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Management and Conservation Article

From Wiens to Robel: A Review of Grassland-Bird Habitat Selection

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ABSTRACT Efforts to stabilize or increase grassland bird populations require identification of suitable habitat as a first step. Although the number of studies examining grassland-bird habitat selection has increased substantially in recent years, much uncertainty exists regarding local-scale habitat variables that researchers should consider. We reviewed 57 studies and identified important vegetation features correlated with grassland bird abundance, density, occurrence, and nest and territory selection. Our objectives were to 1) guide future studies of grassland-bird habitat use by providing a reduced set of relevant vegetation characteristics, 2) challenge researchers to critically think about what variables to consider, and 3) highlight the need to include consistent definitions of terms used to describe grassland bird habitat. We identified 9 variables that were important predictors of habitat use by grassland birds: coverage of bare ground (important in 50% of the instances where it was included), grass (34% of instances), dead vegetation (33% of instances), forbs (31% of instances), and litter (29% of instances), along with an index of vegetation density (39% of instances) and volume (39% of instances), litter depth (36% of instances), and vegetation height (41% of instances). Only 25% of studies provided information on effects sizes and measures of variance. Furthermore, definitions of measured habitat variables were not consistent among studies. We provide definitions of the 9 important variables and implore authors to report effect size and measures of variance. Standardization of terms and reporting of meaningful results will facilitate replication of wildlife research and enhance our ability to recognize general patterns that emerge from observational studies of habitat use.

KEY WORDS Daubenmire, grassland passerines, habitat models, habitat use, litter depth, vegetation density, vegetation height, vegetation structure.

The widespread decline of grassland birds in North America has been referred to as an unfolding "conservation crisis" (Brennan and Kuvlesky 2005:1). The continent-wide nature of these declines suggests that the causes are not local isolated phenomena and likely involve the loss and degradation of grassland habitat (Vickery et al. 1999*b*, Vickery and Herkert 2001, Brennan and Kuvlesky 2005). Hence, efforts to stabilize or increase grassland bird populations require identification of remaining habitat as a first step (Vickery and Herkert 2001), followed by habitat management and restoration (Brennan and Kuvlesky 2005). Not surprisingly, the number of studies examining grassland-bird habitat selection has increased substantially in recent years.

Two important questions researchers must answer before conducting any type of habitat study are these: 1) what features of the habitat should be measured, and 2) what is the best method for measuring those features. Wiens (1969) contended that a description of bird habitat should provide sufficient detail to differentiate among habitats used by multiple species, yet be suitably flexible and precise to reduce the need to artificially classify and categorize habitat. Furthermore, researchers should consider those habitat features deemed important to the animals being studied (Wiens 1969). Stemming from these requirements, Wiens (1969) developed a protocol for quantifying grassland bird habitat based on structural vegetation characteristics such as density, height, and dispersion. The system is both efficient and easy to use in the field, making it one of the preferred methods for quantifying grassland bird habitat. Many of the structural characteristics included by Wiens (1969) are still perceived to be important for contemporary assessments of grassland-bird habitat use.

Although Wiens' (1969:86) system included a set of carefully chosen variables, he suggested that "…it does not seem proper to restrict consideration, a priori, to a few readily-measurable habitat features which may or may not have any direct relevance to the activity of birds." Numerous studies conducted since Wiens' (1969) monograph have identified relevant vegetation features influencing habitat use that should aid researchers in defining a priori hypotheses regarding grassland-bird habitat selection. This approach would allow development of more robust habitat selection models that could be used to make informed decisions regarding habitat management. Even so, grassland bird researchers still conduct exploratory analyses because they are uncertain of important habitat variables. This is particularly apparent in the grassland-bird Breeding Biology Research and Monitoring Database (BBird) protocol where >40 vegetation parameters are measured at each nest (Martin et al. 1997). Continued use of exploratory analyses and measurement of all potentially important vegetation variables suggests that either no pattern regarding grassland-bird habitat relationships has emerged, or that apparent trends are not being recognized, or are being ignored.

