significance of comparisons designated by: *=p<0.05, **=p<0.01.

Species	Vegetation Features	(units)	Grazed x̄ (SD) Nest	vs Random[a]	Successful	vs Depredated[b]	Ungrazed x̄ (SD) Nest	vs Random	Successful	vs Depredated	Grazed vs Ungrazed[b]
Western Meadowlark			n = 14	n = 14	n = 7	n = 5	n = 6	n = 6	n = 3	n = 6	
	Nest HD	(dm)	1.02 (0.53)	0.30 (0.34)**	1.21 (0.58)	0.78 (0.45)	1.06 (0.81)	1.17 (1.00)	1.67 (0.72)	0.77 (0.39)*	
	Litter Depth	(cm)	3.86 (3.86)	0.50 (0.65)**	6.28 (4.27)	1.40 (0.55)*	4.33 (3.50)	1.33 (1.37)	6.67 (1.53)	4.50 (3.67)	
	Litter Cover	(%)[c]	4.29 (1.20)	2.71 (1.33)**	4.29 (1.11)	4.00 (1.41)	5.00 (1.10)	4.00 (1.67)	5.67 (0.58)	4.83 (0.98)	
	Grass Cover	(%)	2.07 (0.83)	2.14 (0.66)	2.29 (0.95)	1.60 (0.55)	2.17 (0.75)	1.67 (1.03)	2.33 (0.58)	2.17 (0.75)	
	Forb Cover	(%)	1.93 (1.21)	1.71 (0.83)	2.00 (1.41)	2.40 (0.55)	1.67 (0.82)	1.67 (1.03)	1.67 (1.53)	1.17 (0.75)	
			n = 24		n = 8	n = 7	n = 24		n = 7	n = 15	
	Nest HD Loc.[d]	(dm)	1.07 (0.42)		1.00 (0.50)	1.10 (0.78)	1.24 (0.53)		1.36 (0.71)	1.14 (0.44)	
Savannah Sparrow			n = 46	n = 46	n = 10	n = 18	n = 19	n = 19	n = 11	n = 16	
	Nest HD	(dm)	1.08 (0.46)	0.60 (0.61)**	1.36 (0.40)	1.01 (0.47)*	1.21 (0.51)	1.34 (0.62)	1.42 (0.56)	1.12 (0.40)*	
	Litter Depth	(cm)	2.00 (1.51)	0.80 (1.08)**	2.70 (1.70)	1.56 (1.25)*	5.21 (2.72)	4.79 (2.82)	5.82 (3.46)	5.19 (2.14)	**
	Litter Cover	(%)	4.09 (1.49)	3.56 (1.69)*	4.60 (1.51)	3.89 (1.45)	5.68 (0.75)	5.16 (1.17)	5.55 (0.93)	5.81 (0.40)	**
	Grass Cover	(%)	2.85 (1.30)	2.57 (1.00)	3.40 (1.51)	2.61 (1.20)	2.37 (0.83)	2.74 (0.73)	2.27 (0.65)	2.44 (0.81)	
	Forb Cover	(%)	2.13 (1.38)	1.76 (1.18)	1.80 (1.93)	2.33 (1.24)	1.84 (0.69)	0.68 (0.89)**	1.82 (0.87)	1.75 (0.77)	
			n = 44		n = 11	n = 24	n = 57		n = 20	n = 19	
	Nest HD loc.	(dm)	1.05 (0.52)		1.12 (0.53)	0.93 (0.49)	1.15 (0.33)		1.25 (0.30)	1.03 (0.36)*	
Gadwall			n = 13	n = 13	n = 7	n = 5	n = 14	n = 14	n = 7	n = 6	
	Nest HD	(dm)	2.15 (1.59)	0.40 (0.37)**	2.93 (1.68)	1.40 (0.97)*	2.32 (0.95)	1.62 (1.05)*	2.23 (1.11)	2.21 (0.79)	
	Litter Depth	(cm)	0.54 (0.78)	0.85 (1.35)	0.29 (0.76)	0.80 (0.84)	1.50 (1.29)	3.00 (3.01)	1.71 (1.60)	1.17 (0.98)	*
	Litter Cover	(%)	2.23 (0.83)	2.92 (1.32)	2.42 (0.98)	2.00 (0.71)	3.57 (1.51)	3.93 (1.59)	3.43 (1.62)	3.67 (1.63)	*
	Grass Cover	(%)	1.38 (1.19)	1.85 (1.07)	1.00 (1.41)	1.80 (0.84)	2.71 (1.07)	2.07 (0.92)	2.71 (1.11)	2.50 (1.05)	**
	Forb Cover	(%)	3.00 (1.22)	2.15 (0.56)*	2.71 (1.11)	3.40 (1.52)	1.79 (1.25)	1.21 (1.05)	1.71 (1.25)	2.17 (1.17)	*
	Shrub Cover[e]	(%)	1.15 (1.86)	0.00 (0.00)*	2.14 (2.12)	0.00 (0.00)*	0.00 (0.00)	0.07 (0.27)	0.00 (0.00)	0.00 (0.00)	*
			n = 18		n = 10	n = 7	n = 158		n = 56	n = 76	
	Nest HD loc.	(dm)	2.97 (1.50)		3.74 (1.51)	2.19 (0.69)*	3.09 (0.96)		3.18 (1.01)	2.95 (0.96)	
Short-eared Owl			n = 8	n = 8	n = 2	n = 5	n = 15	n = 15	n = 11	n = 3	
	Nest HD	(dm)	1.89 (0.88)	1.05 (0.57)*	1.63 (1.06)	1.78 (1.12)	2.22 (0.82)	1.23 (0.76)**	2.18 (0.95)	2.38 (0.33)	
	Litter Depth	(cm)	2.13 (3.36)	0.88 (0.84)	1.50 (2.12)	2.80 (4.09)	2.27 (1.62)	2.87 (2.92)	1.63 (1.21)	3.67 (1.52)*	
	Litter Cover	(%)	4.25 (1.58)	3.87 (1.46)	4.50 (0.71)	4.60 (1.67)	4.87 (0.92)	3.53 (1.60)*	4.73 (0.90)	5.67 (0.58)	
	Grass Cover	(%)	4.25 (1.39)	3.13 (1.25)*	4.00 (0.00)	4.20 (1.79)	2.93 (0.80)	1.93 (0.59)**	3.00 (0.89)	2.67 (0.58)	*
	Forb Cover	(%)	1.63 (0.92)	1.75 (1.28)	1.00 (1.41)	2.00 (0.71)	1.33 (1.05)	1.40 (0.91)	1.36 (0.92)	1.67 (1.53)	
			n = 12		n = 4	n = 6	n = 98		n = 61	n = 16	
	Nest HD loc.	(dm)	1.58 (0.41)		1.17 (0.19)	1.65 (0.57)	2.15 (0.88)		2.16 (0.94)	2.22 (1.02)	**

[a] For all nests vs. paired random points: paired t-test to compare nestHD and litter depth, and Wilcoxon signed rank test to compare percent cover variables.
[b] For all nests in grazed vs. all nests ungrazed and successful vs. depredated: t-test, or ANCOVA when date was a significant covariate ($p < 0.05$) to compare nest HD, t-test to compare litter depth, and Mann-Whitney U-test to compare percent cover variables.
[c] Percent cover category: 0 = 0%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, and 6 = 96-100%.
[d] HD measured when nests were located for study plot and supplemental nests in 1993 and 1994.
[e] Only Gadwall had shrub cover > 0.

chose nest sites with greater HD and grass cover than at random sites on both grazed and ungrazed plots, and greater litter cover on ungrazed plots.

