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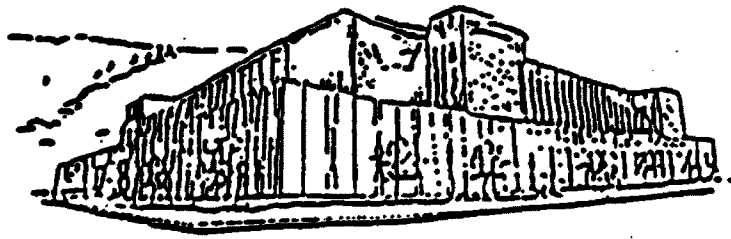
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Nest Habitat Selection by Grassland Birds:

The Role of Vegetation Structure and Floristics

By

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B.S., Davidson College, 1989

Presented in partial fulfillment of the requirements

for a degree of

Master of Science

THE UNIVERSITY OF MONTANA

1999

Approved by:

Chairman, Board of Examiners

Chairman, Board of Examiners

Dean, Graduate School

Dean, Graduate School

12-30-99

Date

UMI Number: EP37763

UMI

Dissertation Publishing

UMI EP37763

ProQuest

ABSTRACT

Hoekman, Steven T., M.S., Fall 1999   Wildlife Biology

Nest Habitat Selection by Grassland Birds: The Role of Vegetation Structure and

Floristics (49pp.).

Director: Dr. I J. Ball

       I studied nest habitat selection of a grassland bird community in fields of ungrazed, cool season grasses in westcentral Montana. Bird species included Cinnamon Teal (*Anas cyanoptera*), Gadwall (*A. strepera*), Mallard (*A. platyrhynchos*), Northern Shoveler (*A. clypeata*), Short-eared Owl (*Asio flammeus*), Savannah Sparrow (*Passerculus sandwichensis*), and Western Meadowlark (*Sturnella neglecta*). Vegetation characteristics (structure, structural heterogeneity, and floristics) were sampled at the nest site (<50 cm radius around nest) and nest patch (10 m radius). I compared nests of each species to available vegetation and compared selection among species. Each species selected nest sites nonrandomly (P <0.003 in all cases). Nest site choice differed among species: 9 of 10 pairs of species were significantly different (P <0.10) in 1996, and 20 of 21 in 1997. Canopy cover, heterogeneity of plant growth form, and vegetation density at varying heights best discriminated among species. At nest patches, selection by each species and differences among species were relatively weak and generally reflected patterns at nest sites. For most ducks and Short-eared Owls, vegetation volume immediately around nests was significantly lower (P <0.10) to the southeast than to the northwest or southwest. I conclude that nest habitat selection was operating primarily at a fine scale (the nest site). Nest site selection was nonrandom and was expressed through selection of plant growth form, placement of the nest relative to vegetation, and active manipulation of vegetation by birds. I suggest that managers need to provide fine scale diversity of vegetation characteristics within fields because of increased need to manage grasslands for mutual benefits to a diversity of breeding birds.

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Considerable conservation effort to manage upland vegetation for birds in grassland-wetland systems of the northern prairies has focused on providing tall, dense, monotypic stands of vegetation. This goal has largely been pursued by limiting disturbance on managed grasslands or through restoration programs planting grass or grass/legume mixtures, commonly referred to as Dense Nesting Cover, or DNC (Higgins and Barker 1982, Kirby et al. 1992, Hartley 1994, Reynolds et al. 1994). This emphasis has occurred largely because ducks were thought to benefit from such conditions (Duebbert 1969, Duebbert and Lokemoen 1976), but site-specific benefits expected from this approach often have not accrued (Klett et al. 1988, Clark and Nudds 1991, Sargeant 1996). Additional reasons to suggest that fundamental re-evaluation of grassland conservation practices is in order include recent evidence of substantial population declines in many species of grassland birds (Johnson and Schwartz 1993, Knopf 1995) and growing interest in providing suitable habitat for a diversity of bird species in grasslands (Tome et al. 1994, Hartley 1994, Reynolds et al. 1994).

Despite the importance of detailed knowledge of habitat preferences by individual species for developing unambiguous "targets" for grassland management, much of the available information on this topic is difficult to synthesize meaningfully. Most studies which that measured vegetation characteristics address only one (or a few -- closely related) species, and methods used to measure and analyze vegetation usually differs among studies. Differing ecological scales (Wiens et al. 1987) further complicate attempts to compare among studies, and hence among species. Finally, habitat preferences of

1

grassland birds often have been inferred from density or occupancy of breeding birds in relation to habitat manipulations such as grazing, haying, or burning (Kantrud 1981, Pylypec 1991, Gilbert et al. 1995, Kruse and Bowen 1996, Dale et al. 1997). Apparent responses by individual species to specific manipulations often differ, however, probably because birds respond to changes in vegetation structure rather than to the manipulation *per se* (Wiens 1973, Kantrud 1981, Kirby et al. 1992, Saab et al. 1995, but see Bowen and Kruse 1993). Differences in the timing and intensity of a manipulation may alter the effect (Bowen and Kruse 1993, Kruse and Bowen 1996), and manipulation may have different effects different habitats or moisture regimes (Wiens 1973, Biondini et al. 1998)

Habitat preferences may be reflected at multiple ecological scales (Johnson 1980, Kotliar and Wiens 1990). At intermediate scales, correlating presence or density of breeding birds to some measure of "average" structure within a field is commonly used to demonstrate general habitat preferences by groups of species with similar preferences (Rotenberry and Wiens 1980, Renken and Dinsmore 1987, Delisle and Savidge 1997). However, wide overlap in preferences is common at such broad scales: preferences of individual species can not be discerned, and responses to specific manipulations are difficult to predict (Rotenberry and Wiens 1980). I therefore chose the more powerful approach of measuring vegetation at sites used by individual birds (James 1971, Larson and Bock 1986, Sedgwick and Knopf 1992) to investigate habitat preferences of nesting birds. Because selection of nest habitat may involve the area immediately around the nest site or a much larger area (Martin and Roper 1988, Knopf and Sedgwick 1994, Badyaev 1995), I sampled vegetation at the scale of the nest site (<50 cm around nest) and nest

patch (10 m from nest). My goal was to describe nesting habitat preferences of a diverse community of ground-nesting birds in grassland, using objective measures of vegetation characteristics (structure, structural heterogeneity, and floristics). Specifically, I asked: do species select vegetation characteristics at nest sites and nest patches nonrandomly relative to availability?; do preferences for vegetation characteristics at nest sites and nest patches differ among species?; and does directional orientation of vegetation volume immediately surrounding nest sites differ from random?

STUDY AREA AND METHODS

Study Area and Species

I conducted research during the 1996 and 1997 breeding seasons on 227 ha of ungrazed grassland habitat on the Flathead Indian Reservation in the lower Mission Valley of westcentral Montana, 80 km north of Missoula. Glacial topography characterizes the area, which exhibits low relief and high densities of wetlands (Lokemoen 1962). Management of the study area and other local state and federal land focused primarily on providing breeding habitat for upland nesting ducks and Ring-necked pheasant (*Phasianus colchicus*). I searched for nests and sampled vegetation in seven contiguous fields supporting varying combinations of tame, cool season grasses, primarily Intermediate Wheatgrass (*Agropyron intermedium*), Smooth Brome (*Bromus inermis*), Kentucky Bluegrass (*Poa pratensis*), Quackgrass (*Agropyron repens*), and Orchard Grass (*Dactylis glomerata*); differing combinations of plant species created a wide diversity of vegetation structure within and among fields. No shrubs or trees existed on the study area, but

locally common exotic forbs occurred at low densities in all fields. The breeding bird community included both grassland species and wetland species. I chose study species that were common on the study area, but also attempted to maximize diversity of taxa and life history traits. I sampled nests of Mallard , Gadwall , Northern Shoveler (hereafter "Shoveler"), Cinnamon Teal (hereafter "Teal"), Short-eared Owl (hereafter "Owl"), Savannah Sparrow (hereafter "Sparrow") and Western Meadowlark (hereafter "Meadowlark"). Observers often could not distinguish between female Cinnamon and Blue-winged Teal (*Anas discors*), which are closely related and behaviorally similar (Connelly and Ball 1984). I assumed that our sample of teal nests reflected the consistent 7:1 ratio of Cinnamon to Blue-winged Teal observed in the area (Forman 1993; U. S. Fish and Wildlife Service, unpublished data). In 1996, I searched 5 fields (162 ha) and sampled nests of ducks and Owls. Two adjacent fields were acquired for conservation purposes in 1997, allowing us to enlarge the search area to 227 ha. Consequently, I was able to obtain sufficient samples of ducks, Owls, Sparrows, and Meadowlarks in 1997.

Methods

I conducted nest searches on the study area three times each breeding season (at 21-25 day intervals) using a cable-chain device (Higgins et al. 1969). This technique was effective for finding duck and Owl nests but was less efficient for finding passerine nests. Consequently, I observed parental behavior (Martin and Geupel 1993) from tower blinds (Fondell et al. *In prep*) to find most Sparrow and some Meadowlark nests. I mapped all Sparrow territories early in the breeding season, and searched each territory for nests throughout the breeding season.

Vegetation sampling occurred when nests were no longer active because I suspected that intensive sampling provided visual and olfactory cues that could increase nest predation. Vegetation sampling plots were centered on nest sites and on available sites randomly located within the study area. To locate available sites, I generated random coordinates for a grid superimposed on an aerial photo of the study area. I used topographical features to get to the indicated locations. Then, the plot center was located by tossing a stick behind me in a randomly selected direction. Nest and available plots were sampled within 3 days to account for temporal change in vegetation, which can be rapid in grassland. I assumed that rates of change in vegetation characteristics were similar at nest and available sites. Furthermore, I sampled only under suitable conditions relative to wind (<25 km/h), light (>1 h from sunrise or sunset), and moisture (i.e. I avoided periods when moisture caused vegetation to droop). Transects extended from each plot center at intercardinal directions with sampling points at 0 and 10 m. Sampling points at 0 m characterized the nest site or available site, and sampling points at 10 m characterized the nest patch or available patch.