We reviewed studies of habitat selection by grassland birds in North America to 1) summarize methods used by researchers for quantifying grassland bird habitat, and 2) identify patterns of grassland-bird vegetation associations. Our results are intended to 1) guide future studies of grassland-bird habitat use by providing a reduced set of relevant vegetation characteristics for researchers to consider, 2) challenge researchers to critically think about what variables to consider, and 3) highlight the need to include

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consistent definitions of terms used to describe grassland bird habitat.

METHODS

We gathered peer-reviewed literature via online search engines (Institute for Scientific Information Web of Science, Searchable Ornithological Research Archive, and Google Scholar) that directly tested effects of vegetation characteristics on occurrence, relative abundance, density, or habitat selection (e.g., nest, territory, or postfledgling habitat) of grassland passerines in North America. We included passerines considered grassland or successional and shrub-breeding species by Sauer et al. (2007) or obligate or facultative grassland species by Vickery et al. (1999*b*). We did not consider winter habitat because few studies were reported in published literature.

The paucity of information on effect sizes, particularly for statistically nonsignificant variables, precluded use of a formal statistical meta-analysis. Instead, we used a vote-counting procedure to determine which vegetation factors were consistent correlates of grassland-bird habitat use (Gurevitch and Hedges 1999). This vote-counting procedure provided a descriptive summation of the importance of individual variables. Our sample size for the vote-counting procedure was the total number of instances a vegetation variable was examined with respect to a bird species response, not the total number of articles. Thus habitat associations of multiple species included in one article each added 1 to the overall sample size. Similarly, if authors developed separate models for a species' response to a vegetation variable over multiple years or at different sites, each model added 1 to the overall sample size for that vegetation variable. Although models of habitat use that are developed for a single species over multiple years or sites are not independent, our focus was to identify consistent vegetation features that could reliably predict bird use across years and locations.

We used 2 sets of statistical criteria that were most commonly reported when assessing variables for inclusion into our analyses. For papers reporting statistical hypothesis testing procedures, we judged individual variables to be important if they had P-values <0.05. When an information-theoretic approach (Akaike's Information Criterion [AIC]; Burnham and Anderson 1998) was used, we included variables that appeared in models with ΔAIC <2. If a variable was included in multiple models with ΔAIC <2, we only included it once in our determination of importance. In all analyses, we calculated the importance of an individual vegetation variable as the number of instances a variable was deemed important (following criteria above) divided by the total number of instances the variable was included as an explanatory variable in all studies.

RESULTS

We evaluated 57 studies (Appendix A) spanning 39 years (1969–2008), which included 31 grassland bird species (Appendix B) found in a variety of grassland types (Appendix A). The number of variables measured by researchers averaged 7.6 (SE = 0.6) but ranged from 2 to 23. We included 310 species responses to vegetation structure (i.e., habitat models) in our analyses (Appendix A). The most common techniques used to assess grassland habitat were Daubenmire frame (Daubenmire 1959), Robel pole (Robel et al. 1970), and Wiens pole (Wiens 1969; Fig. 1). We identified 118 different vegetation variables included in models of grassland-bird habitat use (Appendix C). These variables measured 8 broad characteristics of vegetation structure and composition: density, height, volume, horizontal canopy coverage of biotic or abiotic factors, patchiness (spatial heterogeneity), litter depth, and vegetation community composition (richness, evenness, or diversity; Appendix C).

Each of the 8 vegetation categories was composed of individual explanatory variables (Appendix C). We examined whether these individual variables were consistent predictors of grassland-bird habitat use. We restricted our analyses to those variables that had a sample size ≥ 30 (approx. 10% of all species–habitat models). Of 14 variables analyzed, 9 were considered important predictors of grassland-bird habitat use in $\geq 29\%$ of models where they were included (Table 1).