All four abundant species chose more features at the nest than at adjacent areas. Pooling the four species and all vegetation features measured, 22 features were chosen: 16 at the nest, 5 at 2.5 m, 0 at 5 m, and 1 at 10 m. Values of chosen features at adjacent areas were in all cases intermediate between values at nest sites and random points.

In comparisons of vegetation features at the nest on grazed and ungrazed plots, only Western Meadowlarks nests had no differences (Table 4). Savannah Sparrow nests had lower litter depth and litter cover at the nest on grazed plots than on ungrazed plots. Gadwall nests had lower litter depth, litter cover, and grass cover, and greater forb and shrub cover at the nest on grazed than on ungrazed plots. Short-eared Owl nests had lower nest HD on grazed than on ungrazed plots, providing the only instance where nest HD differed by grazing regime. Three other species with $\geq$5 nests on both grazed and ungrazed plots also did not differ in nest HD between grazed and ungrazed plots: Cinnamon Teal (*Anas cyanoptera*; 1.95 $\pm$ 0.68 vs. 2.27 $\pm$ 0.83, n=9,130; t=1.14, P=0.21), Northern Shoveler (*Anas clypeata;* 1.55 $\pm$ 0.53 vs. 2.02 $\pm$ 0.75, n=5,153; t=1.93, P=0.12), and Common Snipe (1.25 $\pm$ 0.37 vs. 1.35 $\pm$ 0.66, n=5,24; t=0.44, P=0.67).

Comparisons of vegetation features between nests on grazed and ungrazed plots were different more often at adjacent areas than at the nest for all four abundant species. At $\geq$2.5 m, Western Meadowlark and Savannah Sparrow nests had lower HD, litter depth, and litter cover, and Short-eared Owls had lower HD, on grazed than on ungrazed plots. At $\geq$5.0 m, Gadwall nests had lower HD on grazed than on ungrazed plots.

Short-eared Owls initiated nests later on grazed than on ungrazed plots, by 23 days in 1993 (U=52.5, P=0.05) and by 26 days in 1994 (U=86.5, P=0.01). The date of earliest initiation was also later on grazed than on ungrazed plots, by 17 days in 1993 and 26 days in 1994. No consistent differences were noted for the other abundant species.

Nest Success

Predation was the greatest source of nest mortality on grazed and ungrazed plots for all four abundant species (Table 5). Among Western Meadowlarks on grazed plots, successful nests had greater litter depth than depredated nests; on ungrazed plots, successful Western Meadowlark nests had greater HD than depredated nests. Among Savannah Sparrows on grazed plots, successful nests had greater HD and litter depth than depredated nests; on ungrazed plots, successful nests had greater HD than depredated nests. Among Gadwalls on grazed plots, successful nests had greater

Table 5. Sources of nesting mortality for Western Meadowlarks, Savannah Sparrows, Short-eared Owls, and Gadwalls in grazed and ungrazed plots for 1993 and 1994 pooled.

		Nests	Exposure	Daily Mortality Rates (SE)				
Species	Plot Type	*n*	Days	All Sources	Predation	Parasitism	Trampling	Other[a]
Western Meadowlark	Grazed	18	246.5	0.041 (0.013)	0.033 (0.011)	0.000	0.008 (0.006)	0.000 (0.000)
	Ungrazed	22	326.0	0.049 (0.012)	0.046 (0.012)	0.000	0.000 (0.000)	0.003 (0.003)
			χ^2 (df)	0.20 (1)	0.74 (1)	-	1.97 (1)	0.94 (1)
			P	0.651	0.387		0.161	0.333
Savannah Sparrow	Grazed	57	472.5	0.097 (0.014)	0.051 (0.010)	0.019 (0.006)	0.017 (0.006)	0.011 (0.005)
	Ungrazed	43	460.5	0.050 (0.010)	0.041 (0.010)	0.004 (0.003)	0.000 (0.000)	0.004 (0.003)
			χ^2 (df)	7.46 (1)	0.53 (1)	4.56 (1)	8.03 (1)	1.55 (1)
			P	0.006	0.466	0.033	0.005	0.214
Gadwall	Grazed	18	265.0	0.030 (0.011)	0.023 (0.009)	0.000	0.004 (0.004)	0.004 (0.004)
	Ungrazed	143	2037.5	0.032 (0.004)	0.029 (0.004)	0.000	0.000 (0.000)	0.003 (0.001)
			χ^2 (df)	0.22 (1)	0.06 (1)	-	1.11 (1)	0.26 (1)
			P	0.640	0.806		0.293	0.613
Short-eared Owl	Grazed	12	191.5	0.042 (0.015)	0.037 (0.014)	0.000	0.000	0.005 (0.005)
	Ungrazed	82	1797.5	0.009 (0.002)	0.009 (0.002)	0.000	0.000	0.001 (0.001)
			χ^2 (df)	4.76 (1)	4.13 (1)	-	-	0.58 (1)
			P	0.029	0.042			0.445

[a] Includes: abandoned, flooded, and non-viable eggs.

HD, forb cover, and shrub cover than depredated nests; on ungrazed plots, vegetation features did not differ between successful and depredated Gadwall nests. Among Short-eared Owls on grazed plots, successful nests did not differ from depredated nests; on ungrazed plots, successful nests had lower litter depth than depredated nests.

Comparisons of vegetation features between successful and depredated nests were more often different at the nest than in adjacent areas. Pooling results from all four abundant species, 17 comparisons of features differed: 41% were at the nest, 41% were at 2.5 m, 18% were at 5 m, and none were at 10 m. In most cases where a feature differed at adjacent areas, the same variable differed, and in greater magnitude, at the nest.

To examine the relationship between species predation rates and nest density for Western Meadowlarks, Savannah Sparrows, and Gadwalls I pooled grazed and ungrazed plots because nest predation did not differ between grazing regimes for these species (Table 4). Daily predation rates were unrelated to nest densities in Western Meadowlarks (r_S=0.10, n=12, P=0.77), Savannah Sparrows (r_S=-0.01, n=13, P=0.968), and Gadwalls (r_S=0.32, n=15, P=0.25). Predation rates differed between grazing regimes for Short-eared Owls, but daily predation rates were unrelated to nest densities on grazed plots (r_S=-0.10, n=5, P=0.87) or ungrazed plots (r_S=-0.14, n=9, P=0.73).

Frequency of nest parasitism was greater on grazed than on ungrazed plots for Western Meadowlarks (16% vs. 0%; χ^2=3.91, df=1, *P*=0.05) and Savannah Sparrows (40% vs. 16%; χ^2=6.76, *df=1, P*=0.01). Vegetation features did not differ (*P*>0.10) between parasitized and unparasitized nests for either Western Meadowlarks or Savannah Sparrows. I was unable to detect any correlation between frequency of parasitism and nest densities among grazed or ungrazed plots for Western Meadowlarks (r_S=0.48, n=8, *P*=0.23 on grazed plots, and no parasitism on ungrazed plots) or for Savannah Sparrows (r_S=0.41, n=7, *P*=0.36 on grazed, and r_S=0.70, *n*=6, *P*=0.12 on ungrazed). However, effect sizes were relatively large and sample sizes were small, especially for Savannah Sparrows on ungrazed plots.