I estimated vegetation characteristics at each sampling point. A pole marked in 2 cm intervals (modified from Robel et al. 1970) was used to estimate vegetation volume. From a height of 1 m and a distance of 2 m, I recorded the lowest interval not completely obscured by vegetation. The pole was placed at each sampling point, and readings were taken facing the plot center. A rod marked in 10 cm intervals (Wiens 1969) was used to estimate vertical structure, a measure of vegetation density, in 1997. At each sampling point, I lowered the rod vertically to the ground and recorded the number of vegetation

"hits" on the pole in each 10 cm interval between 0-50 cm, hits above 50 cm, and the highest vegetation hit. At plot center, estimates of vertical structure were taken 10 cm from plot center to measure structure immediately around the nest bowl. Canopy cover at the nest was estimated at the time of nest location as the percentage of the nest bowl obscured by vegetation from 1 m above the nest. I defined structural heterogeneity as variation in volume and in vertical structure among sampling points: heterogeneity variables were calculated as the standard deviation of volume and of vertical structure variables after transformation to remove positive correlations between means and variances at random plots. Floristics were recorded only on a single transect. From 1 m above each sampling point, the observer estimated percent cover of the ground in a 0.5 m diameter circle by each plant species independent of others. Cover was estimated by category (0-5%, 5-25%, 25-50%, 50-75%, 75-95%, and 95-100%; Mueller-Dumbois and Ellenburg 1974), then transformed into mid-point percentages (Huberty 1994). Litter cover and litter depth were not measured because Fondell (1997) had demonstrated that litter was abundant in all of the fields and that litter characteristics of nest sites did not differ from available sites for most species.

I used logical and statistical screening procedures for variable selection and reduction (Huberty 1994). I dropped from consideration plant species with <5% mean cover and occurring at <5% of nest plots because these species probably contributed little to analysis of nest site preferences. I also found that subjectivity in estimating vertical structure increased with height (due mainly movement of vegetation caused by wind). Therefore, I dropped estimates of highest vegetation hit and restricted analysis of

structural heterogeneity to hits below 20 cm. I used correlation analysis to indicate

variables that measured similar characteristics and therefore could be combined. Adjacent

intervals of vertical structure that were highly correlated were lumped. Grass species with

similar growth forms showed similar patterns of preference among bird species, so I

lumped cover estimates from those species in statistical analysis (Table 1).

Statistical Analysis

I tested for differences between nest and available habitat for each species and

among nest habitat preferences of all species using univariate Analysis of Variance and

descriptive Discriminant Function Analysis (DFA; Huberty 1994, Norusis/SPSS 1997).

Comparison of habitat preferences among species was based on difference variables

created by subtracting available habitat variables from nest habitat variables. Univariate

analysis of variance showed which variables were significantly different among groups. I

presented univariate results and descriptive statistics for comparisons among habitat

preferences of species to show effect sizes of individual variables for each species. I did

not present comparisons of nest and available habitat for each species because qualitatively

similar interpretations can be reached from comparisons of preferences among species. I

used DFA to derive the linear combination of variables that best separated groups.

Although I used a stepwise procedure that maximized Mahalonobis distance between

group centroids as the basis of variable selection, I also utilized best subsets analysis and

judgement to select parsimonious and biologically interpretable final models (Huberty

1994, Norusis/SPSS 1997). *F*-statistics were used to test if Mahalonobis locations in

discriminant space differed between each pair of species. Experimentwise Type I error

Table 1. Variables used in statistical analysis of nest site (< 50cm around nest) and nest patch (10 m from nest) characteristics.

Measurement Type	Variable	Description
Structure	Volume	Mean vegetation volume
	Surface Structure	Mean Wiens hits from 0-10 cm
	Low Structure	Mean Wiens hits from 10-20 cm
	Intermediate Structure	Mean Wiens hits from 20-40 cm
	High Structure	Mean Wiens hits above 40 cm
	Canopy[a]	Percent of nest bowl obscured from above
Heterogeneity	SD Volume	Standard deviation of squareroot (*Volume*)
	SD Surface Structure	Standard deviation of log (*Surface Structure*)
	SD Low Structure	Standard deviation of log (*Low Structure*)
Floristic	Bunchgrass Cover[b]	Percent cover by Intermediate Wheatgrass and Orchard Grass
	Broadleaf Grass Cover[c]	Percent cover by Smooth Brome and Quackgrass
	Bluegrass Cover	Percent cover by Kentucky Bluegrass

[a]Estimated only at nest sites.
[b]Cespitose grasses with robust, erect culms.
[c]Rhizomatous grasses with long, broad leaves.

rates of 10% were maintained for univariate and pairwise tests on a tablewide basis.

Classification of groups was presented as an index to effect size (Huberty 1994).

Covariance matrices were tested for homogeneity using Box's M criterion. Because some

matrices showed significant heteroscedasticity, separate group covariance matrices were

employed for classification. Although some of the DFA analyses violated assumptions of

normality and homoscedasticity ($P < 0.05$), parallel analyses using Canonical

Correspondence Analysis, which assumes only unimodal distributions (ter Braak and

Verdonschot 1986, Palmer 1993), yielded virtually identical results. Structure correlations

showed the most important component variables for each discriminant function. Analysis

was separated by year because of differences between years in study area size, study

species, and habitat measurements. For species sampled in both years, I plotted 1997

samples on the 1996 discriminant function to facilitate comparisons between years.

I tested if Volume around nest sites of ducks and Owls (for which $n > 20$) or

random sites varied by direction using one-way Analysis of Variance (Norusis/SPSS

1997). I combined years for this analysis because patterns were similar between years.

Where significant differences existed, I tested for pairwise differences using Tukey's

method to maintain a Type I error rate of 10% for each species (Day and Quinn 1989).

RESULTS

Nest Vegetation Preferences

Differences between nest site and available vegetation for each species (Table 2)

were highly significant in 1996 ($P \le 0.0016$) and 1997 ($P \le 0.0029$). High mean rates for

correct classification from DFA for all species in 1996 (86% relative to 50% expected by

Table 2. Summary results of Discriminant Function Analysis in separating nest site (<50 cm around nest) from available vegetation for grassland birds in westcentral Montana in 1996 and 1997.

Species	*n*	Wilk's Lambda	*P*	% correct classification
1996				
Cinnamon Teal	28	0.57	0.0008	79
Gadwall	42	0.47	<0.0001	86
Mallard	42	0.37	<0.0001	93
Northern Shoveler	46	0.51	<0.0001	78
Short-eared Owl	16	0.29	0.0016	94
Overall	174			86[a]
1997				
Cinnamon Teal	30	0.33	<0.0001	93
Gadwall	32	0.62	0.0026	76
Mallard	28	0.27	<0.0001	93
Northern Shoveler	24	0.54	0.0024	88
Short-eared Owl	28	0.37	<0.0001	93
Savannah Sparrow	36	0.38	<0.0001	94
Western Meadowlark	24	0.50	0.0029	83
Overall	202			89[b]

[a]72% reduction in error relative to correct classification expected by chance (50%).
[b]78% reduction in error relative to correct classification expected by chance (50%).

chance) and 1997 (89% relative to 50% expected by chance) demonstrated low overlap between nest site and available vegetation. Structure correlations showed strength of association of vegetation variables with each discriminant function in 1996 (Table 3) and

1997 (Table 4). For species sampled in both years, patterns of selection generally were biologically similar between years.

Differences between nest patch and available vegetation for each species in 1996 and 1997 were weaker in all cases (Table 5) than between nest site and available vegetation, but nest patch preferences in 1996 (Table 6) and 1997 (Table 7) generally reflected nest site preferences. Low mean rates for correct classification from DFA for all species in 1996 (66% relative to 50% expected by chance) and 1997 (67% relative to 50% expected by chance) indicated high overlap between nest patch and available vegetation.

Because Canopy was estimated only at nests (1996, Table A1; 1997, Table A2), it was not included in DFA. For species sampled in both years, Canopy was similar between years. Averaging across years, Canopy was very high for Sparrows (84%) and Meadowlarks (87%), high for Teals (65%) and Shovelers (58%), moderate for Gadwalls (35%) and Mallards (39%), and low for Owls (12%).

Volume at nest sites varied by direction for Teals ($F = 4.2$; df $= 3,122$; $P = 0.007$), Gadwalls ($F = 3.7$; df $= 3,135$; $P = 0.013$), Shovelers ($F = 2.9$; df $= 3,136$; $P = 0.04$), and Owls ($F = 13.5$; df $= 3,84$; $P < 0.0001$), but not for Mallards ($F = 1.4$; df $= 3,139$; $P = 0.24$) or at random points ($F = 2.0$; df $= 3,764$; $P = 0.11$). Volume was lowest to the southeast and highest to the southwest or northwest for all species. For Teals, Volume to the southeast was 3.4 cm less than to the southwest ($P = 0.10$) and 5.1 cm less than to the northwest ($P = 0.004$). Volume to the southeast of Gadwall sites was 5.8 cm less than to the northwest ($P = 0.008$) and 4.4 cm less than to the northeast ($P = 0.075$). For Shovelers, Volume to the southeast was 3.1 cm less than to the southwest ($P = 0.019$).

