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Nest habitat selection by grassland birds in the northern Great Plains

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Summary

Effective conservation of bird populations requires a detailed understanding of the relationships between habitat conditions and density and productivity. Ideally, studies of habitat requirements should be integrated into a standardized system such that comparisons among species or among sites are not confounded by different sampling approaches. Here, I discuss the use of the standardized Breeding Bird Research and Monitoring Database (BBIRD) habitat sampling protocol as a method for describing nest site use of grassland birds. In general, the BBIRD protocol was effective in describing interspecific variation in nest site use, although I was only able to identify non-random nest site selection for two species. Furthermore, I was unable to identify features of the nest site that correlated with reproductive success. This is the most problematic finding, as information on the habitat conditions that promote reproductive success are sorely lacking for grassland systems. I suggest a number of reasons why successful and depredated nests may have similar vegetation structure, including potentially overwhelming processes operating at larger spatial scales. In addition, I identify a number of ways in which this protocol can be streamlined so that it may gain broader acceptance among researchers and managers, and suggest that further thought be given to identifying additional habitat variables that may be better predictors of reproductive success.

Introduction

Effective conservation of bird populations requires a detailed understanding of the relationships between habitat conditions and density and productivity of the species of interest. However, because management for one species invariably affects co-existing species, any comprehensive conservation effort requires information about the habitat needs of multiple species. Ideally, studies of habitat requirements would be integrated into a standardized system such that comparisons among species or among sites are not confounded by different sampling approaches. In forested habitats, the Breeding Biology Research and Monitoring Database (BBIRD) program has provided a successful model for using an integrated approach to understanding habitat needs of multiple species at multiple scales. A similar protocol exists for grassland environments, but has been used infrequently (e.g., Logan 2001). The need for information on habitat requirements is especially pressing in grasslands: most grassland-breeding bird species are experiencing significant population declines (Sauer and Link 2002), yet we know little of the habitat conditions that attract desired species and promote self-sustaining populations.

Here, I report on the use of the BBIRD grassland protocol to describe patterns of nest site selection for a suite of grassland birds at two sites: Lostwood National Wildlife Refuge, North Dakota and Medicine Lake National Wildlife Refuge, Montana. In particular, I address four main objectives: first, to describe nest site use for a variety of species at both sites; second, to determine if species show non-random use of particular habitat features when choosing a nest site; third, to determine if habitat features selected by individuals are associated with increased reproductive success; and fourth, to examine the efficacy of

the BBIRD protocol as a standardized system for measuring habitat use of grassland birds.

Study area

Medicine Lake National Wildlife Refuge is located on the glaciated plains north of the Missouri River in eastern Montana and consists of approximately 8100 ha of terrestrial habitats, including native mixed-grass prairie (dominant species include *Stipa* spp., *Agropyron smithii*, *Koeleria cristata*, and *Bouteloua gracilis*), monocultures of *Agropyron cristatum*, hayfields, small agricultural fields, and a variety of seasonal and permanent wetlands surrounding a large (c.a. 3200 ha) freshwater lake.

Lostwood National Wildlife Refuge is located approximately 110 miles west of Medicine Lake in northwestern North Dakota and is characterized by a pronounced knob-and-kettle topography. The Refuge covers approximately 10,900 ha and contains numerous small wetland basins, clumps of aspen (*Populus tremuloides*), native prairie (dominant genera are *Stipa* and *Agropyron*), old agricultural fields dominated by exotic grasses (notably *Bromus inermis* and *Poa pratensis*), and stands of large shrubs, mostly *Symphoricarpos occidentalis*.

Methods

Nest searching. – Nest searching was conducted on 9 plots at Lostwood and 13 plots at Medicine Lake during 1999-2002. Plot size ranged from 12-25 ha. I located nests using both systematic searches and, in the case of passerines, behavioral observations of adult

birds. During systematic searches, we flushed adults off of the nest by dragging a weighted rope across the plot. Each plot was searched systematically at least 3 times between early May and late June of each year, but I continued to locate nests until late July using behavioral observations. I marked the location of each nest with 1 or 2 small pieces of flagging placed 1-2 m from the nest cup. To determine the fate of nests we returned every 2-3 days in the case of passerines, or every 4-6 days for shorebirds and ducks, to inspect the contents of the nest. When hatching or fledging was expected I visited daily or every other day. Nests were considered successful if at least 1 young fledged.