Among grazed plots, daily nest mortality rates from trampling for all species combined was lower where stocking rates were low than where they were high (0.001 $\pm$ 0.001 [SE] vs. 0.020 $\pm$ 0.006 [SE]; χ^2=10.3, *df*=1, *P*=0.001). Frequency of trampling was 11%, 14%, 6%, and 0% of Western Meadowlark, Savannah Sparrow, Gadwall, and Short-eared Owl nests on grazed plots, and accounted for 20%, 18%, 13%, and 0% of total nest mortality for these species. Trampling mortality rates on grazed plots (Table 5) differed among species (χ^2=10.8, df=3, *P*=0.01); Savannah Sparrows suffered greater trampling mortality than Short-eared Owls (χ^2=8.03, df=1, *P*=0.005) and possibly Gadwall (χ^2=3.25, df=1, *P*=0.07).

Daily nest survival rates of Western Meadowlarks and Gadwalls did not differ between grazed and ungrazed plots in 1993, 1994, or years pooled ($P>0.10$, Fig. 1). Daily nest survival rates of Savannah Sparrows were lower on grazed than on ungrazed plots in 1993 ($\chi^2=3.75$, $P=0.053$), in 1994 ($\chi^2=3.67$, $P=0.056$), and for years pooled ($\chi^2=7.46$, $P=0.006$). Daily nest survival rates of Short-eared Owls were lower on grazed plots in 1994 ($\chi^2=3.62$, $P=0.057$) and for years pooled ($\chi^2=4.76$, $P=0.029$). Savannah Sparrow nests suffered higher rates of mortality due to parasitism and trampling on grazed than on ungrazed plots (Table 5). Short-eared Owl nests suffered greater predation on grazed than on ungrazed plots.

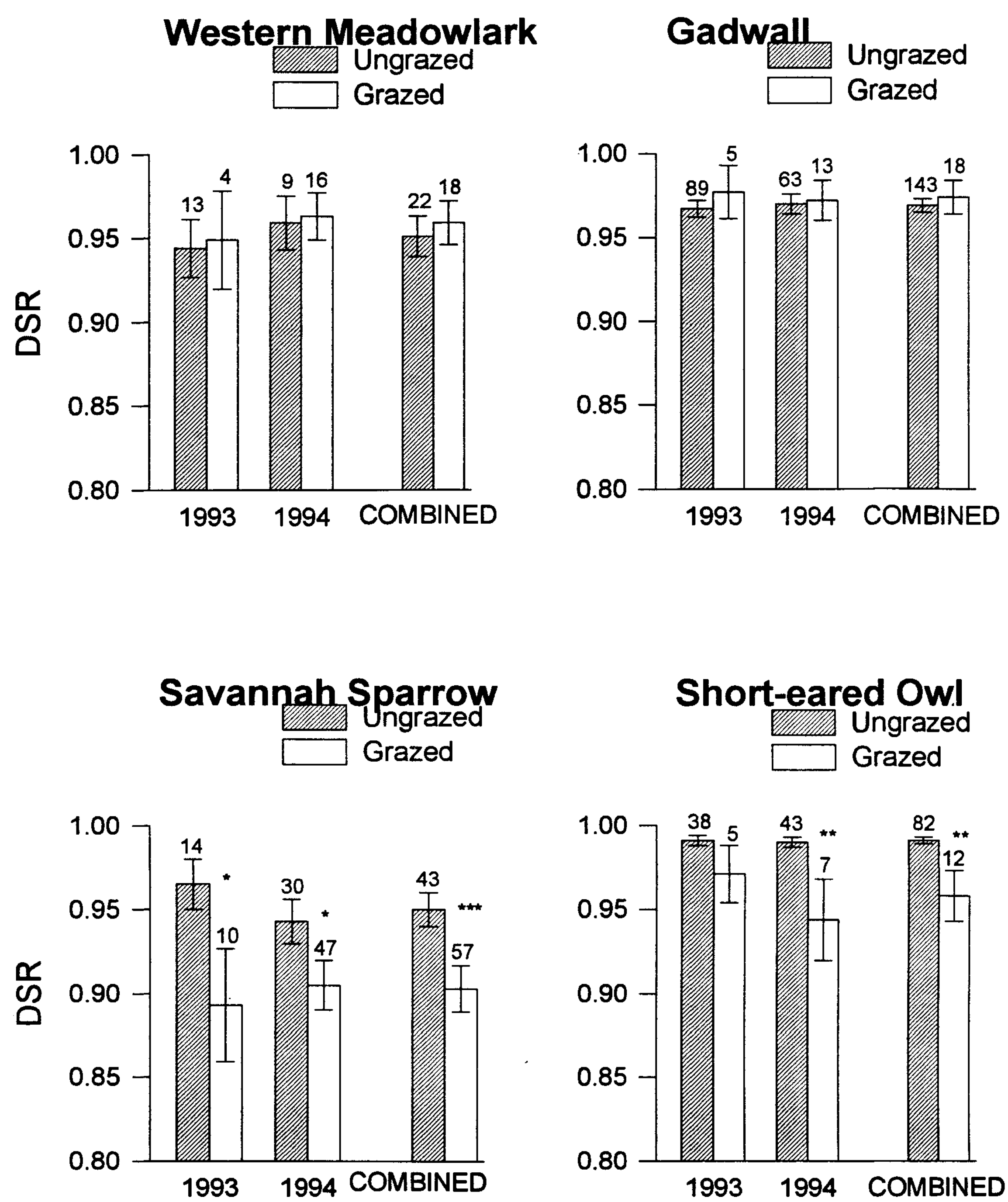

Figure 1. Daily survival rates (DSR, +/- se) in grazed and ungrazed plots in 1993, 1994, and years combined. Significance indicated by: * p < 0.10, ** p < 0.05, *** p < 0.01. The number above bar indicates the number of nests used to calculate DSR.

DISCUSSION

Effects of Grazing on Vegetation

I found that grazing strongly affected the structure and density of vegetation, reducing HD, litter depth, and litter cover. Grazing also influenced floristics, increasing forb and shrub cover (see also Holechek et al. 1989, Ryder 1980, Fleischner 1994, Vavra et al. 1994). However, the ranges of all vegetation features overlapped between grazed and ungrazed plots.

Nest Density

I evaluated potential grazing effects on breeding bird density based on densities of nests found, and substantial bias could occur if detectability differed among cover types (Skinner 1975, Kantrud and Higgins 1992). However, any bias in detectability should have been most evident for species such as Western Meadowlarks and Savannah Sparrows with small, well-concealed nests that are difficult to find. The positive correlation between nest densities and mean point counts was strong for both species, and I suspect that part of the variation noted for meadowlarks arose because they were difficult to count accurately using point counts. Overall, nest density appeared to provide a reasonable index to breeding density in this study.

Average nest densities for most bird species differed between grazed and ungrazed plots. These differences seem to reflect direct response to differences in vegetation between grazed and ungrazed plots given that nest densities were more strongly correlated with vegetation than with grazing regime *per se* (see Cody 1968, Wiens 1969, Balda 1975, Saab et al. 1995).