Table 3. Structure correlations from Discriminant Function Analysis separating nest sites (<50 cm around nest) and available vegetation for grassland birds in westcentral Montana in 1996. Structure correlations are presented for variables included by stepwise procedures (or with structure correlations >0.25).

Variable	Species				
	Cinnamon Teal	Gadwall	Mallard	Northern Shoveler	Short-eared Owl
Volume		0.45	0.48		0.59
SD Volume			0.23		0.22
Bunchgrass Cover	-0.53	0.40	0.48	(-0.51)	
Broadleaf Grass Cover	0.85	-0.13		1.00	0.28
Bluegrass Cover	0.36	-0.38	-0.41		

Table 4. Structure correlations from Discriminant Function Analysis separating nest sites (<50 cm around nest) and available vegetation for grassland birds in westcentral Montana in 1997. Structure correlations are presented for variables included by stepwise procedures (or with structure correlations >0.25).

Variable	Species						
	Cinnamon Teal	Gadwall	Mallard	Northern Shoveler	Short-eared Owl	Savannah Sparrow	Western Meadowlark
Volume	0.59	0.43	0.43	(0.43)	0.38	0.57	
Surface Structure	(0.28)				-0.53	0.62	0.66
Low Structure	(0.38)					(0.50)	(0.38)
Intermediate Structure	0.59		(0.30)		0.44	(0.31)	
High Structure	-0.14		(0.39)	0.72			
SD Volume		0.60	0.34				-0.44
SD Surface Structure				0.63			
SD Low Structure	0.31	(0.34)				-0.26	0.44
Bunchgrass Cover		(0.48)	0.68		(-0.25)	-0.62	
Broadleaf Grass Cover				0.43	0.33		
Bluegrass Cover		-0.47				(0.52)	

Table 5. Summary results of Discriminant Function Analysis in separating nest patch (10 m from nest) from available vegetation for grassland birds in westcentral Montana in 1996 and 1997.

Species	n	Wilk's Lambda	P	% correct classification
1996				
Cinnamon Teal	28	0.81	0.022	68
Gadwall	42	0.94	0.10	59
Mallard	42	0.66	0.0010	74
Northern Shoveler	46	0.86	0.012	65
Short-eared Owl	16	0.77	0.072	63
Overall	174			66[a]
1997				
Cinnamon Teal	28	0.80	0.015	70
Gadwall	34	0.90	0.068	65
Mallard	28	0.81	0.020	65
Northern Shoveler	22	0.86	0.075	64
Short-eared Owl	28	0.93	0.11	61
Savannah Sparrow	34	0.57	0.0001	81
Western Meadowlark	22	0.94	0.26	63
Overall	196			67[a]

[a] 34% reduction in error relative to correct classification expected by chance (50%).

Mallards showed a pattern and effect size similar to other ducks, but high variance resulted in low power. Directional orientation of vegetation was strongest for Owls: Volume to the southeast was 12.4 cm less than to the southwest ($P < 0.0001$) and 6.6 cm less than to the northwest ($P = 0.007$).

Table 6. Structure correlations from Discriminant Function Analysis separating nest patches (10 m from nest) and available vegetation for grassland birds in westcentral Montana in 1996. Structure correlations are presented for variables included by stepwise procedures (or with structure correlations >0.25).

Variable	Species				
	Cinnamon Teal	Gadwall	Mallard	Northern Shoveler	Short-eared Owl
Volume	(0.45)	1.00			
SD Volume			0.33		
Bunchgrass Cover			0.60		-1.00
Broadleaf Grass Cover	1.00			1.00	(0.44)
Bluegrass Cover			-0.58		

Table 7. Structure correlations from Discriminant Function Analysis separating nest patches (10 m from nest) and available vegetation for grassland birds in westcentral Montana in 1997. Structure correlations are presented for variables included by stepwise procedures (or with structure correlations >0.25).

Variable	Species						
	Cinnamon Teal	Gadwall	Mallard	Northern Shoveler	Short-eared Owl	Savannah Sparrow	Western Meadowlark
Volume	1.00					(0.26)	
Surface Structure							
Low Structure						0.77	
Intermediate Structure	(0.46)		(0.56)				-1.00
High Structure							
SD Volume							
SD Surface Structure							
SD Low Structure		1.00	0.64				
Bunchgrass Cover				1.00			
Broadleaf Grass Cover					1.00		
Bluegrass Cover							

Differences in Preferences Among Species

Species preferences at nest sites differed for all variables collected in 1996 (Table A1). DFA included all variables except Broadleaf Grass Cover (Figs. 1A and 1B) and significantly discriminated among species ($\Lambda = 0.21$, $P < 0.0001$). Three significant discriminant axes (Axis 1: $\chi^2 = 125.6$, $P < 0.0001$; Axis 2: $\chi^2 = 29.1$, $P = 0.0038$; Axis 3: $\chi^2 = 12.3$, $P = 0.056$) discriminated between all pairs of species except Mallards and Gadwalls (Table 8). The 68% mean rate of correct classification from DFA (Table 9) for all species, relative to 20% expected by chance, demonstrated low overlap among species. Mallards and Gadwalls had similar scores on all axes, but all other species occupied unique locations in discriminant space. Low scores on axis 1 showed a preference for increased Canopy and decreased Volume that separated Teals and Shovelers from Gadwalls, Mallards, and Owls. Teals and Shovelers differed on axes 2 and 3, reflecting preference

Table 8. Comparisons of nest site (<50 cm around nest) characteristics between pairwise combinations of grassland birds in westcentral Montana in 1996. F-statistics and P-values show the significance of Mahalanobis distances between nest sites in discriminant space. Of 10 pairs, only Mallard and Gadwall nest sites were not significantly different at the $\alpha = 0.10$ level. For all tests, df = 5, 78.

	Species							
	Cinnamon Teal		Gadwall		Mallard		Northern Shoveler	
Species	F	P	F	P	F	P	F	P
Gadwall	12.8	<0.0001						
Mallard	17.7	<0.0001	0.8	0.59				
Northern Shoveler	2.8	0.021	12.2	<0.0001	18.0	<0.0001		
Short-eared Owl	17.3	<0.0001	4.1	0.0024	3.8	0.0040	16.1	<0.0001
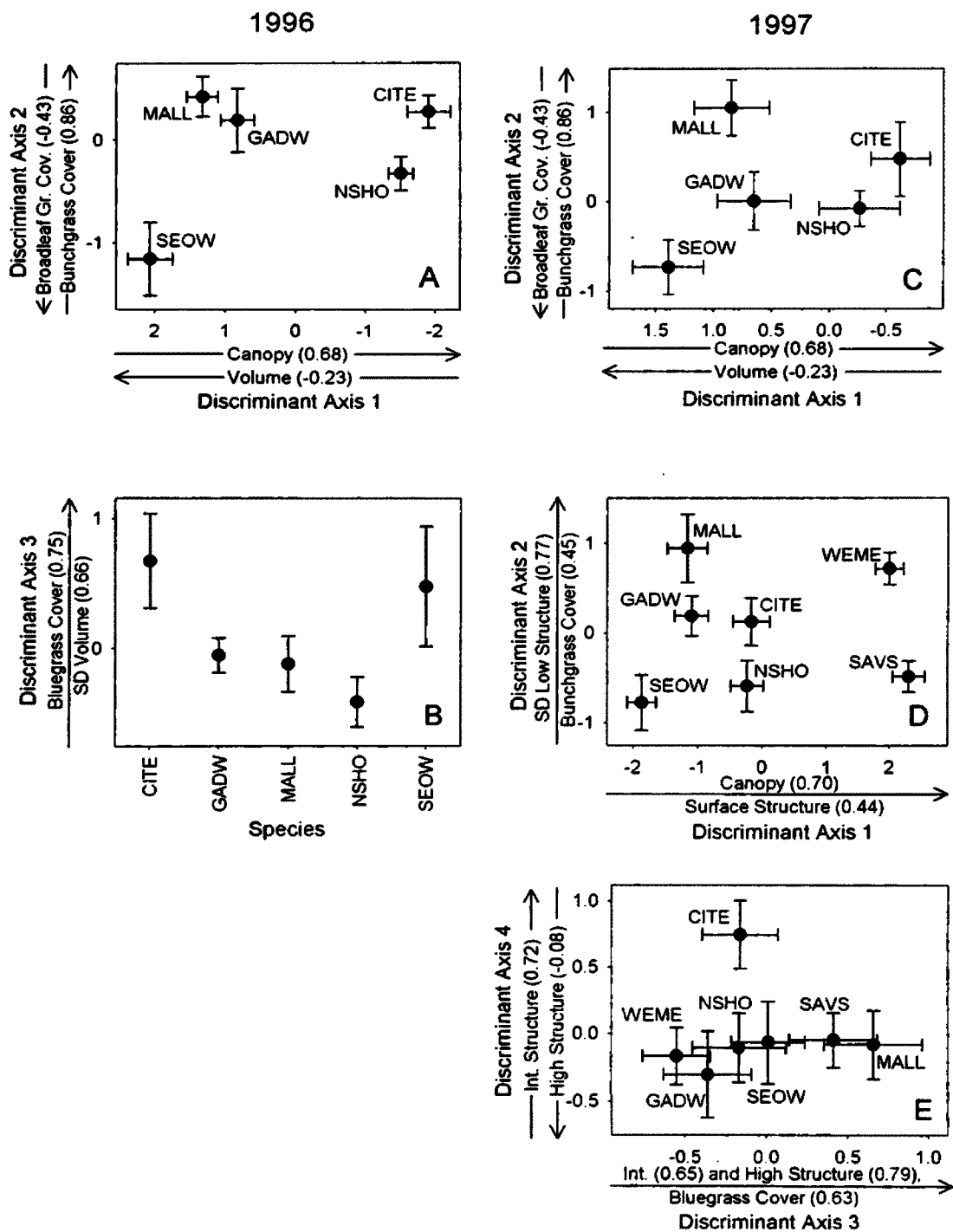
Figure 1. Discriminant function analysis of nest sites (< 50cm around nests) of grassland birds in westcentral Montana, 1996 (A and B) and 1997 (D and E). To facilitate comparisons between species sampled in both years, 1997 samples were plotted on the first two discriminant functions from 1996 (C). Variables most strongly correlated with each axis are shown with structure correlations. Vectors emphasize the direction of correlation. Centroids show the mean location on each axis with standard errors. Abbreviations: CITE=Cinnamon Teal, GADW=Gadwall, MALL=Mallard, NSHO=Northern Shoveler, SEOW=Short-eared Owl, SAVS=Savannah Sparrow, and WEME=Western Meadowlark.