Habitat measurements. – I collected data on nest-site selection within a habitat using the standardized BBIRD protocol (Martin et al. 1997). All vegetation sampling was conducted within 1 week of the day that the nesting attempt terminated. Along 4 perpendicular 5 m transects radiating in cardinal directions out from the nest, I measured the following variables at 5 points (0.01 m, 0.25 m, 1 m, 3 m, and 5 m from the edge of the nest) along each transect: litter depth; aboveground volume of vegetation, measured by the height of visual obstruction (dm) of vegetation against a wooden pole (Robel et al. 1970); and the vertical structure of the vegetation, measured by the number of contacts made by vegetation at different heights against a 60 cm metal rod held perpendicular to the ground (Wiens 1969). I also measured the overhead concealment of the nest (percentage of a 5 cm radius cardboard disc that was occluded when viewed from directly above) and the lateral concealment of the nest (percentage of a 5 cm radius cardboard disc that was occluded when viewed 1 m from the nest bowl along the aforementioned

transects). To examine what features of the environment individuals select when choosing a nest site, I measured the same variables (excepting nest concealment) at a randomly located point within the same territory but at least 10 m from the nest.

Data analysis. – The BBIRD sampling protocol generates a large number of non-independent habitat metrics. Correlations among putatively independent habitat variables pose a significant problem for the interpretation of standard statistical tests, and including an excessive number of independent variables also increases the likelihood of finding spurious correlations. Thus, I examined correlation matrices for all variables to identify sources of collinearity and eliminate unnecessary variables. A number of measured variables appeared to provide redundant information. First, estimates of vegetation structure at different heights are highly correlated ($r = 0.432\text{--}0.786$, all P 's < 0.05). Furthermore, estimates of vegetation volume and the overall vertical structure of the vegetation (total hits at all heights) were significantly correlated ($r = 0.185$, $P = 0.001$). The fact that these variables were correlated is not surprising, but it does suggest that measuring both vegetation volume and vertical structure is unnecessary.

During field work, I also became concerned that the method for estimating vertical structure was not repeatable. Indeed, an experiment in which a second observer repeated the measurements of a first observer showed no correlation between the total number of vegetation hits recorded at the same point ($r = 0.135$, $n = 12$, $P = 0.676$). In addition, results of ANOVA indicated insignificant variation in total vegetation hits across the randomly placed measurement points ($F_{1,11} = 1.285$, $P = 0.342$) but significant variation among estimates generated by the two observers ($F_{1,11} = 11.033$, $P = 0.007$). In

other words, the variation in estimates between observers at the same point exceeds the variation among points, some of which were more than 5 km apart. This suggests that the Wiens (1969) method of estimating vertical structure is unlikely to provide biologically meaningful information about the habitat preferences of grassland birds, especially when multiple observers are collecting data. Given these preliminary results, in addition to the evidence of a strong correlation between vegetation volume and vertical structure, I did not use estimates of vertical structure in subsequent analyses.

Except for percent cover of shrubs, all cover estimates were highly correlated (all P 's < 0.0001). Using MANOVA, I found that percent bare ground surrounding the nest explained more variation among species than did the other variables (adjusted r^2 values: bare ground, 0.205; moss, 0.184; grass, 0.069; forb, 0.01), and thus retained only percent shrub cover and percent bare ground for subsequent analyses. Lateral concealment of the nest was also eliminated as a variable because it was highly correlated ($r = 0.346$, $P < 0.001$) with overhead concealment. Finally, I eliminated estimates of litter depth as an independent variable because of among-year variation in the methods used to estimate litter depth. The final suite of independent variables included percent bare ground (arcsin transformed), percent shrub cover (arcsin transformed), vegetation volume (square-root transformed), and percent overhead cover at the nest (arcsin transformed). I only used estimates of vegetation volume taken 0.01 m from the nest because I found that these estimates were nearly identical to estimates from the rest of the sampling patch ($r = 0.702$, $n = 546$, $P < 0.001$), and because other studies have found that features immediately surrounding the nest site are often the best predictors of differences in habitat use among species (Hoekman 1999, Logan 2001).