If availability of suitable nest sites is a primary determinant of breeding bird density (Martin 1988, 1993), and birds are settling on plots as a function of the availability of suitable nest sites, then density should be positively related with the habitat features characterizing nest sites. This study, and one by Granfors et al. (1996), generally support this prediction. For example, I found that species that chose tall-dense, medium, and short-sparse cover at nests, also tended to nest in greater density on plots with similar characteristics. Birds should also show non-random selection of nest sites, and important vegetation features of nest sites should remain similar across locally varying habitats (i.e. grazing regime). If bird densities are not determined by nest sites, then substantial lowering of plot HD through grazing, as seen in this study, should have been reflected in lower HD at nests on grazed plots. Nest HD did not differ significantly between grazed and ungrazed plots for most species in my study. Similarly, Eastern Meadowlarks (*Sturnella magna*) in Kansas also had similar vegetation structure at nest sites between grazed and ungrazed fields (Granfors et al. 1996). This pattern would occur if species selected nest sites with suitable HD, irrespective of plot-level conditions; consequently, nest densities would vary by plot HD but nest HD would not vary by plot condition. Only Short-eared Owl nest HD differed by grazing regime, and this appeared to be due to density-dependent displacement (see below). Given the latter, we should be able to infer bird response to grazing from the effects of grazing on potential nest sites. Most ducks, Ring-necked Pheasants, and Northern Harriers chose high nest HD and nest density was positively correlated with plot HD. A negative response to grazing would be expected in this group and it occurred: Redheads and harriers nested only on ungrazed plots, and densities of the others were 4 to 18 times higher on ungrazed than on grazed plots (see also Kirsch et al. 1978, Saab et al. 1995). Gadwalls presented an apparent exception to the pattern: like other ducks they chose high nest HD yet they nested at relatively high densities on some grazed plots. Nest density of Gadwalls was most strongly correlated with plot forb cover rather than plot HD, and they selected forb and shrub cover at nests in grazed plots. Apparently, their ability to use forbs and shrubs (Duebbert et al. 1986, Kruse and Bowen 1996), cover types that often are promoted by grazing, allows them to locate nest sites with high HD, and hence to nest at relatively high densities, on grazed plots.

Short-eared Owls chose high nest HD and their nest densities were positively correlated with plot HD; therefore, they would be expected to respond negatively to grazing (see Saab et al. 1995). Yet, as with Gadwalls, I found reasonably high densities of owl nests on grazed plots. I suspect that density-dependant displacement of nesting owls accounted for this unexpected pattern of habitat occupancy. In the two years of the study Short-eared Owls nested at high densities (35-40 nests per km^2) on a favored ungrazed area, greater than any previously reported densities (Holt and Leasure 1993). Owls initiated nests an average of 24 days later on grazed than on ungrazed plots, and both nest HD and nest success were lower on grazed than on ungrazed plots. In addition, in 1995 when Short-eared Owls nested at low densities at Ninepipe, apparently because populations of voles (*Microtus montanus, M. pennsylvanicus*) were low, I found no owl nests on grazed plots.

Savannah Sparrows chose nest sites with intermediate HD, and they nested in highest density in plots with intermediate HD. More grazed than ungrazed plots fell in the intermediate HD range and, as would be expected, Savannah Sparrows nested at greater density on grazed plots although, only marginally so. My results conflict with Saab et al. (1995) who summarized the response of Savannah Sparrows to grazing as always negative. However, an examination of Savannah Sparrow response over a comparable range of plot HD values shows a similarity in species response. Most ungrazed plots in my study were managed to provide tall dense cover, with plot HD often $\geq$ 2.0 dm. Ungrazed plots in past studies of grazing effects were mostly in native mixed-grass prairie (Saab et al. 1995); from one of those studies (Owens and Myers 1973) I was able to estimate an approximate plot HD of 1.0 dm. If that is typical of the other study sites, then densities of Savannah Sparrows were highest at approximately 1.0 dm HD and declined with increasing HD; this approximates the pattern that I observed.

Western Meadowlarks chose intermediate nest HD, and their densities were negatively correlated with plot HD. Furthermore, as would be expected, they nested in greater density on grazed plots. Saab et al. (1995) characterized meadowlark response to grazing from slightly to highly negative. As in Savannah Sparrows, this pattern probably occurred because the cover in the ungrazed fields I studied had greater HD than the vegetation surveyed in past studies, mostly conducted in short and mixed grass prairie.

Killdeer chose low nest HD and their nest densities were negatively correlated with plot HD. As expected, and in concordance with previous studies (Saab et al. 1995), Killdeer nested in greatest densities in grazed plots.

Overall, my results fit the hypothesis that availability of suitable nest sites is a primary determinant of nesting density (Martin 1988, 1993) and that responses of ground-nesting grassland birds to grazing primarily reflect the effects of grazing on nest sites (Kantrud and Kologiski 1982). Species response to grazing may depend less upon grassland type or grazing intensity (Saab 1995) than to the resulting vegetation structure. HD was the most important habitat variable measured in explaining bird response and selection patterns (also see Kantrud and Higgins 1992).

Nest Success

My investigation of nest success relative to grazing was largely limited to the four abundant species: Western Meadowlarks, Savannah Sparrows, Gadwalls, and Short-eared Owls. Predation was the primary source of mortality for all species on both grazed and ungrazed plots, accounting for 50%-99% of nest loss. Predation is the primary source of nest mortality over a wide range of species, habitats, and geographic locations, and therefore, should be a significant influence on nest site selection (Martin and Roper 1988, Martin 1992). Grazing often reduces density and structural heterogeneity of vegetation, which could increase predator efficiency by reducing nest concealment or decreasing the number of potential nest sites (Clark and Nudds 1991, Martin 1992).

My findings suggest that areas adjacent to nests may influence nest site selection and the probability of predation (see also Martin and Roper 1988, Norment 1993, Badyaev 1995). In comparisons of nest sites and random sites, vegetation features differed at areas adjacent to the nest (2.5-10.0 m) for three of the four major species. The number of features which differed between nest sites and random sites were considerably more numerous at the nest than at adjacent areas, and those at adjacent areas had values intermediate between the nest and random site (see also Badyaev 1995). In comparisons of successful and depredated nests, vegetation features which differed were more numerous at adjacent areas than at the nest, but in most of the differences at adjacent areas, the same feature at the nest differed to a greater degree. In comparisons both between nest sites and random sites, and between successful and depredated nests vegetation features rarely differed beyond 2.5 m, and patterns of features which differed at adjacent areas appeared to be similar between grazed and ungrazed plots. However, my results could also be due simply to patterns in patchiness of nesting habitats, with selection and risk of predation related only to features at nests.

Several lines of evidence suggest that risk of predation should have increased with grazing. First, on grazed plots one or more of the vegetation features chosen was also associated with reduced risk of predation in Western Meadowlarks (litter depth), Savannah Sparrows (HD and litter depth), and Gadwalls (HD and shrub cover). This relationship was not observed on ungrazed plots, suggesting that availability of suitable nest sites was reduced in grazed plots. Among Short-eared Owls, however, vegetation features were unrelated to risk of predation on grazed plots: furthermore, litter depth was actually lower at successful nests than at failed nests on ungrazed plots. This probably reflects the confounding effect of increased trampling of nest vegetation by adult and nestling owls at successful nests. Second, grazing negatively impacted many of the nest vegetation features selected for and associated with reduced predation risk. Finally, negative impacts demonstrated in comparisons of vegetation on grazed and ungrazed plots were reflected in comparisons of nest sites on grazed and ungrazed plots. Nests on grazed plots had reduced values for vegetation features associated with reduced predation risk at $\geq$0 m for Savannah Sparrows and Short-eared Owls, at $\geq$2.5 m for Western Meadowlarks, and at $\geq$5 m for Gadwalls. The primary exception to the negative impacts of grazing was that grazing favored shrub and forb cover which were selected for and related to reduced predation risk for Gadwalls on grazed areas. Overall, the availability of quality nest sites appeared to be reduced by grazing.