DISCUSSION

Increased awareness of population declines of grassland species has likely contributed to an increased number of studies on grassland-bird habitat selection (Vickery and Herkert 2001). Even so, a lack of information in reported statistical results made it impossible to conduct meta-analyses using effect sizes. Johnson (2002) advocated the importance of replication in wildlife research and the use of meta-analytic procedures. These procedures allow researchers to tease apart consistent versus inconsistent effects of explanatory variables on the response variable of interest (Johnson 2002). However, effect sizes were presented in only 25% of the studies that we examined. The lack of basic information such as means and measures of variance in published articles is surprising considering the number of articles highlighting the need to include such information in wildlife research (Anderson et al. 2001, Chamberlain 2008).

Methods

We found substantial overlap in the methods used to assess habitat use by grassland birds. The primary methods (Daubenmire frame, Robel pole, and Wiens method) efficiently and quantitatively describe grassland habitat. These are important considerations given that habitat studies are often subject to time and resource limitations (Herrick et al. 2005). Furthermore, reduction in time conducting habitat measurements may allow researchers to increase sample sizes.

The vegetation measurement techniques we reviewed were often standardized, but we found inconsistencies in 1) the size of Daubenmire frames (standard size 50 cm × 20 cm; Daubenmire 1959), 2) the distance and height where a visual-obstruction reading was taken for a Robel measurement (4-m distance and 1-m ht provided the best

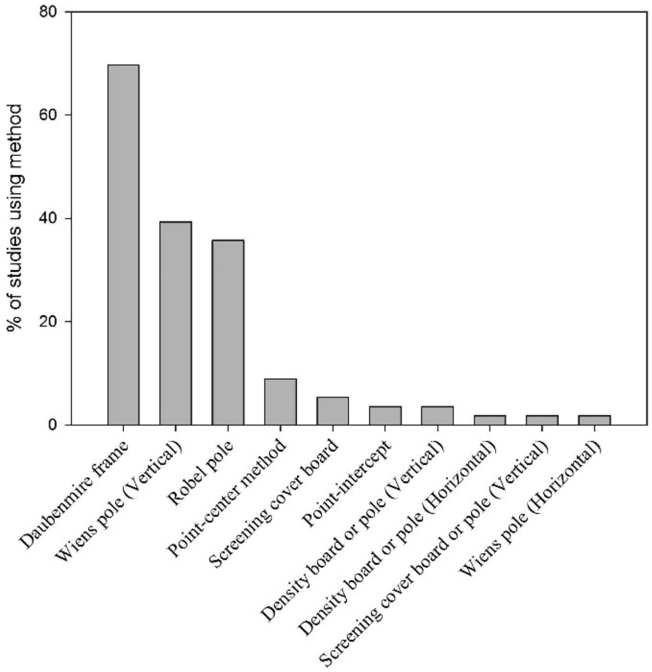

Figure 1. Field techniques used for measuring vegetation structure by grassland bird researchers (n = 57 studies) from articles published between 1969 and 2007.

correlation with vegetation volume; Robel et al. 1970), 3) the shape, diameter, and color of the Robel pole, and 4) the increments on the Wiens and Robel poles (dm increments were used in the original development of these methods; Wiens 1969, Robel et al. 1970). We applaud development of new techniques to measure vegetation (e.g., digital photography; Luscier et al. 2006), but continued use of standardized, common techniques will provide common metrics among future studies. We believe that standardized techniques are 1) useful for maintaining consistency of data sets in long-term studies, 2) allow for easier replication of study design, and 3) reduce ambiguity among published literature. Along with use of standardized techniques, we also advocate that researchers determine a suitable sampling intensity for their studies.

Table 1. We evaluated vegetation variables using a vote-counting procedure to identify important predictors of grassland-bird habitat use. We considered variables important if the percent of cases in which the variable was deemed important (%) exceeded 25 (n = no. of cases in which the variable was examined).