I used MANOVA to compare habitat variables among species, between nests and random points, and between successful and depredated nests. When MANOVA indicated significant differences among groups, I used univariate ANOVA, corrected for multiple tests, to determine which variables were significantly different. In addition, discriminant function analysis (DFA) was used to examine how combinations of habitat variables contributed to differences among species in nest site use. For DFA classifications, Box's M criterion indicated significant heteroscedasticity in covariance matrices and thus I used separate group covariance matrices.

Results

Habitat features at the nest varied significantly among species ($F_{36, 748} = 7.171$, $P < 0.001$; Appendix A). Shrub cover was the strongest predictor of variation among species ($F_{9, 187} = 27.015$, $P < 0.001$), followed by the percent bare ground ($F_{9, 187} = 8.225$, $P < 0.001$), overhead cover at the nest ($F_{9, 187} = 7.861$, $P < 0.001$), and finally vegetation volume ($F_{9, 187} = 7.861$, $P < 0.001$). The results of the DFA showed two main axes of variation, explaining 75% (Wilks lambda = 0.241, $P < 0.001$) and 18% (Wilks lambda = 0.626, $P < 0.001$) of variation among species, respectively. The first axis was most strongly correlated with the percent shrub cover (0.881; Fig. 1) and effectively served to separate the shrub-nesting Clay-colored Sparrow (*Spizella pallida*) from the remaining ground-nesters. The second axis was most strongly associated with increasing amounts of bare ground (0.596) and decreasing vegetation volume (-0.732).

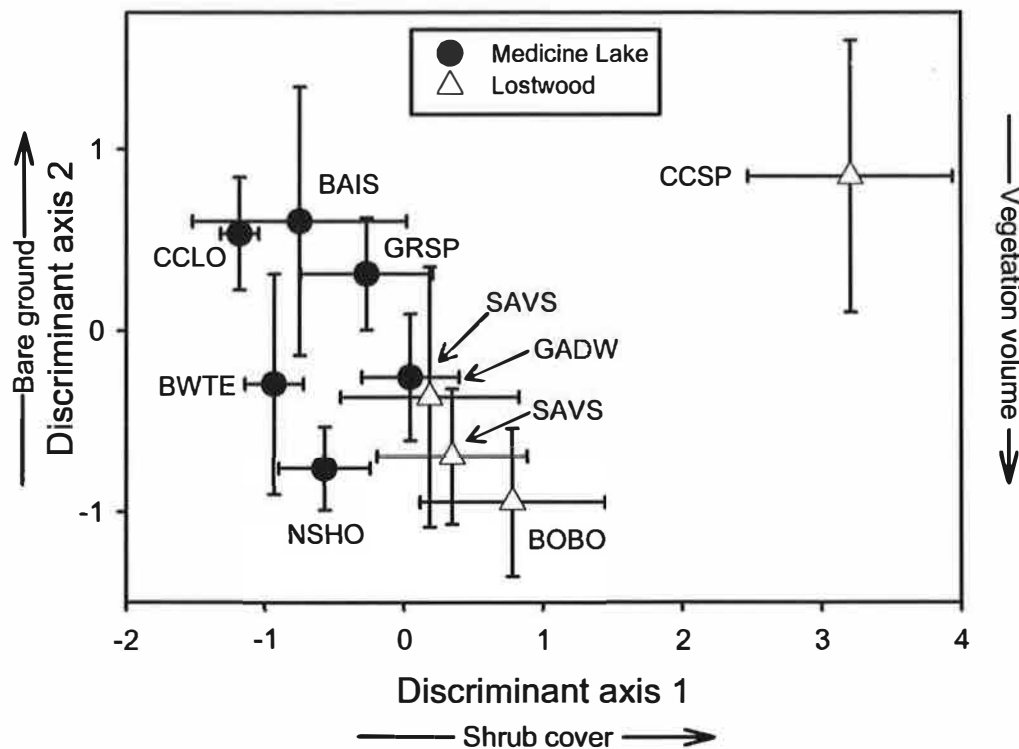


Fig. 1. Group centroids (\pm 95% CI) plotted against the first two discriminant function axes, which show linear combination of habitat variables that best explain variation among species in nest site characteristics. The habitat variables most strongly correlated with each discriminant function are shown along the axes of the figure; the arrows represent the direction of the correlation.