Table 9. Rate of correct classification (%) of nest sites (<50 cm from nest) from Discriminant Function Analysis of 7 grassland birds in 1996 and 1997 based on separate covariance matrices. Classification rates indicate the amount of overlap of each species with others.

Year	Mean	Species						
		Cinnamon Teal	Gadwall	Mallard	Northern Shoveler	Short-eared Owl	Savannah Sparrow[a]	Western Meadowlark[a]
1996	68[b]	79	52	52	83	88		
1997	70[c]	47	56	57	75	86	83	91

[a]Sampled only in 1997.

[b]60% reduction in error relative to correct classification expected by chance (20%).

[c]65% reduction in error relative to correct classification expected by chance (14%).

by Teals relative to Shovelers for increased Bunchgrass Cover, SD Volume, and Bluegrass Cover. Among species with high scores on axis 1, Owls preferred lower Canopy and higher Volume relative to Gadwalls and Mallards. Owls were strongly separated from Gadwalls and Mallards on axis 2 by preference for Broadleaf Grass Cover rather than Bunchgrass Cover and on axis 3 by preference for highest SD Volume.

Species preferences at nest sites differed for 10 of 12 variables measured in 1997 (Table A2). DFA included 6 variables and significantly discriminated among species (Λ = 0.15, $P < 0.0001$). Four significant axes (Figs. 1D and 1E; Axis 1: $\chi^2 = 178.6$, $P < 0.0001$; Axis 2: $\chi^2 = 62.8$, $P < 0.0001$; Axis 3: $\chi^2 = 32.1$, $P = 0.0098$; Axis 4: $\chi^2 = 17.7$, $P = 0.038$) discriminated between 20 of 21 pairs of species (Table 10): only Teals and Shovelers ($P = 0.12$) did not differ at the $\alpha = 0.10$ level. The 70% mean rate of correct classification from DFA for all species, relative to 14% expected by chance, demonstrated low overlap between species (Table 9). Increased Canopy and Surface Structure segregated Meadowlarks and Sparrows from other species on axis 1. Meadowlarks were separated from Sparrows by preference for increased Bunchgrass Cover and SD Low Structure, shown on axis 2, and increased structure above 20 cm and Bluegrass Cover by Sparrow, shown on axis 3. Among ducks and Owls, Teals and Shovelers had the highest preference for Canopy and Surface Structure, Owls had the lowest, and Gadwalls and Mallards were intermediate. Differences among these species on axis 2 reflected relative preferences for bunchgrasses and the consequent increased SD Low Structure. Mallards had higher scores on axis 2 relative to Shovelers and Owls, and Gadwalls and Teals were intermediate. Increased preference for vertical structure above 20 cm isolated Mallards

Table 10. Comparisons of nest site (<50 cm around nest) characteristics between pairwise combinations of grassland birds in westcentral Montana in 1997. F-statistics and P-values show the significance of Mahalanobis distances between nest sites in discriminant space. Twenty of 21 pairs were significantly different at the $\alpha = 0.10$ level. For all tests, df = 6, 89.

Species	Cinnamon Teal		Gadwall		Mallard		Northern Shoveler		Short-eared Owl		Savannah Sparrow	
	F	P	F	P	F	P	F	P	F	P	F	P
Gadwall	2.5	0.030										
Mallard	3.5	0.0040	2.0	0.079								
Northern Shoveler	1.8	0.12	2.0	0.068	4.3	0.0007						
Short-eared Owl	5.2	0.0001	2.2	0.047	4.6	0.0004	4.0	0.0015				
Savannah Sparrow	9.6	<0.0001	16.9	<0.0001	17.5	<0.0001	8.3	<0.0001	22.0	<0.0001		
Western Meadowlark	6.3	<0.0001	10.7	<0.0001	11.8	<0.0001	7.1	<0.0001	17.9	<0.0001	2.8	0.014

from other ducks and Owls on axis 3. Teals were unique relative to other ducks and Owls

on axis 4 because of preference for increased Intermediate Structure in conjunction with

low preference for High Structure. Samples of ducks and Owls from 1997 plotted on the

1996 discriminant function (Fig. 1C) showed that relative preferences remained similar

between years.

Nest patches of bird species differed significantly only in Bunchgrass Cover in

1996 (Table A3). DFA included Bunchgrass Cover and (Fig. 2a) discriminated among

species (Λ = 0.83, χ^2 = 15.9, P = 0.0031) and the single axis discriminated between 6 of

10 pairs of species (Table 11). However, the 30% mean rate of correct classification

indicated almost complete overlap among species (Table 12). Mallard preferred nest

patches with increased Bunchgrass Cover and decreased Broadleaf Grass Cover relative to

Teal, Shoveler, and Owl; Gadwall preferred intermediate values. Species preferences at

nest patches differed only for Bluegrass Cover in 1997 (Table A4). However, DFA

Table 11. Comparisons of nest patch (10 m from nest) characteristics between pairwise combinations of grassland birds in westcentral Montana in 1996. F-statistics and P-values show the significance of Mahalanobis distances between nest patches in discriminant space. Six of 10 pairs were significantly different at the α = 0.10 level. For all tests, df = 1, 82.

	Species							
	Cinnamon Teal		Gadwall		Mallard		Northern Shoveler	
Species	F	P	F	P	F	P	F	P
Gadwall	2.9	0.093						
Mallard	8.0	0.0059	1.6	0.21				
Northern Shoveler	0.0	0.93	4.2	0.045	11.1	0.0013		
Short-eared Owl	0.3	0.56	4.2	0.045	8.8	0.0039	0.3	0.58
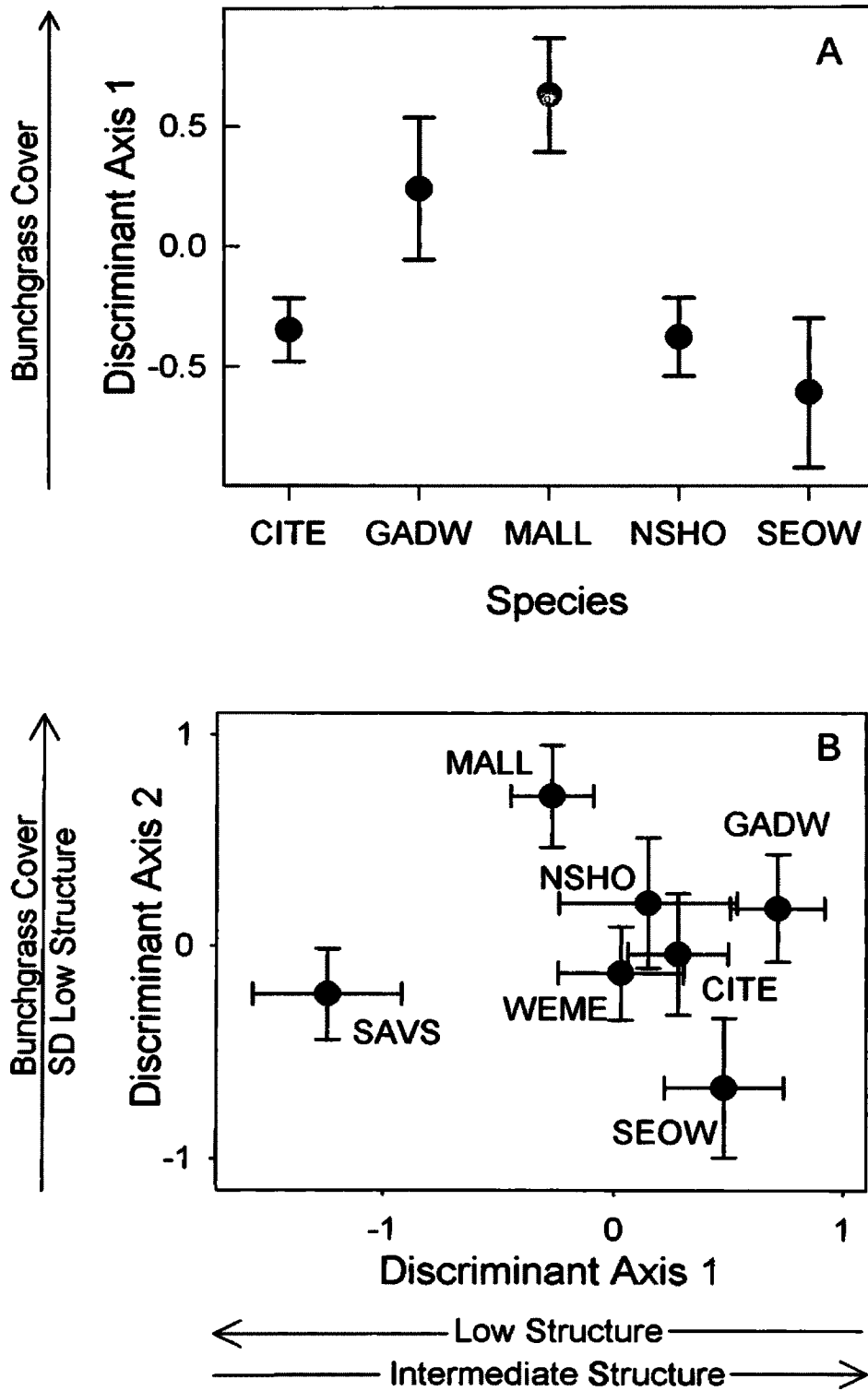
Figure 2. Discriminant function analysis of nest patches (10 m from nest) of grassland birds in westcentral Montana, 1996 (A) and 1997 (B). Variables most strongly correlated with each axis are shown with structure correlations. Vectors emphasize the direction of correlation. Centroids show the mean location on each axis with standard errors. Abbreviations: CITE=Cinnamon Teal, GADW=Gadwall, MALL=Mallard, NSHO=Northern Shoveler, SEOW=Short-eared Owl, SAVS=Savannah Sparrow, and WEME=Western Meadowlark.