Vegetation variable	%	*N*
% bare ground	50	130
% grass[a]	34	143
% dead vegetation	33	30
% forbs	31	139
% litter[b]	29	102
% shrub	23	56
% vegetation cover[c]	23	37
Vegetation density[d]	39	74
Grass density[a]	30	30
Forb density	23	40
Shrub density	12	51
Vegetation volume	39	126
Litter depth[b]	36	190
Vegetation ht[e]	41	202

[a] Grass cover and density were used by authors to describe coverage of all grass types, without separation into narrower grass categories (e.g., live, dead, native, exotic, etc.).

[b] Litter was based on authors' descriptions of the variable they were measuring. Despite different definitions of litter (see Discussion), if authors reported measuring litter, we included it in this category.

[c] Vegetation cover was a general term used by authors when pooling all vegetation types into one category. This category included all types of vegetation cover, except bare-ground exposure.

[d] Vegetation density, as used by authors, included density of all vegetation types. Different plant types were not separated in this category.

[e] Vegetation ht included several definitions (see Discussion), but all were combined into this one category for our analysis.

Important Vegetation Factors for Birds

Of 118 individual vegetation variables identified by our review and the 14 variables we used in the vote-counting procedure, 9 appeared to be consistent predictors of grassland-bird habitat use and should be considered in future studies. Bare-ground exposure, vegetation height, and litter depth were 3 of the most consistent predictors of habitat use by grassland birds. Reduced bare-ground exposure and increased vegetation height could both provide concealment and cover from predators or wind for adults and young birds (Nelson and Martin 1999, Davis 2005, Warren and Anderson 2005). However, moderate levels of bare ground and vegetation height are likely preferable for some species because of the trade-off between concealment, the need for vigilance, and foraging efficiency (Lusk et al. 2003). The biological relevance of litter depth for grassland birds is unclear. We found few explanations of why litter depth was included in studies of grassland-bird habitat relationships, but Winter (1999) suggested litter (i.e., horizontally lying dead-plant material) provides a suitable nesting substrate. However, litter (as we define it) also provides a stable soil microclimate, materials for nutrient cycling, a substantial input of organic matter, and food for microorganisms in a healthy rangeland; thus, it may also be an index of overall grassland health (Pellant et al. 2000).

Coverages of grass, forbs, litter, and dead vegetation, as well as vegetation density, were important in 29–39% of the species responses examined. Grassland birds may respond to grass cover and density because grass is used as a nesting substrate, and provides concealment (Davis 2005) and abundant prey (Cody 1974). The low percentage of studies (34%) finding that grass cover is important for grassland birds may seem unusual, but given that measurements at used and unused or random locations were all within grassland habitat, it is not surprising that few differences in grass cover were found. Some forbs may provide singing and display perches or a suitable nesting substrate for some species, but they could also be avoided by other species that prefer habitats with high grass:forb ratios (Wiens 1973, Patterson and Best 1996). Horizontal coverage of dead vegetation may be important because it is the only source of available cover at the beginning of the breeding season, whereas other factors, such as live grass coverage, only become important for concealment as the breeding season progresses (Davis 2005). Similar to litter, dead vegetation cover may also reflect overall grassland health and different grazing intensities in rangelands (Schuman et al. 1999).

We found little evidence for a consistent influence of vegetation community composition (i.e., evenness, richness, and diversity) or vegetation patchiness on grassland-bird habitat use. However, vegetation community composition is likely often linked to vegetation structure. Also, the absence of an effect of vegetation patchiness may result from the small scales at which these parameters are usually measured (i.e., within the same plot or even within the same territory), whereas studies examining habitat heterogeneity at larger scales have found an important influence on grassland-bird distribution patterns (Fuhlendorf et al. 2006).

We acknowledge that scale may play an important role in the variables we found important. For example, the presence of (or distance to) woody vegetation can negatively affect grassland-bird habitat use, but may be more important at a larger landscape scale than within the small scales we examined (Coppedge et al. 2001). Grassland birds likely select habitat in a hierarchical manner, and so variables at different scales can be incorporated into models of habitat use to potentially explain variation (Cunningham and Johnson 2006).