Nonetheless, I found that of the four primary species only Short-eared Owls suffered greater predation rates on grazed than on ungrazed plots. These owls were the only species with lower nest HD, suggesting they may be especially susceptible to grazing effects on vegetation because the grassy sites they select are favored foraging areas for cattle. In contrast, Gadwalls nesting on grazed areas selected shrubs and forbs (often thistle) at nest sites; these vegetation forms appear to provide high cover value and also to be avoided by cattle.

The lack of difference in rates of nest predation between grazed and ungrazed plots could reflect a confounding interaction between cover quality and nest density. If ungrazed plots provided a larger number of suitable nest sites (and hence attracted higher densities of most nesting species) then the security benefits accompanying higher quality nest sites may have been offset by increasing risks associated with increased nest density (Martin 1988, Clark and Nudds 1991). I was unable to detect a relationship between nest density and nest predation in any of the four abundant species. However, my study was not designed to examine density effects.

Differences in abundance of predators or alternate prey between grazed and ungrazed areas also can influence predation rates. In New Mexico, garter snakes were 5 times more abundant on ungrazed than on grazed sites (Szaro et al. 1985). Populations of small mammals also may decline with grazing (Krapu et al. 1970, Reynolds and Trost 1980, Medin and Clary 1989). Density of alternate prey can act in two opposing fashions, by attracting predators to an area and increasing incidental predation (Roseberry and Klimstra 1970, Vickery et al. 1992) or by buffering predation of nests (Byers 1974, Weller 1979, Crabtree and Wolfe 1988).

Nest parasitism by Brown-headed Cowbirds is a second nest mortality factor associated with grazing. Frequency of parasitism is often greatest near concentrations of cattle (Robinson et al. 1995), and I found that parasitism frequency was greater on grazed than on ungrazed plots for Western Meadowlarks and Savannah Sparrows. Yet, given that all ungrazed plots had adjacent grazed areas, I suspect that factors other than proximity to cattle also were involved. Cowbird abundance also is strongly correlated with host abundance (Robinson et al. 1995), and increased parasitism frequency on grazed plots could reflect greater Western Meadowlark and Savannah Sparrow nest density on grazed plots. Furthermore, Savannah Sparrows nested in higher densities and had higher parasitism frequency than Western Meadowlarks, on both grazed and ungrazed plots. However, sample sizes did not allow me to adequately test for correlation between parasitism frequency and nest density. Increased parasitism frequency in Savannah Sparrows might also be due to variability in host vulnerability (Robinson et al. 1995). In summary, frequency of nest parasitism increased on grazed plots, but my data fit predictions from several competing hypothesis about the factors responsible. In agreement with Robinson et al. (1995), I found no evidence that nest concealment was related to probability of being parasitized.

Western Meadowlarks and Savannah Sparrows, are considered uncommon cowbird hosts (Ehrlich et al. 1988, Wheelright and Rising 1993). Among Western Meadowlarks, parasitism frequency was relatively low and resulted in no nest mortality. However, frequency of parasitism was high among Savannah Sparrows on grazed plots, resulted in significant nest mortality, and was similar to estimates reported previously (see Johnson and Temple 1990). Thus Savannah Sparrows appear, at least in some situations, to be common cowbird host.

Nest trampling, unlike nest predation and parasitism, is a direct effect of livestock presence and appears to be positively correlated to stocking rates (Jenson et al. 1990, Shrubb 1990, Koerth et al. 1983, this study). However, I also found that nest daily mortality rates from trampling differed among species. Variation in species vulnerability to trampling may in part be explained by habitat selection. For example, Savannah Sparrows nested in highest density on plots with high stocking rates and suffered high trampling. In contrast, Gadwalls nesting on grazed plots, nested at highest density on plots with low stocking rates, selected nest sites with shrub and forb cover, and suffered relatively little trampling. However, Short-eared Owls selected grazed plots with medium to high stocking rates and grassy nest sites, yet were not trampled. This suggests that species behavioral characteristics may be important in reducing vulnerability to trampling. Nest mortality from trampling was substantial among Savannah Sparrows nesting on grazed plots, less important for Western Meadowlarks, and inconsequential for Gadwalls and Short-eared Owls. Finally, nest trampling may be underestimated and mistakenly labeled predation if trampled eggs or young are quickly removed from nests. On several occasions carrion beetles (*Nicrophorus sp.)* had almost completely buried trampled Savannah Sparrow nestlings or eggs within a few days after trampling. Nest predators could also quickly remove nest remains.

Relatively little research has examined the effects of grazing on nest success, and results have varied. Among ducks, for example, Sedivac (1989) found greater duck nest success in grazed than in ungrazed areas, Gilbert et al. (1996) found the opposite, and Kruse and Bowen (1996) found no difference. Nest success did not differ between grazed and ungrazed areas for Eastern Meadowlarks (Roseberry and Klimstra 1970, Grandfors et al. 1996) or Upland Sandpipers (Bowen and Kruse 1993). Conversely, nest success was lower on grazed than on ungrazed areas for Upland Sandpipers (Kirsch and Higgins 1976, Kantrud and Higgins 1992) and Lapwings (Shrubb 1990). Decreased nest success in grazed areas was attributed to increased predation (Kirsch and Higgins 1976, Kantrud and Higgins 1992), trampling, and abandonment (Shrubb 1990) on grazed areas.

I found that nest success of Western Meadowlarks did not differ between grazed (27%) and ungrazed plots (21%), and was within the range of previously reported values for meadowlarks (13-52%; Lanyon 1957, Roseberry and Klimstra 1970, Knapton 1988, Johnson and Temple 1990). Gadwall nest success also did not differ between grazed (34%) and ungrazed (32%) plots, and was well above the 15-20% thought necessary to maintain duck populations (Cowardin et al. 1985). Nest success for Savannah Sparrows was lower on grazed (7%) than on ungrazed (20%) plots, primarily because of greater mortality due to parasitism and trampling, and was lower on both grazed and ungrazed than most previous estimates (18-37%; Dixon 1978, Wray et al. 1982, LaPointe and Bedard 1986, Johnson and Temple 1990); and (90%; Welsh 1975). Nest success for Short-eared Owls was lower on grazed (19%) than on ungrazed (70%) plots because of greater mortality due to predation. The figure from grazed plots was lower than all but one account in the literature (8%; Lockie 1955); on ungrazed plots it was similar to most past estimates (>50%; see Holt and Leasure 1993).

Management and Research Implications

Grassland managers attempting to predict the effects of grazing on breeding grassland birds should examine grazing effects on nest site availability. Grazing intensity and the original grassland type appear to be less important than the vegetation structure that results from grazing. Habitat measures should consider the vegetation structure (Cody 1968, Wiens 1969, Balda 1975, Kantrud and Higgins 1992), especially HD and litter, and also percent cover type.