Table 12. Rate of correct classification (%) of nest patches (10 m from nest) from Discriminant Function Analysis of grassland birds in 1996 and 1997 based on separate covariance matrices. Classification rates indicate the amount of overlap of each species with others.

Year	Mean	Species						
		Cinnamon Teal	Gadwall	Mallard	Northern Shoveler	Short-eared Owl	Savannah Sparrow[a]	Western Meadowlark[a]
1996	30[b]	71	0	62	0	38		
1997	45[c]	50	47	57	36	43	53	18

[a]Sampled only in 1997.
[b]13% reduction in error relative to correct classification expected by chance (20%).
[c]36% reduction in error relative to correct classification expected by chance (14%).

24

Table 13. Comparisons of nest patch (10 m from nest) characteristics between pairwise combinations of grassland birds in westcentral Montana in 1997. F-statistics and P-values show the significance of Mahalanobis distances between nest patches in discriminant space. Eight of 21 pairs were significantly different at the $\alpha = 0.10$ level; however, Savannah Sparrow nest patches accounted for 6 of the 8 significant differences. For all tests, df = 4, 88.

Species	Cinnamon Teal		Gadwall		Mallard		Northern Shoveler		Short-eared Owl		Savannah Sparrow	
	F	P	F	P	F	P	F	P	F	P	F	P
Gadwall	0.8	0.52										
Mallard	1.5	0.20	2.6	0.042								
Northern Shoveler	1.3	0.28	2.0	0.11	1.3	0.27						
Short-eared Owl	1.0	0.44	1.9	0.11	4.1	0.0038	1.7	0.15				
Savannah Sparrow	4.5	0.0022	8.3	<0.0001	3.4	0.012	4.4	0.0029	6.0	0.0003		
Western Meadowlark	0.8	0.51	1.0	0.40	1.7	0.17	1.4	0.26	1.3	0.26	2.9	0.027

included 4 variables (Fig. 2b) which significantly discriminated among species ($\Lambda = 0.53$, $P = 0.0001$). The first discriminant axis was highly significant ($\chi^2 = 58.9$, $P = 0.0001$), the second marginally significant ($\chi^2 = 25.2$, $P = 0.047$). These axes significantly discriminated between 8 of 21 pairs of species (Table 13), but separation of Sparrows from other species accounted for 6 of these differences. The 45% mean rate of correct classification indicated moderate overlap between species (Table 12). Low scores on axis 1 separated Sparrow from all other species. Sparrow preferred increased Low Structure but decreased Intermediate Structure, reflecting preference for dense but not tall patches. High scores on axis 2 indicated Mallard preferred patches with increased structural heterogeneity, reflected in increased Bunchgrass Cover and SD Low Structure, relative to Owl. Scores for other species were intermediate. Discrimination between species was much weaker at the scale of the nest patch relative to the scale of the nest site, and nest patch differences generally reflected nest site differences.

DISCUSSION

Nest Site Preferences

Vegetation characteristics at nest sites of all seven species showed little overlap with vegetation characteristics of available vegetation. Vegetation characteristics at nest sites should reflect preferences within available habitat, expressed primarily through nest placement and secondarily through manipulation of vegetation. Nonrandom selection of nest sites based on numerous microhabitat characteristics (e.g. vegetation structure, heterogeneity, floristics, relief, orientation of vegetation) has been demonstrated across

many systems (Peterson and Best 1985, Rodrigues 1994, Badyaev 1995, Martin 1998). However, studies of nesting grassland birds have generally focused on preferences for vegetation volume and broad floristic groups.

Mallards and Gadwalls often have been considered to prefer nest sites with tall, dense vegetation (Duebbert and Lokemoen 1976, Crabtree et al. 1989, Kruse and Bowen 1996): in our study, this pattern was reflected in preference for increased Volume at nest sites by Mallards and Gadwalls and preference for increased vertical structure above 20 cm by Mallards. Mallards and Gadwalls typically placed nests between clumps of bunchgrasses. This patchy growth form resulted in moderate Canopy and high SD Volume for Mallards and moderate Canopy and moderate SD Volume for Gadwalls. Mallards and Gadwalls have also shown high use of shrubs for nesting, suggesting that plants with clumped growth forms are attractive to these species (Kruse and Bowen 1996). Teals and Shovelers have been reported to prefer moderately tall grasses at nest sites (Livezey 1981, Kruse and Bowen 1996). Teals typically placed nests beneath overhanging grass and showed preference for high Canopy, increased SD Low Structure, and increased vertical structure from 0-40 cm, but decreased vertical structure above 40 cm. The preference for dense but not tall vegetation is consistent with studies showing higher use of grazed and hayed areas relative to other upland nesting ducks (Kirsch et al. 1978). Shovelers placed nests in Broadleaf grasses and manipulated leaves to form loose domes (Sowls 1955), resulting in high Canopy. Shovelers also showed preference for increased vertical structure above 40 cm and increased SD Surface Structure, but decreased SD Volume. Previous observations of Owl nests have suggested a preference

for sites with tall grasses (Kantrud and Higgins 1992). In our study, Owls typically selected nest sites with low canopy cover adjacent to a large tuft of broadleaf grasses. Increased vertical structure was preferred at 20-40 cm, but nest sites had relatively little structure near the ground apart from the tuft, resulting in increased SD Volume.

Sparrows often place nests under grass tufts with a tunnel entrance, but nests in dense cover may be simple open cups (Wheelwright and Rising 1993). Sparrows typically placed open cup nests in Kentucky Bluegrass with increased Volume. The numerous basal leaves of Kentucky Bluegrass provided extreme high Canopy and abundant, uniform vertical structure below 20 cm. Meadowlarks often construct domed nests in grass of moderate volume with low variation in volume (Lanyon 1994, Granfors et al. 1996). I found that Meadowlarks preferred nest sites with increased vertical structure below 20 cm, and nests typically adjoined a small tuft of grass, which increased SD Low Structure but not SD Volume. Meadowlarks constructed nearly complete domes over nests, resulting in almost complete Canopy.

Studies of bird habitat preferences have commonly related habitat use to vegetation structure (Anderson and Shugart 1974, Whitmore 1975, Rotenberry and Wiens 1980). However, because vegetation structure is largely derived from plant growth form, preferences for floristics may be driving apparent preferences for vegetation structure (Wiens and Rotenberry 1981, Rice et al. 1984, Rotenberry 1985). I observed that plant growth form did not dictate vegetation structure at nests. For example, both Shovelers and Owls preferred Broadleaf grasses, but Owls placed nests next to tufts of residual grass, resulting in higher SD Volume than at Shoveler nests. Shovelers actively

constructed domes over nests, resulted in much higher Canopy than at Owl nests. In addition to plant growth form, vegetation structure at nest sites was influenced largely by placement of the nest in vegetation and partly by manipulation of vegetation.

Birds in many systems have demonstrated nonrandom selection of nest patches (Martin and Roper 1988, Knopf and Sedgwick 1994, Badyaev 1995). However, I found little preference for vegetation characteristics at the scale of the nest patch, and I conclude that the primary nest vegetation preferences occurring among these 7 species in ungrazed, seeded grass cover occurred at a scale <10 m around the nest site. Because preferences at nest sites often reflected placement relative to vegetation immediately around the nest or manipulation of vegetation over the nest, selection appeared to be most strongly influenced by vegetation in a diameter <50 cm around the nest.

Differences in Preferences Among Species

Species showed strong segregation of preferences for vegetation characteristics at nest sites. Species with similar preferences for one vegetation characteristic usually differed in preferences for others. Because of differences in species and variables included, the DFA models I constructed in each year can not be directly compared. However, comparisons of locations of 1996 and1997 samples in 1996 discriminant space show that although preferences changed somewhat between years, the relative preferences of ducks and Owls were consistent. In addition, the first two discriminant axes derived from the 1996 and 1997 data sets were biologically similar. Canopy was strongly correlated in both years with the first discriminant axis, the most important in

discriminating among species. In both years, Canopy increased with decreasing body size, with the exception of the Owls. The second discriminant axis in each year was correlated positively with Bunchgrass Cover and described a gradient of increasing variation in vegetation structure. The negative correlation of Broadleaf Grass Cover in 1996 showed decreasing preference for plant species with more uniform structure, and the positive correlation of SD Low Structure in 1997 quantitatively reflected the increase in patchiness of structure due to the "clumped" growth form of bunchgrasses. Measures of vertical structure showed these species differed in preferences for vegetation at different heights above the ground. In particular, preference for Surface Structure increased with decreasing body size. I found that Volume, which has been the primary vegetation characteristic used to compare nest sites of grassland species (especially ducks) (Kantrud and Higgins 1992, Gilbert et al. 1995, Kruse and Bowen 1996) contributed relatively little to segregating among these species.