MANAGEMENT IMPLICATIONS

We suggest that editors and reviewers implore authors to report effect sizes of both significant and nonsignificant variables in ecological literature to facilitate quantitative reviews, similar to recent policies in medical publications (Gates 2002). Many of the studies we examined included multiple species with multiple explanatory variables, making the reporting of this information difficult in a typical space-limited, 5–6-page article. To alleviate this problem, we recommend inclusion of supplementary data in electronic format appendices as occurs in some electronic ecological journals (e.g., *Ecological Archives* in support of the journals *Ecology*, *Ecological Applications*, and *Ecological Monographs*) and is currently being implemented by *The Journal of Wildlife Management*.

We recognize that advocating a completely standardized methodology for quantifying grassland habitat may not be prudent given the diversity of habitats, species, study objectives, and logistics. However, we strongly recommend researchers use standardized terms to describe vegetation, or at the very least, provide explicit descriptions of these terms. For example, the term "vegetation height" in our review included measures such as maximum vegetation height (Davis 2005), mean vegetation height (Whitmore 1981), and the dm at which the tallest vegetation contacted the Robel or Wiens pole (Martin and Forsyth 2003). Litter also had several definitions: mulch (Wiens 1969); unconsolidated plant material (Davis 2005); dead plant material that was oriented 0–45° to the ground (Winter et al. 2005*b*); unattached dead vegetation (Sutter 1997); and dead vegetation that was standing, but no longer vertical (Madden et al. 2000). Most studies simply did not define litter or vegetation height.

In light of these discrepancies in variable descriptions, we recommend the following definitions: grass coverage as all graminoids not separated into more detailed categories of grass type (e.g., narrow- vs. broad-leaved); litter as the organic debris on the soil surface (i.e., the freshly fallen or slightly decomposed vegetal material on the soil surface [Smith et al. 1995]), and dead vegetation as standing dead vegetation that is attached to the soil; bare ground as any land surface not covered by vegetation, rock, or litter (Smith et al. 1995); forbs as any flowering plants that are not a graminoid (percent ground coverage should be estimated using a Daubenmire frame [Daubenmire 1959]); vegetation density as the number of stems per unit area measured using the Wiens (1969) method (a single density measurement of grass and forb vegetation types is likely sufficient to predict grassland-bird habitat use); vegetation volume as g/m^2, measured indirectly using the Robel et al. (1970) methodology; vegetation height (as often defined in plant ecology) as the height where approximately 80% of vegetation is growing below (and measured directly, accurately, and consistently using a ruler [Stewart et al. 2001]). Consistent and clearly defined terminology is required to facilitate communication amongst stakeholders and researchers (Hall et al. 1997). Standardization of terms will facilitate replication of wildlife research and enhance our ability to make broader generalizations and have greater confidence in general patterns that emerge from observational studies (Madden et al. 2000, Johnson 2002).

The large number of vegetation characteristics that have been measured in past grassland studies suggest uncertainty regarding what should be measured. Furthermore, it was unclear why authors included certain variables in their analyses (e.g., litter depth). We could not determine whether variables were related to a priori hypotheses, metrics used by land managers, or were simply replication of past measurements. We are not questioning the choices of these authors to include these variables in their analyses, but we recommend authors present the ecological reasoning regarding these choices. Such reasoning will facilitate understanding of patterns and processes behind habitat selection of grassland birds (Clark and Shutler 1999). Current analytical paradigms reinforce the need to determine in advance what variables are likely important and develop a priori hypotheses and models (Burnham and Anderson 1998). Reduction of the number of variables examined in observational studies decreases analytic complexity, as well as the probability of finding spurious relationships (Anderson et al. 2000).

Land managers must balance the cost of collecting a large number of samples or measuring a large number of vegetation characteristics (although these are not necessarily mutually exclusive) with the benefits of developing habitat selection models with relatively high predictive ability to allow informed decisions. Interestingly, few researchers evaluated whether their habitat selection models adequately predicted abundance, occurrence, or nest-site selection across time and space, even though the primary focus of the research was to inform management. Inclusion of these

9 habitat variables and standardized terminology should allow researchers to reduce their number of a priori hypotheses and ultimately provide land managers with useful decision-support tools.