Nest site characteristics are poorly differentiated among species along the second axis, as indicated by the broadly overlapping confidence intervals, but three roughly defined groups were apparent. Nest sites of Chestnut-collared Longspur (CCLO; *Calcarius ornatus*), Baird's Sparrow (BAIS; *Ammodramus bairdii*), and Grasshopper Sparrow (GRSP; *Ammodramus savannarum*) form one group distinguished by low amounts of shrub cover, less vegetation, and more bare ground. Savannah Sparrow (SAVS;

Passerculus sandwichensis; from both sites, with nests from each site treated as a separate “species”), Gadwall (GADW; *Anas strepera*), and Bobolink (BOBO; *Dolichonyx oryzivorus*) nests formed a variable group with tendencies towards less bare ground, more vegetation, and intermediate levels of shrub cover. Blue-winged Teal (BWTE; *Anas discors*) and Northern Shoveler (NSHO; *Anas clypeata*) nest sites were characterized by low amounts of shrub cover and bare ground, and relatively dense vegetation.

Overall, 45% of nests were correctly classified to species by the DFA, a 35% improvement over that expected by chance (Table 1), but only Chestnut-collared

Table 1. Summary of nest site classifications produced by DFA, expressed as the percentage of cases classified to each category. Rows in boldface indicate species for which more nests were classified correctly than expected by chance.

Species	Predicted Species									
	BAIS	BWTE	CCLO	CCSP	GADW	GRSP	NSHO	SAVS (M.L)	BOBO	SAVS (LW)
BAIS (n = 12)	0	8.3	66.7	8.3	0	0	8.3	0	8.3	0
BWTE (n = 8)	0	25.0	62.5	0	0	0	12.5	0	0	0
CCLO (n = 151)	2.0	0	95.9	0	0	0	2.0	0	0	0
CCSP (n = 19)	0	0	0	89.5	0	0	0	0	10.5	0
GADW (n = 23)	0	23.1	0	23.1	0	7.7	7.7	15.4	15.4	7.7
GRSP (n = 21)	0	0	38.1	14.3	0	4.8	0	23.8	9.5	9.5
NSHO (n = 13)	0	15.4	53.8	0	0	0	23.1	0	7.7	0
SAVS – M.L. (n = 23)	4.3	4.3	26.1	13.0	4.3	0	13.0	17.4	17.4	0
BOBO (n = 21)	0	5.0	5.0	20.0	0	0	0	0	70.0	0
SAVS – LW (n = 20)	0	15.8	10.5	10.5	0	0	0	15.8	47.4	0

Longspur, Clay-colored Sparrow, and Bobolink had a majority of nests classified correctly. Two species, Baird's Sparrow and Savannah Sparrows from Lostwood, had none of their nests classified correctly by the DFA. However, because DFA seeks the linear combination of variables that maximize differences between species, the location of species centroids and the resultant classification rate is dependent upon the species included in the analysis (e.g., Grill and Rush 2000). Thus, nest site descriptions produced by DFA are best viewed as heuristic.

Comparing nest sites and random sites provides a better indication of the habitat characteristics that distinguish among species. Clay-colored Sparrows selected nest sites with vegetation characteristics that differed from random points ($F_{3,34} = 23.36$, $P < 0.001$). In particular, nests of Clay-colored Sparrows were surrounded by significantly more shrub cover than random points ($F_{1,36} = 66.292$, $P < 0.001$), which is unsurprising given this species dependence on shrubs as nesting substrate. On average, shrub cover in Clay-colored Sparrow nest patches was 56% (range: 20-89%), as opposed to an average of 8.5% (range: 0-37%) at random points within the territory. Bobolink nest sites also differed from random points ($F_{3,38} = 3.335$, $P = 0.029$), having a significantly greater volume of vegetation surrounding the nest ($F_{1,40} = 5.954$, $P = 0.019$; nest = 3.0 dm (1-5.25 dm); random = 2.3 dm (1.1-4.6 dm)). None of the other species showed significant differences between habitat characteristics at the nest site and habitat characteristics at random points (all P 's > 0.24).