Partitioning of resources has seemed to be largely absent in grassland systems. In forested systems, competition for food has traditionally been invoked as the process driving partitioning of vegetation and, ultimately, community structure (MacArthur and MacArthur 1961, James 1971, Willson 1974). In prairie ecosystems, coexisting species show wide overlap in food resources and foraging habitat, food resources are not limiting in most years, and competition for food does not appear to drive community structure (Wiens 1973, Wiens 1977, Rotenberry and Wiens 1980, Wiens and Rotenberry 1980, Dubowy 1988). However, nest sites are also a resource that can influence habitat selection and community structure. Partitioning of habitat selected for nesting based on

vegetation characteristics has been demonstrated in forested systems (Martin 1998). In many systems the availability of or competition for suitable nest sites has a strong role in determining patterns of occupancy and community structure (Parker 1985, Arnold and Higgins 1986, Martin 1988, Martin 1993). Given the broad overlap in foraging preferences among species (and because many waterfowl forage in wetlands rather than grasslands), I suggest that differences in nest site preferences may play an important role in determining habitat occupancy and hence community structure in grasslands.

Potential Adaptive Significance of Preferences at Nest Sites

Because reproductive success directly influences fitness, natural selection should favor choices of nest sites that minimize reproductive failure (Martin 1993). Extreme nest microclimates can stress adults and young, and birds appear to place nests in vegetation to moderate nest microclimate (Walsberg 1985, Gloutney and Clark 1997). Orientation of increased Volume to the NW or SW relative to the SE by ducks and Owls may facilitate heat gain in the morning but provide shading against excessive insolation in the afternoon (Peterson and Best 1985, Facemire et al. 1990, With and Webb 1993). Orientation of Volume also may minimize convective heat loss during cold periods by sheltering nests (Cannings and Threlfall 1981, Sakai and Noon 1991) from prevailing westerly winds. Because overhead cover may provide shading from mid-day sun and protection radiative heat loss at night and because smaller birds are more subject to thermal stress, the trend of increasing Canopy with decreasing body size suggests that Canopy may become increasingly important in thermal regulation with decreasing body size.

Nest predation is the primary cause of nest failure in grasslands (Ricklefs 1969) and hence should exert strong selective pressure on nest site preferences. If increases in concealment of nests by vegetation, vegetation density, or vegetation heterogeneity cause decreased nest predation (Schrank 1972, Bowman and Harris 1980, Crabtree et al. 1989, Clark and Nudds 1991), I would expect species with similar suites of nest predators to converge on similar nest sites. However, nests sites of each species in this study were usually unique. Differences among species could be related to different microclimate needs, foraging needs, or differences in predation pressures; however, the closely related dabbling ducks have similar life histories, nest microclimates, and predator communities. Density dependent nest predation has been shown to drive partitioning of nest site characteristics among species in a forested system (Martin 1988, Martin 1993). For nests that are closely spaced or have similar characteristics, predators may concentrate search efforts where nests have already been found or develop search images for common nest types (Goransson et al. 1975, Dunn 1977, Knapton 1979, Sugden and Beyersbergen 1986, Martin 1993). Therefore, coexisting species would be expected to diverge in nest site preferences and nest initiation dates.

Management Implications

Management of grasslands has focused on providing tall, high volume, monotypic vegetation for upland nesting ducks (Higgins and Barker 1982), either by limiting disturbance on existing managed grasslands or through restoration programs for wildlife management (e.g. Waterfowl Production Areas) or for limiting crop surpluses and soil

erosion (e.g., Conservation Reserve Program) involving seeding of DNC (Kirby et al. 1992, Hartley 1994, Gilbert et al 1995). Typically, DNC has been composed of forage plant species that are relatively easy and inexpensive to establish and that produce tall, high volume stands (Reynolds et al. 1994, Patterson and Best 1996).

However, I observed strong preferences at nest sites for a wide variety of vegetation characteristics rather than just height and volume. Knowledge of preferred vegetation characteristics allows managers to provide attractive nesting habitat for species that are habitat limited or can benefit from managed vegetation. For species attracted to "ecological traps" (e.g. habitats such as cropland and hayland which attract breeding birds but result in poor reproduction and survival), knowledge of preferences should allow managers to provide vegetation that more effectively "competes" for breeding birds (Best 1986). Furthermore, increasing concerns for a broad spectrum of species highlights the need to manage habitat in ways that are mutually beneficial to a diversity of species (Ball et al. 1994, Tome et al. 1994). The distinct segregation of preferences at nest sites among species suggests that providing a wider diversity of vegetation characteristics within managed stands of vegetation can allow a wider diversity of bird species to utilize the vegetation for nesting (Tome et al. 1994). Because preferences involved relatively small areas around the nest site, diversity of vegetation characteristics at a relatively fine scale could provide suitable nesting habitat for multiple species within a single field, probably without detriment to other species.

Desired vegetation characteristics can be achieved by altering floristics or by directly manipulating vegetation structure. Because breeding birds respond to plant

growth form and because growth forms are the primary determinant of fine scale heterogeneity, plant species for restoration should be chosen in part based on desired growth form (Patterson and Best 1996). A 'landscaping approach"of seeding distinct mixtures of plant species in relation to topography would create microhabitats with distinct vegetation characteristics and could more closely mimic natural prairie vegetation zones (Tome et al. 1994). Disturbances (e.g. grazing, burning) have been shown to have dissimilar, but interacting, effects on plant species composition and diversity (Collins and Barber 1986, Collins 1987, Collins 1992, Biondini et al. 1998). Disturbance regimes (e.g. frequency and intensity of grazing, burning, and haying) can also be used to directly alter vegetation structure. Although grazing, burning, and haying are known to cause short term reductions in vegetation volume and litter cover (Collins 1987, Bowen and Kruse 1993, Kruse and Bowen 1996, Biondini et al. 1998), their effects on vegetation characteristics such as vertical structure and variation in structure have not been documented.

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Table A1. Mean vegetation characteristics (with standard error) and univariate F-statistics for nest sites (< 50 cm around nest) of 5 grassland birds in westcentral Montana, 1996 . All variables except Canopy show the difference of nest sites from available habitat. Variables are ordered from highest to lowest by univariate F-statistic.

Species	Canopy		Bunchgrass Cover		Broadleaf Grass Cover		SD Volume		Bluegrass Cover		Volume	
Cinnamon Teal	73	(4.8)	-8	(4.8)	38	(10.4)	0.15	(0.17)	9	(6.3)	2.5	(2.8)
Gadwall	37	(5.7)	23	(12.1)	11	(9.1)	0.12	(0.12)	-5	(2.1)	14.3	(4.4)
Mallard	33	(4.6)	34	(9.3)	2	(6.3)	0.30	(0.14)	-10	(2.8)	15.0	(2.3)
Northern Shoveler	65	(2.8)	-15	(7.3)	45	(7.9)	-0.32	(0.12)	-6	(4.2)	6.2	(3.1)
Short-eared Owl	8	(4.4)	-20	(12.3)	18	(10.7)	0.52	(0.41)	-5	(2.3)	15.8	(5.1)
F	22.9		6.1		5.0		3.5		2.9		2.5	
P value[a]	<0.0001		0.0013		0.0048		0.030		0.055		0.045	

[a] P values corrected for multiple comparisons using a sequential Bonferroni procedure (Rice 1989) to maintain an experimentwise Type I error rate of 10%; df = 1,4 for all tests.

APPENDIX A

42

Table A2. Mean vegetation characteristics (with standard error) and univariate F-statistics for nest sites (< 50cm around nest) of 7 grassland birds in westcentral Montana, 1997. All variables except Canopy show the difference of nest sites from available habitat. Variables are ordered from highest to lowest by univariate F-statistic.

Species	Canopy	Surface Structure	Bluegrass Cover	SD Low Structure	Bunchgrass Cover	High Structure	Low Structure	SD Volume	Volume	SD Surface Structure	Intermediate Structure	Broadleaf Grass Cover
Cinnamon Teal	58 (7.9)	0.7 (1.0)	-8 (4.9)	0.11 (0.03)	19 (12)	0.5 (0.41)	2.7 (0.63)	0.01 (0.14)	11.5 (2.2)	0.04 (0.04)	2.6 (0.60)	19 (9.3)
Gadwall	33 (6.3)	-1.2 (1.0)	-15 (5.9)	0.09 (0.03)	23 (11)	0.6 (0.39)	0.6 (0.72)	0.15 (0.19)	4.4 (2.4)	0.10 (0.04)	0.4 (0.82)	7 (6.7)
Mallard	45 (7.9)	-1.7 (0.8)	-1 (4.4)	0.16 (0.06)	46 (8)	2.2 (0.65)	1.2 (0.42)	0.47 (0.23)	8.7 (2.4)	0.15 (0.05)	2.2 (0.71)	-16 (8.3)
Northern Shoveler	46 (6.1)	-0.4 (1.2)	-13 (8.6)	-0.06 (0.05)	13 (8)	0.6 (0.18)	1.1 (0.78)	-0.13 (0.10)	7.4 (2.6)	0.14 (0.05)	1.2 (0.82)	21 (9.4)
Short-eared Owl	13 (3.3)	-2.6 (0.7)	-9 (5.9)	0.03 (0.05)	2 (12)	0.4 (0.37)	0.1 (0.58)	0.40 (0.19)	2.4 (2.1)	0.03 (0.05)	1.5 (0.41)	21 (9.5)
Savannah Sparrow	84 (4.2)	4.1 (1.0)	35 (9.2)	-0.05 (0.02)	-14 (5)	0.5 (0.38)	2.9 (0.64)	-0.18 (0.13)	9.0 (2.7)	-0.03 (0.03)	2.3 (0.57)	15 (10.5)
Western Meadowlark	87 (4.2)	3.9 (1.1)	16 (8.7)	0.11 (0.03)	-1 (8)	-0.1 (0.23)	1.8 (0.52)	-0.28 (0.12)	-0.3 (2.6)	0.03 (0.04)	0.3 (0.35)	17 (11.3)
F	20.6	7.6	7.2	4.9	4.7	3.0	2.9	2.8	2.7	2.6	2.1	1.9
P value[a]	<0.0001	<0.0001	<0.0001	0.0020	0.0028	0.077	0.072	0.073	0.068	0.066	0.13	0.19

[a] P values corrected for multiple comparisons using a sequential Bonferroni procedure (Rice 1989) to maintain an experimentwise Type I error rate of 10%; df = 1,6 for all tests.