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LITERATURE CITED

Ahlering, M. A., and J. A. Faaborg. 2006. Avian habitat management meets conspecific attraction: if you build it, will they come? Auk 123:301–312.

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems prevalence and an alternative. Journal of Wildlife Management 64:912–923.

Anderson, D. R., W. A. Link, D. H. Johnson, and K. P. Burnham. 2001. Suggestions for presenting the results of data analysis. Journal of Wildlife Management 65:373–378.

Bajema, R. A., T. L. Devault, P. E. Scott, and S. L. Lima. 2001. Reclaimed coal mine grasslands and their significance for Henslow's sparrows in the American Midwest. Auk 118:422–431.

Bakker, K. K., D. E. Naugle, and K. F. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. Conservation Biology 16:1638–1646.

Bollinger, E. K. 1995. Successional changes and habitat selection in hayfield bird communities. Auk 112:720–730.

Bossenbroek, J. M., H. H. Wagner, and J. A. Wiens. 2005. Taxon-dependent scaling: beetles, birds, and vegetation at four North American grassland sites. Landscape Ecology 20:675–688.

Brennan, L. A., and W. P. Kuvlesky. 2005. North American grassland birds: an unfolding conservation crisis? Journal of Wildlife Management 69:1–13.

Bryan, G. G., and L. B. Best. 1994. Avian nest density and success in grassed waterways in Iowa rowcrop fields. Wildlife Society Bulletin 22:583–592.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer Science+Business Media, New York, New York, USA.

Camp, M., and L. B. Best. 1994. Nest density and nesting success of birds in roadsides adjacent to rowcrop fields. American Midland Naturalist 131:347–358.

Chamberlain, M. J. 2008. Are we sacrificing biology for statistics? Journal of Wildlife Management 72:1057–1058.

Chapman, R. N., D. M. Engle, R. E. Masters, and D. M. Leslie. 2004. Grassland vegetation and bird communities in the southern Great Plains of North America. Agriculture Ecosystems and Environment 104:577–585.

Clark, R. G., and D. Shutler. 1999. Avian habitat selection: pattern from process in nest site use by ducks? Ecology 80:272–287.

Cody, M. L. 1974. Competition and structure in bird communities. Princeton University Press, Princeton, New Jersey, USA.

Coppedge, B. R., D. M. Engle, R. E. Masters, and M. S. Gregory. 2001. Avian responses to landscape change in fragmented southern Great Plains grasslands. Ecological Applications 11:47–59.

Cunningham, M. A. 2005. A comparison of public lands and farmlands for grassland bird conservation. The Professional Geographer 57:51–65.

Cunningham, M. A., and D. H. Johnson. 2006. Proximate and landscape factors influence grassland bird distributions. Ecological Applications 16:1062–1075.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43–64.

Davis, S. K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. Condor 107:605–616.

Davis, S. K., and D. C. Duncan. 1999. Grassland songbird occurrence in native and crested wheatgrass pastures of southern Saskatchewan. Studies in Avian Biology 19:211–218.

Davis, S. K., D. C. Duncan, and M. Skeel. 1999. Distribution and habitat associations of three endemic grassland songbirds in southern Saskatchewan. Wilson Bulletin 111:389–396.

Delisle, J. M., and J. A. Savidge. 1997. Avian use and vegetation characteristics of Conservation Reserve Program fields. Journal of Wildlife Management 61:318–325.

Dieni, J. S., and S. L. Jones. 2003. Grassland songbird nest site selection patterns in north-central Montana. Wilson Bulletin 115:388–396.

Fletcher, R. J., and R. R. Koford. 2002. Habitat and landscape associations of breeding birds in native and restored grasslands. Journal of Wildlife Management 66:1011–1022.