Managing for a diverse grassland bird community requires a variety of habitats (Saab et al. 1995, Knopf 1996b). One group of species at Ninepipe, which included ducks, raptors, and pheasants, was associated with tall and dense cover. These species nested mostly on ungrazed plots, but Gadwalls and Short-eared Owls nested in relatively high densities on grazed plots as well. Public lands managed for wildlife with tall and dense cover usually were the only ungrazed sites available. A second group of species, which included several species of passerines and shorebirds, was associated with cover of short to medium height and relatively low density. These species appeared to be dependant on periodic disturbance, and grazing was the major disturbance factor in the Valley. Moreover, because public lands were relatively undisturbed, such species were associated primarily with grazed sites. Disturbance from grazing and fire can benefit many grassland species (Kantrud

1981, Johnson and Temple 1990, Kantrud and Higgins 1992, Knopf 1996b). Even for species associated with tall dense cover, excessive accumulations of vegetation can become detrimental (Kirsch and Kruse 1972), and many grassland habitats require periodic disturbance to maintain long-term vigor (Knapp and Seastedt 1986). Also, once grazing has ended vegetation and breeding bird populations can quickly recover (Kruse and Bowen 1996). However, disturbance from grazing may hold the disadvantages of increased risk of predation, parasitism, and trampling. Indeed, the continuously grazed sites at Ninepipe were an ecological trap (Gates and Gysel 1978) for Savannah Sparrows and a sink (Pulliam 1988) for Short-eared Owls. Grazing may have fewer negative impacts on breeding birds if conducted outside of the nesting season (Mundinger 1976) or a grazing system is utilized (Brown 1978, Sedivac 1989, Messmer 1990). In some cases fire may be a better disturbance tool because of added benefits to vegetation and insect populations (Risser et al. 1981).

At present, our ability to predict the effects of grazing on nest success is limited. Grazing can effect nest density, cover at nest sites, predator community (Szaro et al. 1985), and alternate prey community (Krapu et al.1970, Reynolds and Trost 1980, Medin and Clary 1989). All of these factors can influence nest predation rates (Martin 1988, Clark and Nudds 1991). More research into the effects of grazing on these factors and the interactions among them is needed. In grazed grasslands, cowbird parasitism may be a larger problem than is commonly believed. Relationships between cowbird parasitism and proximity to cattle, host nest density, and species vulnerability needs further research (Robinson et al. 1995). Trampling also can be an important mortality factor (this study, Lanyon 1957, Shrubb 1990), and research into variation in species vulnerability is needed. Finally, managers should realize that predation, parasitism, and trampling could interact in a compensatory manner; thus a decrease in one factor may not result in an equivalent decrease in the overall mortality rate.

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Appendix A. Mean (SD) of vegetation features at 2.5 m from nests and paired random points in grazed and ungrazed plots for Western Meadowlarks, Savannah Sparows, Gadwalls, and Short-eared Owls. Significance of comparisons designated by: *=p<0.05, **=p<0.01.

Species	Vegetation Features	(units)	Grazed x̄ (SD)				Ungrazed x̄ (SD)				Grazed vs Ungrazed[b]
			Nest vs	Random[a]	Successful vs	Depredated[b]	Nest vs	Random	Successful vs	Depredated	
Western Meadowlark			n = 14	n = 14	n = 7	n = 5	n = 6	n = 6	n = 3	n = 6	
	Nest HD	(dm)	0.72 (0.37)	0.31 (0.38)**	0.66 (0.44)	0.71 (0.33)	1.02 (0.46)	1.14 (0.80)	1.48 (0.36)	0.82 (0.21)**	*
	Litter Depth	(cm)	1.64 (1.95)	0.75 (1.31)*	1.50 (1.96)	0.90 (1.02)	3.50 (2.28)	1.83 (2.30)	5.83 (1.15)	3.17 (1.86)	**
	Litter Cover	(%)[c]	3.25 (1.52)	2.75 (1.31)	2.85 (1.52)	3.10 (1.29)	5.33 (0.98)	3.58 (2.01)	5.83 (0.29)	5.17 (0.93)	**
	Grass Cover	(%)	2.00 (0.65)	1.96 (0.87)	1.92 (0.61)	1.70 (0.45)	1.83 (0.52)	1.92 (0.97)	2.00 (1.00)	2.00 (0.32)	
	Forb Cover	(%)	1.96 (1.28)	2.00 (0.94)	1.92 (1.51)	2.60 (0.42)	1.42 (0.86)	1.83 (0.93)	1.50 (1.32)	1.17 (0.68)	
Savannah Sparrow			n = 46	n = 46	n = 10	n = 18	n = 19	n = 19	n = 11	n = 16	
	Nest HD	(dm)	0.55 (0.43)	0.63 (0.54)	0.73 (0.47)	0.49 (0.43)*	1.18 (0.59)	1.37 (0.68)	1.45 (0.65)	1.00 (0.50)*	**
	Litter Depth	(cm)	1.00 (1.30)	1.09 (1.47)	1.65 (2.29)	0.50 (0.45)	4.29 (2.45)	4.18 (2.41)	4.77 (2.83)	3.91 (2.26)	**
	Litter Cover	(%)	3.58 (1.36)	3.53 (1.46)	4.10 (1.31)	3.47 (1.51)	5.25 (0.80)	5.08 (1.00)	5.45 (0.69)	5.13 (0.85)	**
	Grass Cover	(%)	2.63 (0.96)	2.60 (1.03)	2.75 (1.21)	2.44 (0.89)	2.36 (0.68)	2.53 (0.57)	2.32 (0.60)	2.28 (0.60)	
	Forb Cover	(%)	1.85 (0.95)	1.96 (1.08)	1.65 (1.05)	1.94 (1.04)	1.71 (0.90)	0.97 (0.84)**	1.95 (0.91)	1.59 (0.80)	
Gadwall			n = 13	n = 13	n = 7	n = 5	n = 14	n = 14	n = 7	n = 6	
	Nest HD	(dm)	1.51 (1.65)	0.68 (0.66)	2.21 (2.03)	0.64 (0.35)*	2.15 (0.65)	1.57 (1.12)	1.95 (0.59)	2.11 (0.34)	
	Litter Depth	(cm)	1.12 (1.37)	0.85 (0.80)	1.71 (1.65)	0.40 (0.42)	3.50 (1.95)	4.00 (3.45)	3.79 (2.29)	3.33 (1.81)	**
	Litter Cover	(%)	3.00 (0.84)	3.38 (1.28)	3.43 (0.53)	2.40 (0.96)*	4.32 (1.05)	4.21 (1.27)	4.21 (1.29)	4.50 (0.89)	**
	Grass Cover	(%)	1.42 (0.93)	2.00 (1.19)	1.14 (1.11)	1.70 (0.67)	2.64 (1.01)	1.96 (0.41)*	2.64 (1.28)	2.42 (0.49)	**
	Forb Cover	(%)	2.27 (0.78)	2.31 (0.66)	2.36 (1.07)	2.20 (0.27)	1.82 (1.22)	1.25 (0.89)	1.50 (1.19)	2.33 (1.25)	
	Shrub Cover[d]	(%)	1.08 (1.75)	0.00 (0.00)*	2.00 (2.00)	0.00 (0.00)*	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	*
Short-eared Owl			n = 8	n = 8	n = 2	n = 5	n = 15	n = 15	n = 11	n = 3	
	Nest HD	(dm)	1.01 (0.66)	0.74 (0.69)	1.00 (0.44)	1.08 (0.82)	1.65 (0.68)	1.47 (0.85)	1.63 (0.65)	1.56 (0.98)	*
	Litter Depth	(cm)	1.44 (1.86)	1.13 (1.09)	1.41 (1.00)	2.16 (0.97)	3.07 (2.47)	3.17 (2.22)	2.18 (1.50)	5.67 (3.88)	
	Litter Cover	(%)	3.88 (1.36)	3.75 (1.34)	3.75 (1.06)	4.20 (1.52)	4.67 (1.08)	4.00 (1.36)	4.41 (1.04)	5.83 (0.29)	
	Grass Cover	(%)	3.38 (1.33)	2.69 (0.96)	2.75 (0.35)	3.30 (1.48)	2.10 (0.43)	2.20 (0.53)	2.14 (0.32)	1.83 (0.76)	*
	Forb Cover	(%)	1.44 (1.21)	2.06 (0.98)	1.00 (1.41)	1.60 (1.38)	1.43 (0.59)	1.27 (0.70)	1.36 (0.32)	1.83 (1.26)	

[a] For all nests vs. paired random points: paired t-test to compare nestHD and litter depth, and Wilcoxon signed rank test to compare percent cover variables.