43

Table A3. Mean vegetation characteristics (with standard error) and univariate F-statistics for nest patches (10 m from nest) of 5 grassland birds in westcentral Montana, 1996. All variables show the difference of nest patches from available habitat. Variables are ordered from highest to lowest by univariate F-statistic.

Species	Variable									
	Bunchgrass Cover		SD Volume		Bluegrass Cover		Broadleaf Grass Cover		Volume	
Cinnamon Teal	-14	(4.8)	0.36	(0.20)	5	(5.4)	24	(7.4)	3.4	(2.6)
Gadwall	7	(10.8)	-0.18	(0.15)	-2	(3.4)	13	(9.0)	4.6	(2.8)
Mallard	21	(8.6)	0.34	(0.16)	-9	(2.3)	4	(8.4)	1.2	(2.9)
Northern Shoveler	-15	(6.0)	-0.05	(0.15)	1	(4.0)	17	(6.6)	2.7	(2.4)
Short-eared Owl	-24	(11.3)	-0.12	(0.26)	0	(2.6)	19	(11.2)	6.8	(3.7)
F	4.3		2.2		1.8		0.8		0.4	
P value[a]	0.016		0.31		0.54		1.0		1.0	

[a]P values corrected for multiple comparisons using a sequential Bonferroni procedure (Rice 1989) to maintain an experimentwise Type I error rate of 10%; df = 1,4 for all tests.

44

Table A4. Mean vegetation characteristics (with standard error) and univariate F-statistics for nest patches (10 m from nest) of 7 grassland birds in westcentral Montana, 1997. All variables show the difference of nest sites from available habitat. Variables are ordered from highest to lowest by univariate F-statistic.

Species		Variable																				
	Bluegrass Cover		Low Structure		Bunchgrass Cover		SD Low Structure		Broadleaf Grass Cover		Volume		SD Volume		Intermediate Structure		High Structure		SD Surface Structure		Surface Structure	
Cinnamon Teal	-4	(5.2)	0.7	(0.38)	1	(7.0)	0.01	(0.03)	10	(8.2)	4.6	(1.8)	0.30	(0.19)	0.5	(0.33)	0.3	(0.19)	-0.05	(0.04)	-0.3	(1.0)
Gadwall	-5	(8.1)	0.0	(0.55)	7	(7.7)	0.08	(0.04)	-1	(4.9)	2.1	(2.3)	0.16	(0.15)	0.0	(0.50)	0.3	(0.50)	0.02	(0.05)	0.4	(1.1)
Mallard	-3	(5.5)	1.4	(0.58)	17	(8.3)	0.03	(0.03)	-10	(7.1)	4.3	(2.1)	-0.07	(0.18)	0.1	(0.52)	0.1	(0.20)	0.03	(0.03)	1.0	(0.7)
Northern Shoveler	-7	(4.6)	-0.1	(0.46)	18	(8.7)	-0.04	(0.04)	-12	(11.2)	-2.8	(1.9)	-0.10	(0.19)	-0.3	(0.51)	-0.4	(0.23)	0.07	(0.05)	0.7	(1.1)
Short-eared Owl	1	(5.7)	-0.4	(0.48)	-9	(9.6)	-0.06	(0.05)	13	(10.1)	1.1	(1.8)	0.12	(0.15	0.1	(0.25)	0.0	(0.10)	0.01	(0.05)	-0.5	(0.9)
Savannah Sparrow	26	(7.4)	1.8	(0.52)	-15	(6.1)	-0.08	(0.03)	16	(8.8)	4.8	(2.1)	-0.11	(0.13)	-0.4	(0.33)	0.1	(0.32)	-0.02	(0.03)	0.0	(0.8)
Western Meadowlark	10	(5.7)	0.1	(0.56)	-6	(10.3)	0.01	(0.04)	1	(9.9)	-0.1	(1.6)	-0.13	(0.19)	-0.7	(0.40)	-0.3	(0.24)	0.01	(0.06)	-1.4	(1.3)
F	3.6		2.8		2.5		2.3		1.7		1.3		0.8		0.8		0.7		0.7		0.6	
P value[a]	0.036		0.16		0.30		0.40		1.0		1.0		1.0		1.0		1.0		1.0		1.0	

[a] P values corrected for multiple comparisons using a sequential Bonferroni procedure (Rice 1989) to maintain an experimentwise Type I error rate of 10%; df = 1,6 for all tests.

45

APPENDIX B

To examine how nest habitat differed from similar available habitat, I compared vegetation measurements at nest plots to nearby paired plots. One paired plot was located 25 m in a randomly selected intercardinal direction from each nest plot. From each plot center, sampling transects were extended in the cardinal directions, with sampling points along each transect at 0, 1, 5, and 10 m. At each sampling point, I took vegetation measurements as described in the Methods. For each distance, I created difference variables by subtracting the mean of the paired plots from the nest plots. These difference variables allow finer resolution for assessing the scale involved in selection of nest habitat.

Table B1. Mean vegetation characteristics relative to nearby available habitat (with standard error) for nest habitat of 5 grassland birds in westcentral Montana, 1996. Variables show mean values for paired plots subtracted from nest plots at each distance from the plot center.

Species	Distance	Volume	SD Volume	Bunchgrass Cover	Broadleaf Grass Cover	Bluegrass Cover
Cinnamon Teal n = 14 nests	0 m	-4.1 (2.8)	0.02 (0.19)	-2.5 (7.7)	20.2 (11.3)	4.3 (3.8)
	1 m	-4.4 (2.5)	0.06 (0.14)	-2.1 (3.6)	-3.6 (7.8)	-1.4 (3.1)
	5 m	-1.6 (2.8)	0.21 (0.16)	-0.5 (4.0)	2.9 (7.7)	0.2 (3.2)
	10 m	-0.8 (2.0)	-0.03 (0.20)	-7.8 (4.5)	2.5 (8.5)	-0.5 (6.3)
Gadwall n = 22 nests	0 m	9.7 (3.4)	0.18 (0.18)	21.7 (7.0)	-4.3 (7.7)	-2.8 (1.2)
	1 m	5.3 (2.6)	0.11 (0.09)	-0.3 (4.8)	12.4 (5.2)	-0.9 (1.1)
	5 m	4.0 (1.9)	0.05 (0.15)	-4.2 (7.0)	10.3 (4.4)	5.5 (4.3)
	10 m	0.9 (1.0)	-0.01 (0.16)	4.3 (6.4)	13.0 (5.6)	2.2 (3.8)
Mallard n = 21 nests	0 m	11.2 (2.8)	0.17 (0.18)	25.4 (6.7)	-0.6 (5.4)	-3.5 (1.4)
	1 m	7.0 (2.7)	0.15 (0.12)	19.9 (6.0)	3.5 (5.6)	-3.3 (1.8)
	5 m	3.5 (1.7)	0.08 (0.20)	4.2 (4.8)	3.7 (4.8)	-0.2 (1.9)
	10 m	-1.1 (1.7)	-0.15 (0.14)	12.4 (6.5)	2.9 (6.5)	-2.9 (2.9)

Table B1 Continued. Mean vegetation characteristics relative to nearby available habitat (with standard error) for nest habitat of 5 grassland birds in westcentral Montana, 1996. Variables show mean values for paired plots subtracted from nest plots at each distance from the plot center.

Species	Distance	Variable									
		Volume		SD Volume		Bunchgrass Cover		Broadleaf Grass Cover		Bluegrass Cover	
Northern Shoveler *n* = 14 nests	0 m	2.4	(1.9)	-0.12	(0.12)	-0.4	(2.6)	27.4	(6.9)	-5.4	(2.7)
	1 m	0.6	(1.7)	0.35	(0.18)	-1.2	(1.9)	8.5	(5.4)	-2.1	(2.5)
	5 m	1.0	(1.7)	0.11	(0.19)	-2.9	(5.4)	2.7	(6.2)	-5.3	(4.5)
	10 m	-1.4	(1.4)	-0.11	(0.14)	-2.1	(4.2)	-3.4	(6.4)	0.5	(2.3)
Short-eared Owl *n* = 21 nests	0 m	11.6	(3.7)	0.80	(0.33)	5.3	(8.0)	14.1	(9.0)	-4.1	(2.4)
	1 m	5.9	(1.0)	0.10	(0.18)	-7.2	(3.5)	13.4	(7.5)	0.0	(3.7)
	5 m	2.6	(2.9)	-0.07	(0.19)	1.3	(8.1)	1.9	(4.7)	5.9	(5.4)
	10 m	5.7	(1.8)	-0.20	(0.17)	-2.2	(1.9)	9.7	(13.3)	-2.5	(1.5)

Table B2. Mean vegetation characteristics relative to nearby available habitat (with standard error) for nest habitat of 7 grassland birds in westcentral Montana, 1997. Variables show mean values for paired plots subtracted from nest plots at each distance from the plot center.