Savannah Sparrows were relatively common at both Medicine Lake and Lostwood, allowing me to compare nest site use between study areas. Nest sites at Lostwood were significantly different from nest sites at Medicine Lake ($F_{4,37} = 3.721$, P

= 0.012), and were surrounded by a significantly greater volume of vegetation ($F_{1,40} = 12.938$, $P = 0.001$; Lostwood = 2.5 dm; Medicine Lake = 1.5 dm). However, the difference in nest sites was paralleled by a similar difference between random points at Lostwood and Medicine Lake. Random points within Savannah Sparrow territories were significantly different between the two study sites ($F_{3,39} = 7.497$, $P < 0.001$); a result driven primarily by a greater volume of vegetation around random points at Lostwood ($F_{1,41} = 9.826$, $P = 0.003$; Lostwood = 2.0 dm; Medicine Lake = 1.22 dm). Thus, the variation in Savannah Sparrow nest sites appears to reflect larger-scale differences between the two study sites.

Chestnut-collared Longspur was the only species for which sample size was large enough to make comparisons of habitat characteristics between successful ($n = 75$) and depredated nests ($n = 76$). There were no significant differences in any of the measured habitat variables between the two nest types ($F_{3,148} = 1.16$, $P = 0.316$), although there was a non-significant trend towards increased vegetation volume at successful nests (successful = 0.95 dm; depredated = 0.86 dm; $P = 0.08$).

Discussion

Progress in understanding the habitat conditions that promote healthy populations of grassland birds has been hindered both by a lack of study and by the lack of a standardized methodology. In the absence of a standard sampling protocol, apparent contradictions may arise among different studies as to what habitat features are important for a given species (examples in Madden et al. 2000). The BBIRD protocol is the only nationwide standard for measuring bird-habitat associations, but it has been used

infrequently in grassland systems. One of the principal objections to its adoption for studies of grassland birds is the amount of time required to complete the sampling protocol. Here, I have found some justification for this view: many of the variables included in the protocol are redundant. Most importantly, much of the information obtained by estimating vertical structure of vegetation (following Wiens 1969), which is by far the most time consuming portion of the protocol, can be obtained by the much simpler estimate of vegetation volume (following Robel et al. 1970). Furthermore, the method used to estimate vertical structure appears to be flawed in a number of ways. First, measures of structure at different heights are highly correlated and thus cannot be considered separate, independent variables. Second, estimates of vertical structure are not repeatable among observers. Most importantly, the variation in estimates between observers measuring the same point is greater than the variation in estimates between widely separated (up to 5 km) points. This last point suggests that estimates of vertical structure will, at best, be an inefficient method for examining habitat use.

In this report, I have eliminated collinear or confounded variables, and thus the results should reflect in part the likely efficacy of a streamlined BBIRD grassland sampling protocol. The measured variables differed among nest sites of different species, and generally coincided with previous descriptions of habitat use. For example, the DFA model performed well in separating Clay-colored Sparrows, the only shrub-nester, from the remaining ground nesters. The placement of Chestnut-collared Longspur, Baird's Sparrow, and Grasshopper Sparrow in a group associated with increased bare ground, reduced vegetation volume and low shrub cover match what is generally known about these species (Hill and Gould 1993, Vickery 1996, Madden et al. 2000). The absolute

values of the habitat measures also coincide well with previous studies. For example, several studies have reported an average visual obstruction of 1.35 dm and shrub cover from 1-20% in areas occupied by Baird's Sparrow (summarized in Madden et al. 2000); average visual obstruction at Baird's Sparrow nests in this study was 1.19 dm and shrub cover ranged from 0-40% (Appendix A). The consistency of these habitat variables across studies suggests that data gathered within a standardized protocol may be generalizable across sites, although the between-site variation in Savannah Sparrow nest sites poses a counterargument. However, Savannah Sparrows breed throughout North America and are rather plastic in their selection of nesting habitat (Wheelwright and Rising 1993, Madden et al. 2000) and as a consequence may show little consistency in small-scale habitat features at the nest.