[b] For all nests in grazed vs. all nests ungrazed and successful vs. depredated: t-test, or ANCOVA when date was a significant covariate ($p < 0.05$) to compare nest HD, t-test to compare litter depth, and Mann-Whitney U-test to compare percent cover variables.

[c] Percent cover category: 0 = 0%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, and 6 = 96-100%.

[d] Only Gadwall had shrub cover > 0.

Appendix B. Mean (SD) of vegetation features at 5.0 m from nests and paired random points in grazed and ungrazed plots for Western Meadowlarks, Savannah Sparrows, Gadwalls, and Short-eared Owls. Significance of comparisons designated by: *=p<0.05, **=p<0.01.

Species	Vegetation Features	(units)	Grazed x̄ (SD) Nest	vs Random[a]	Successful	vs Depredated[b]	Ungrazed x̄ (SD) Nest	vs Random	Successful	vs Depredated	Grazed vs Ungrazed[b]
Western Meadowlark			n = 14	n = 14	n = 7	n = 5	n = 6	n = 6	n = 3	n = 6	
	Nest HD	(dm)	0.62 (0.44)	0.46 (0.43)	0.53 (0.39)	0.75 (0.42)	0.92 (0.64)	1.14 (0.90)	1.54 (0.50)	0.61 (0.36)**	
	Litter Depth	(cm)	1.82 (2.18)	0.82 (1.20)	1.71 (2.45)	1.40 (1.19)	2.92 (2.71)	1.92 (1.43)	3.67 (1.04)	2.75 (2.62)	
	Litter Cover	(%)[c]	3.43 (1.40)	3.07 (1.30)	3.35 (1.46)	3.20 (1.10)	5.17 (0.93)	3.92 (1.39)	6.00 (0.00)	4.83 (0.93)	**
	Grass Cover	(%)	2.00 (0.65)	1.96 (0.75)	1.93 (0.61)	1.80 (0.45)	2.00 (0.32)	1.83 (0.93)	2.50 (0.50)	1.92 (0.38)	
	Forb Cover	(%)	1.89 (1.20)	2.11 (1.02)	1.71 (1.29)	2.70 (0.44)	1.50 (0.63)	1.33 (0.75)	1.33 (1.15)	1.33 (0.61)	
			n = 22		n = 8	n = 7	n = 23		n = 7	n = 15	
	Nest HD Loc.[d]	(dm)	0.80 (0.52)		0.65 (0.56)	1.12 (0.44)	1.30 (0.79)		1.15 (1.02)	1.20 (0.66)	*
Savannah Sparrow			n = 46	n = 46	n = 10	n = 18	n = 19	n = 19	n = 11	n = 16	
	Nest HD	(dm)	0.62 (0.50)	0.67 (0.46)	0.66 (0.43)	0.56 (0.55)	1.28 (0.68)	1.51 (0.77)	1.56 (0.69)	1.13 (0.64)	**
	Litter Depth	(cm)	0.98 (0.85)	1.18 (1.28)	1.20 (1.03)	0.83 (0.80)	5.04 (3.06)	4.74 (2.71)	5.05 (3.09)	5.13 (3.22)	**
	Litter Cover	(%)	3.41 (1.31)	3.51 (1.27)	4.05 (1.28)	3.31 (1.26)	5.29 (0.98)	5.08 (1.04)	5.32 (0.93)	5.31 (0.83)	**
	Grass Cover	(%)	2.72 (1.08)	2.63 (1.04)	3.00 (1.15)	2.50 (1.00)	2.39 (0.57)	2.50 (0.53)	2.55 (0.57)	2.28 (0.52)	
	Forb Cover	(%)	1.80 (0.97)	1.93 (1.11)	1.45 (1.04)	1.86 (1.10)	1.64 (0.83)	1.16 (0.71)	1.91 (1.04)	1.44 (0.87)	
			n = 56		n = 11	n = 24	n = 56		n = 20	n = 19	
	Nest HD loc.	(dm)	0.66 (0.54)		0.60 (0.58)	0.57 (0.46)	1.08 (0.48)		1.19 (0.52)	0.99 (0.49)	**
Gadwall			n = 13	n = 13	n = 7	n = 5	n = 14	n = 14	n = 7	n = 6	
	Nest HD	(dm)	1.08 (1.34)	0.65 (0.71)	1.51 (1.75)	0.59 (0.29)	2.11 (0.98)	1.68 (0.97)	2.11 (1.16)	2.32 (0.79)	*
	Litter Depth	(cm)	0.85 (0.66)	0.54 (0.48)	1.07 (0.53)	0.40 (0.65)	3.00 (2.39)	3.71 (3.46)	3.64 (3.06)	2.42 (1.53)	**
	Litter Cover	(%)	2.88 (1.06)	3.19 (1.11)	3.42 (1.02)	2.10 (0.74)*	4.25 (1.27)	4.00 (1.41)	4.64 (1.28)	3.92 (1.32)	**
	Grass Cover	(%)	1.46 (0.72)	1.96 (1.07)	1.43 (0.84)	1.40 (0.65)	2.21 (0.64)	1.89 (0.56)	2.07 (0.67)	2.25 (0.61)	*
	Forb Cover	(%)	2.38 (0.87)	2.42 (0.89)	2.14 (1.03)	2.60 (0.65)	1.54 (1.15)	1.25 (0.87)	1.36 (0.98)	2.00 (1.22)	*
	Shrub Cover[e]	(%)	0.62 (1.10)	0.00 (0.00)	1.14 (1.31)	0.00 (0.00)*	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	*
			n = 18		n = 10	n = 7	n = 156		n = 56	n = 76	
	Nest HD loc.	(dm)	1.29 (1.27)		1.67 (1.56)	0.87 (0.56)	2.39 (1.08)		2.58 (1.16)	2.19 (0.98)*	**
Short-eared Owl			n = 8	n = 8	n = 2	n = 5	n = 15	n = 15	n = 11	n = 3	
	Nest HD	(dm)	0.86 (0.42)	0.89 (0.80)	0.97 (0.13)	0.73 (0.47)	1.55 (0.61)	1.57 (0.88)	1.48 (0.61)	1.73 (0.78)	**
	Litter Depth	(cm)	1.56 (0.98)	1.19 (0.80)	2.25 (1.77)	1.30 (0.75)	3.27 (1.52)	2.97 (1.79)	2.86 (1.58)	4.17 (0.29)	*
	Litter Cover	(%)	3.81 (1.36)	3.75 (1.36)	4.50 (1.41)	3.80 (1.44)	4.60 (0.76)	3.83 (1.33)	4.36 (0.67)	5.50 (0.50)	
	Grass Cover	(%)	3.19 (1.28)	3.06 (1.37)	2.75 (1.06)	3.00 (1.27)	2.07 (0.37)	2.10 (0.47)	2.09 (0.30)	1.83 (0.58)	*
	Forb Cover	(%)	1.69 (1.13)	1.56 (0.86)	1.50 (2.12)	1.80 (1.04)	1.70 (0.59)	1.33 (0.72)	1.68 (0.60)	2.00 (0.50)	
			n = 12		n = 4	n = 6	n = 94		n = 61	n = 16	
	Nest HD loc.	(dm)	0.94 (0.56)		1.13 (0.73)	0.94 (0.53)	1.51 (0.89)		1.60 (0.99)	1.47 (0.79)	*

[a] For all nests vs. paired random points: paired t-test to compare nestHD and litter depth, and Wilcoxon signed rank test to compare percent cover variables.
[b] For all nests in grazed vs. all nests ungrazed and successful vs. depredated: t-test, or ANCOVA when date was a significant covariate ($p < 0.05$) to compare nest HD, t-test to compare litter depth, and Mann-Whitney U-test to compare percent cover variables.
[c] Percent cover category: 0 = 0%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, and 6 = 96-100%.
[d] HD measured when nests were located for study plot and supplemental nests in 1993 and 1994.
[e] Only Gadwall had shrub cover > 0.