Species	Distance	Volume	Surface Structure	Low Structure	Intermediate Structure	High Structure	SD Volume	SD Surface Structure	SD Low Structure	Bunchgrass Cover	Broadleaf Grass Cover	Bluegrass Cover
Cinnamon Teal n = 15 nests	0 m	1.9 (3.5)	-0.7 (1.4)	1.7 (0.5)	1.8 (0.5)	0.4 (0.4)	-0.16 (0.16)	0.03 (0.02)	0.08 (0.05)	20.3 (6.7)	3.3 (7.6)	-3.0 (2.8)
	1 m	-1.7 (2.7)	0.6 (0.7)	0.5 (0.5)	0.9 (0.6)	0.2 (0.3)	0.00 (0.13)	-0.02 (0.02)	0.02 (0.04)	4.3 (5.8)	-2.5 (7.3)	-3.0 (2.7)
	5 m	0.2 (2.1)	0.0 (0.6)	0.5 (0.4)	0.4 (0.2)	0.0 (0.2)	0.00 (0.24)	-0.01 (0.04)	0.01 (0.04)	4.2 (6.1)	1.7 (8.1)	-1.7 (4.4)
	10 m	-1.6 (2.3)	-0.8 (0.9)	0.2 (0.3)	0.2 (0.3)	0.3 (0.4)	0.01 (0.18)	0.01 (0.04)	0.02 (0.03)	-3.3 (8.3)	1.7 (10.8)	-2.3 (5.6)
Gadwall n = 17 nests	0 m	-1.0 (1.8)	-3.0 (0.6)	0.1 (0.7)	0.9 (0.8)	0.3 (0.6)	0.30 (0.13)	0.10 (0.04)	0.04 (0.04)	12.1 (8.1)	8.7 (5.9)	-6.0 (4.2)
	1 m	2.8 (1.3)	-0.4 (0.8)	0.2 (0.3)	1.2 (0.4)	0.5 (0.3)	0.14 (0.15)	0.06 (0.03)	0.06 (0.04)	8.4 (6.0)	4.9 (4.2)	-0.1 (1.2)
	5 m	2.4 (1.8)	-1.4 (0.5)	0.0 (0.3)	-0.2 (0.5)	-0.3 (0.3)	0.08 (0.13)	0.01 (0.02)	-0.03 (0.04)	0.8 (4.5)	4.6 (5.5)	-0.6 (3.7)
	10 m	0.2 (1.7)	-0.3 (0.7)	0.2 (0.4)	0.3 (0.4)	0.5 (0.5)	-0.01 (0.11)	0.04 (0.03)	0.03 (0.04)	-0.6 (8.1)	0.3 (8.9)	0.1 (3.3)
Mallard n = 14 nests	0 m	4.6 (1.9)	-1.4 (0.8)	1.1 (0.6)	1.5 (0.8)	1.8 (0.5)	0.49 (0.25)	0.14 (0.05)	0.15 (0.05)	31.6 (8.8)	-7.5 (5.9)	-4.6 (4.5)
	1 m	-0.1 (2.3)	1.3 (0.8)	0.2 (0.3)	0.4 (0.4)	0.2 (0.2)	0.12 (0.18)	0.00 (0.05)	0.03 (0.03)	19.1 (6.7)	-6.8 (3.7)	-2.0 (4.1)
	5 m	-1.4 (1.4)	-0.4 (0.5)	-0.2 (0.5)	-0.5 (0.4)	-0.1 (0.1)	-0.07 (0.09)	0.08 (0.04)	0.02 (0.04)	10.7 (8.6)	-14.3 (5.8)	-1.1 (2.2)
	10 m	-0.9 (1.3)	-0.2 (0.7)	0.6 (0.5)	-0.3 (0.4)	1.6 (0.6)	-0.28 (0.14)	-0.06 (0.03)	0.01 (0.04)	-4.3 (9.6)	-2.3 (5.0)	0.2 (3.3)
Northern Shoveler n = 12 nests	0 m	3.8 (4.7)	0.7 (0.9)	1.9 (0.5)	1.8 (0.5)	0.3 (0.2)	-0.67 (0.48)	0.07 (0.03)	-0.01 (0.04)	8.3 (9.5)	28.5 (6.8)	-7.5 (4.9)
	1 m	5.0 (1.9)	2.9 (1.1)	1.5 (0.3)	1.1 (0.4)	-0.2 (0.2)	0.20 (0.21)	0.01 (0.03)	0.11 (0.03)	9.0 (9.1)	4.8 (6.2)	-3.1 (3.0)
	5 m	0.6 (1.8)	0.0 (0.7)	-0.2 (0.5)	0.3 (0.5)	0.0 (0.1)	-0.30 (0.22)	0.04 (0.03)	-0.03 (0.06)	11.4 (8.2)	-12.3 (6.0)	-6.0 (6.0)
	10 m	-0.2 (1.3)	0.0 (1.1)	-0.4 (0.6)	-0.7 (0.7)	-0.1 (0.3)	-0.14 (0.21)	-0.3 (0.05)	-0.06 (0.04)	10.0 (11.3)	-8.8 (7.9)	-4.3 (8.9)

Table B2 Continued. Mean vegetation characteristics relative to nearby available habitat (with standard error) for nest habitat of 7 grassland birds in westcentral Montana, 1997. Variables show mean values for paired plots subtracted from nest plots at each distance from the plot center.

Species	Distance	Volume		Surface Structure		Low Structure		Intermediate Structure		High Structure		SD Volume		SD Surface Structure		SD Low Structure		Bunchgrass Cover		Broadleaf Grass Cover		Bluegrass Cover	
Short-eared Owl	0 m	4.8	(1.7)	-0.6	(0.5)	0.5	(0.4)	1.9	(0.5)	0.8	(0.3)	0.44	(0.17)	0.06	(0.05)	0.08	(0.04)	3.0	(6.1)	11.1	(5.7)	-7.5	(5.6)
n = 14	1 m	0.6	(1.1)	-1.1	(0.8)	-0.5	(0.3)	0.0	(0.2)	0.2	(0.1)	-0.01	(0.13)	-0.07	(0.03)	0.02	(0.04)	-6.3	(4.7)	7.3	(4.3)	-4.1	(2.4)
	5 m	-0.9	(0.9)	-0.9	(0.7)	-0.6	(0.2)	-0.3	(0.3)	-0.2	(0.1)	-0.17	(0.12)	-0.04	(0.06)	-0.04	(0.03)	0.5	(5.6)	4.3	(7.1)	-3.4	(4.1)
	10 m	0.4	(0.5)	-0.3	(0.4)	0.0	(0.2)	0.0	(0.3)	0.6	(0.3)	0.00	(0.13)	-0.03	(0.03)	-0.04	(0.03)	-4.3	(3.9)	5.0	(6.2)	-0.5	(3.1)
Savannah Sparrow	0 m	2.7	(1.9)	3.6	(0.6)	1.5	(0.5)	1.2	(0.6)	-0.2	(0.4)	0.13	(0.08)	0.00	(0.03)	-0.08	(0.03)	-2.1	(2.1)	4.2	(7.5)	11.3	(4.5)
n = 18	1 m	-1.2	(1.7)	0.6	(0.5)	0.2	(0.3)	-0.2	(0.5)	-0.3	(0.3)	-0.14	(0.14)	0.00	(0.03)	0.02	(0.03)	-2.6	(2.6)	1.3	(6.2)	7.6	(6.2)
	5 m	-0.6	(1.1)	0.4	(0.5)	0.1	(0.4)	0.2	(0.3)	-0.2	(0.3)	0.06	(0.14)	0.00	(0.03)	0.00	(0.04)	-0.1	(0.1)	-3.8	(5.9)	6.5	(5.8)
	10 m	-1.0	(1.1)	0.3	(0.5)	0.5	(0.3)	-0.8	(0.4)	0.2	(0.3)	0.04	(0.09)	0.00	(0.02)	-0.09	(0.04)	2.1	(2.1)	5.3	(5.2)	-0.6	(6.1)
Western Meadowlark	0 m	3.4	(2.2)	2.9	(1.2)	1.5	(0.7)	0.8	(0.5)	0.0	(0.4)	-0.10	(0.11)	0.06	(0.03)	0.09	(0.05)	9.4	(3.3)	19.2	(8.8)	1.3	(8.0)
n = 12	1 m	-1.0	(1.0)	-1.3	(0.7)	-0.4	(0.3)	-0.5	(0.4)	0.0	(0.2)	0.03	(0.11)	0.02	(0.04)	-0.04	(0.03)	3.3	(2.1)	8.5	(7.2)	2.7	(9.5)
	5 m	-0.5	(1.6)	-1.6	(0.9)	0.0	(0.5)	0.3	(0.3)	0.0	(0.1)	0.10	(0.19)	-0.02	(0.05)	-0.01	(0.03)	4.1	(4.0)	3.9	(9.3)	9.8	(7.2)
	10 m	1.7	(1.0)	-1.0	(0.6)	-0.1	(0.3)	-0.2	(0.3)	0.1	(0.2)	0.02	(0.20)	-0.01	(0.06)	0.01	(0.05)	0.7	(7.0)	3.4	(9.1)	-1.6	(6.5)

49