Fondell, T. F., and I. J. Ball. 2004. Density and success of bird nests relative to grazing on western Montana grasslands. Biological Conservation 117:203–213.

Fritcher, S. C., M. A. Rumble, and L. D. Flake. 2004. Grassland bird densities in seral stages of mixed-grass prairie. Journal of Range Management 57:351–357.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie, Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.

Gates, S. 2002. Review of methodology of quantitative reviews using meta-analysis in ecology. Journal of Animal Ecology 71:547–557.

Giuliano, W. M., and S. E. Daves. 2002. Avian response to warm-season grass use in pasture and hayfield management. Biological Conservation 106:1–9.

Granfors, D. A., K. E. Church, and L. M. Smith. 1996. Eastern meadowlarks nesting in rangelands and Conservation Reserve Program fields in Kansas. Journal of Field Ornithology 67:222–235.

Grant, T. A., E. Madden, and G. B. Berkey. 2004. Tree and shrub invasion in northern mixed-grass prairie: implications for breeding grassland birds. Wildlife Society Bulletin 32:807–818.

Greer, R. D., and S. H. Anderson. 1989. Relationships between population demography of McCown's longspurs and habitat resources. Condor 91:609–619.

Gurevitch, J., and L. V. Hedges. 1999. Statistical issues in ecological meta-analyses. Ecology 80:1142–1149.

Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25:173–182.

Herkert, J. R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. Ecological Applications 4:461–471.

Herkert, J. R., and W. D. Glass. 1999. Henslow's sparrow response to prescribed fire in an Illinois prairie remnant. Studies in Avian Biology 19:160–164.

Herrick, J. E., J. W. Van Zee, K. M. Havstad, L. M. Burkett, and W. G. Whitford. 2005. Monitoring manual for grassland, shrubland and savanna Ecosystems. Volume II: design, supplementary methods and interpretation. The University of Arizona Press, Tucson, USA.

Johnson, D. H. 2002. The importance of replication in wildlife research. Journal of Wildlife Management 66:919–932.

Jones, Z. F., and C. E. Bock. 2005. The Botteri's sparrow and exotic Arizona grasslands: an ecological trap or habitat regained? Condor 107:731–741.

Kelly, J. F., D. L. Hawksworth, and R. A. Meyer. 2006. Abundance of non-breeding horned larks and chestnut-collared longspurs on grazed and rested semiarid grassland. Southwestern Naturalist 51:172–180.

Kershner, E. L., and E. K. Bollinger. 1996. Reproductive success of grassland birds at east-central Illinois airport. American Midland Naturalist 136:358–366.

Knick, S. T., and J. T. Rotenberry. 1999. Spatial distribution of breeding passerine bird habitats in a shrub-steppe region of southwestern Idaho. Studies in Avian Biology 19:104–111.

Koper, N., and F. K. A. Schmiegelow. 2006*a*. Effects of habitat management for ducks on target and nontarget species. Journal of Wildlife Management 70:823–834.

Koper, N., and F. K. A. Schmiegelow. 2006*b*. A multi-scale analysis of avian responses to habitat amount and fragmentation in the Canadian dry mixed-grass prairie. Landscape Ecology 21:1045–1059.

Koper, N., and F. K. A. Schmiegelow. 2007. Does management for duck productivity affect songbird nesting success? Journal of Wildlife Management 71:2249–2257.

Luscier, J. D., W. L. Thompson, J. M. Wilson, B. E. Gorham, and L. D. Dragut. 2006. Using digital photographs and object-based image analysis to estimate percent ground cover in vegetation plots. Frontiers in Ecology and the Environment 4:408–413.

Lusk, J. J., K. Suedkamp Wells, F. S. Guthery, and S. D. Fuhlendorf. 2003. Lark sparrow (*Chondestes grammacus*) nest-site selection and success in a mixed-grass prairie. Auk 120:120–129.

Madden, E. M., R. K. Murphy, A. J. Hansen, and L. Murray. 2000. Models for guiding management of prairie bird habitat in northwestern North Dakota. American Midland Naturalist 144:377–392.