Appendix C. Mean (SD) of vegetation features at 10.0 m from nests and paired random points in grazed and ungrazed plots for Western Meadowlarks, Savannah Sparows, Gadwalls, and Short-eared Owls. Significance of comparisons designated by: *=p<0.05, **=p<0.01.

Species	Vegetation Features	(units)	Grazed x̄ (SD) Nest vs	Random[a]	Successful vs	Depredated[b]	Ungrazed x̄ (SD) Nest vs	Random	Successful vs	Depredated	Grazed vs Ungrazed[b]
Western			n = 14	n = 14	n = 7	n = 5	n = 6	n = 6	n = 3	n = 6	
Meadowlark	Nest HD	(dm)	0.77 (0.47)	0.36 (0.33)**	0.75 (0.58)	0.79 (0.41)	0.88 (0.51)	0.98 (0.96)	1.17 (0.42)	0.76 (0.42)	
	Litter Depth	(cm)	1.57 (1.85)	1.04 (1.26)	1.42 (2.41)	1.20 (0.27)	3.42 (2.40)	1.92 (1.69)	5.17 (2.36)	3.00 (2.05)	**
	Litter Cover	(%)[c]	3.18 (1.31)	3.00 (1.06)	3.00 (1.44)	3.00 (1.00)	5.17 (0.68)	3.58 (1.77)	5.33 (1.15)	5.00 (0.55)	**
	Grass Cover	(%)	1.93 (0.70)	2.04 (0.77)	1.93 (0.79)	1.70 (0.67)	2.08 (0.38)	1.67 (0.98)	2.17 (1.25)	2.08 (0.38)	
	Forb Cover	(%)	1.93 (1.19)	1.96 (0.84)	1.86 (1.28)	2.60 (0.65)	1.67 (0.61)	1.58 (1.11)	1.67 (1.52)	1.58 (0.58)	
Savannah			n = 46	n = 46	n = 10	n = 18	n = 19	n = 19	n = 11	n = 16	
Sparrow	Nest HD	(dm)	0.69 (0.60)	0.60 (0.41)	0.75 (0.40)	0.52 (0.45)	1.09 (0.69)	1.53 (0.77)	1.22 (0.49)	1.12 (0.76)	**
	Litter Depth	(cm)	0.99 (1.22)	1.11 (1.28)	1.45 (2.06)	0.86 (0.95)	4.57 (3.05)	5.21 (3.33)	4.82 (2.39)	4.31 (2.04)	**
	Litter Cover	(%)	3.53 (1.41)	3.54 (1.19)	4.30 (1.48)	3.47 (1.44)	4.89 (1.03)	4.92 (0.90)	5.27 (1.19)	5.06 (0.70)	**
	Grass Cover	(%)	2.65 (1.11)	2.73 (0.95)	2.90 (1.02)	2.26 (1.09)	2.32 (0.55)	2.68 (0.69)	2.41 (0.44)	2.19 (0.40)	
	Forb Cover	(%)	2.09 (1.11)	1.88 (0.98)	1.55 (0.83)	2.35 (1.44)	1.43 (0.88)	0.92 (0.69)	1.27 (0.68)	1.50 (0.91)	**
Gadwall			n = 13	n = 13	n = 7	n = 5	n = 14	n = 14	n = 7	n = 6	
	Nest HD	(dm)	0.58 (0.75)	0.61 (0.67)	0.66 (0.98)	0.49 (0.46)	1.78 (0.81)	1.65 (1.10)	1.76 (0.81)	1.67 (0.88)	**
	Litter Depth	(cm)	0.96 (0.85)	1.04 (1.07)	1.00 (1.08)	0.80 (0.57)	3.04 (1.56)	3.82 (3.95)	3.21 (1.65)	3.00 (1.67)	**
	Litter Cover	(%)	3.08 (1.10)	3.50 (1.44)	3.43 (1.06)	2.70 (1.20)	4.25 (0.98)	4.14 (1.43)	4.36 (1.18)	4.25 (0.82)	*
	Grass Cover	(%)	1.92 (0.53)	1.88 (1.00)	1.92 (0.53)	1.90 (0.65)	2.29 (0.55)	2.14 (0.75)	2.14 (0.56)	2.33 (0.61)	
	Forb Cover	(%)	1.92 (0.70)	2.12 (0.87)	1.71 (0.91)	2.10 (0.22)	1.64 (0.63)	1.25 (0.92)	1.43 (0.67)	1.75 (0.52)	
	Shrub Cover[d]	(%)	0.12 (0.30)	0.08 (0.28)	0.21 (0.39)	0.00 (0.00)	0.00 (0.00)	0.14 (0.53)	0.00 (0.00)	0.00 (0.00)	
Short-eared			n = 8	n = 8	n = 2	n = 5	n = 15	n = 15	n = 11	n = 3	
Owl	Nest HD	(dm)	0.69 (0.28)	0.86 (0.78)	0.59 (0.04)	0.66 (0.33)	1.61 (0.73)	1.58 (0.94)	1.60 (0.71)	1.79 (1.04)	**
	Litter Depth	(cm)	1.13 (0.88)	1.19 (0.92)	1.50 (2.12)	1.00 (0.35)	3.70 (1.97)	3.50 (2.08)	3.14 (2.03)	5.17 (0.29)	**
	Litter Cover	(%)	3.56 (1.15)	3.81 (1.44)	3.25 (1.77)	3.90 (1.02)	4.83 (0.79)	4.30 (0.90)	4.68 (0.84)	5.50 (0.50)	*
	Grass Cover	(%)	3.00 (1.23)	3.19 (1.58)	2.25 (1.77)	3.00 (1.00)	2.23 (0.46)	2.13 (0.48)	2.31 (0.34)	1.83 (0.76)	
	Forb Cover	(%)	1.75 (1.17)	1.50 (0.89)	2.00 (2.12)	1.60 (1.08)	1.43 (0.62)	1.37 (0.86)	1.41 (0.63)	1.83 (0.29)	

[a] For all nests vs. paired random points: paired t-test to compare nestHD and litter depth, and Wilcoxon signed rank test to compare percent cover variables.

[b] For all nests in grazed vs. all nests ungrazed and successful vs. depredated: t-test, or ANCOVA when date was a significant covariate ($p < 0.05$) to compare nest HD, t-test to compare litter depth, and Mann-Whitney U-test to compare percent cover variables.

[c] Percent cover category: 0 = 0%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, and 6 = 96-100%.

[d] Only Gadwall had shrub cover > 0.