The weakness of the measured variables in describing nest site use was more evident in the comparison of nest sites with random points within the territory. Of the ten species included, only Clay-colored Sparrow and Bobolink nest sites showed significant differences from random points. Although small sample sizes limit the ability to separate nest sites and random sites (e.g. Clark and Shutler 1999), low power cannot explain the lack of pattern for well-represented species such as Chestnut-collared Longspur. Instead, the similarity of nests and random points may be an artifact of failing to include relevant variables or a reflection of small-scale environmental homogeneity in these grasslands. Using overly coarse estimates of habitat structure may magnify environmental homogeneity; for example, in mixed-grass prairie, estimating vegetation volume from visual obstruction readings taken at 5 cm intervals, as in this study, may obscure meaningful variation.

Whether in the context of evolution, ecology, or conservation, meaningful variation in habitat features can only be defined in relation to reproductive success or other components of fitness. Predation is the primary source of mortality during the breeding season (Ricklefs 1969, Martin 1992), and thus identifying habitat features that reduce predation is essential. Chestnut-collared Longspur was the only species with a large enough sample to compare habitat features at successful and depredated nests, but none of the measured habitat variables were correlated with reproductive success. Given that nest site preferences are generally correlated with increased reproductive success (Martin 1998), the most obvious explanation for the similarity of nest and random points is that critical variables were not measured. Alternatively, failed and successful nests may have similar characteristics if predation on nests is random, if current selection by predators does not reflect selection pressures over evolutionary time, or if vegetation structure around the nest is not the primary determinant of predation risk. For example, landscape level features may be better predictors of intraspecific variation in predation risk (Johnson and Temple 1990, Winter et al. 2000), especially in human-modified environments.

In conclusion, in its current form, the grassland BBIRD protocol contains a number of redundant or, in the case of the vertical structure estimates, unreliable metrics. The goal of standardizing methodology across studies may be achieved more readily if a streamlined, less redundant protocol is developed, and eliminating the estimate of vertical vegetation structure would be a good initial step. In addition, giving more thought to which environmental features are likely to directly influence predation risk may provide better insight into the habitat conditions that promote reproductive success. However, the

results presented here are promising in that they indicate that interspecific variation in nest site characteristics can be described adequately even with a greatly reduced set of variables. The next step is to determine how, if at all, these habitat features relate to reproductive success.

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Appendix A. Mean (range) values for habitat characteristics measured at nest sites during 1999-2002. See text for methods and sample sizes.

Species	Overhead nest concealment (%)	Visual obstruction at nest (dm)	Shrub cover (%)	Bare ground (%)
Baird's Sparrow	20.50 (0-100)	1.19 (0-2)	6.00 (0-40.75)	7.90 (0-25)
Bobolink	43.75 (0-87.5)	3.06 (1-5.25)	19.25 (0-77)	0.06 (0-1.25)
Blue-winged Teal	12.63 (0-63)	1.89 (0.6-3.6)	0.16 (0-1.25)	5.31 (0-15)
Chestnut-collared Longspur	27.30 (0-100)	0.92 (0.13-2)	0.05 (0-1.25)	8.19 (0-35)
Clay-colored Sparrow	76.37 (50-100)	2.35 (0-6.8)	56.33 (20-88.5)	0.03 (0-0.25)
Gadwall	40.46 (0-100)	2.24 (0-6.5)	12.27 (0-50)	1.71 (0-7.5)
Grasshopper Sparrow	50.10 (0-100)	1.19 (0-2.25)	7.44 (0-47.5)	4.58 (0-18.75)
Northern Shoveler	24.08 (0-100)	2.12 (0.88-4)	0.76 (0-5)	2.12 (0-13.75)
Savannah Sparrow (M.L.)	49.48 (0-100)	1.54 (0-3.25)	8.43 (0-36.25)	1.05 (0-5)
Savannah Sparrow (LW)	40.79 (0-100)	2.51 (1.38-3.88)	13.04 (0-73.75)	1.20 (0-15)