Martin, P. A., and D. J. Forsyth. 2003. Occurrence and productivity of songbirds in prairie farmland under conventional versus minimum tillage regimes. Agriculture Ecosystems and Environment 96:107–117.

Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBird field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, USA.

Maurer, B. A. 1996. Predicting habitat quality for grassland birds using density–habitat correlations. Journal of Wildlife Management 50:556–566.

McMaster, D. G., and S. K. Davis. 2001. An evaluation of Canada's Permanent Cover Program: habitat for grassland birds? Journal of Field Ornithology 72:195–210.

Nelson, K. J., and K. Martin. 1999. Thermal aspects of nest-site location for vesper sparrows and horned larks in British Columbia. Studies in Avian Biology 19:137–143.

Nocera, J. J., G. Forbes, and G. R. Milton. 2007. Habitat relationships of three grassland breeding bird species: broadscale comparisons and hayfield management implications. Avian Conservation and Ecology. <http://www.ace-eco.org/vol2/iss1/art7/>. Accessed 1 Oct 2008.

Norment, C. J., C. D. Ardizzone, and K. Hartman. 1999. Habitat relations and breeding biology of grassland birds in New York. Studies in Avian Biology 19:112–121.

Patterson, M. P., and L. B. Best. 1996. Bird abundance and nesting success in Iowa CRP fields: the importance of vegetation structure and composition. American Midland Naturalist 135:153–167.

Pellant, M., P. Shaver, D. A. Pyke, and J. E. Herrick. 2000. Interpreting indicators of rangeland health. Version 3. U.S. Department of the Interior, Bureau of Land Management, National Science and Technology Center Technical Reference 1734-6, Denver, Colorado, USA.

Prescott, D. R. C., and A. J. Murphy. 1999. Bird populations of seeded grasslands in the aspen parkland. Studies in Avian Biology 19:203–210.

Reed, J. M. 1986. Vegetation structure and vesper sparrow territory location. Wilson Bulletin 98:144–147.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–297.

Rotenberry, J. T., and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228–1250.

Sauer, J. R., J. E. Hines, and J. Fallon. 2007. The North American Breeding Bird Survey, results and analysis 1966–2006. Version 10.13.2007. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schuman, G. E., J. D. Reeder, J. T. Manley, R. H. Hart, and W. A. Manley. 1999. Impact of grazing management on the carbon and nitrogen balance of mixed-grass rangeland. Ecology 9:65–71.

Scott, P. E., T. L. Devault, R. A. Bajema, and S. L. Lima. 2002. Grassland vegetation and bird abundances on reclaimed Midwestern coal mines. Wildlife Society Bulletin 30:1006–1014.

Smith, E. L., P. S. Johnson, G. Ruyle, F. Smeins, D. Loper, D. Whetsell, D. Child, P. Sims, R. Smith, L. Volland, M. Hemstrom, E. Bainter, A. Mendenhall, K. Wadman, D. Franzen, M. Suthers, J. Willoughby, N. Habich, T. Gaven, and J. Haley. 1995. New concepts for assessment of rangeland condition. Journal of Range Management 48:271–282.

Stewart, K. E. J., N. A. D. Bourn, and J. A. Thomas. 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. Journal of Applied Ecology 38:1148–1154.

Sutter, B., and G. Ritchison. 2005. Effects of grazing on vegetation structure, prey availability, and reproductive success of grasshopper sparrows. Journal of Field Ornithology 76:345–351.

Sutter, G. C. 1997. Nest-site selection and nest-entrance orientation in Sprague's pipit. Wilson Bulletin 19:462–469.

Sutter, G. C., and R. M. Brigham. 1998. Avifaunal and habitat changes resulting from conversion of native prairie to crested wheat grass: patterns at songbird community and species level. Canadian Journal of Zoology 76:869–875.

Sutter, G. C., T. Troupe, and M. Forbes. 1995. Abundance of Baird's sparrows, *Ammodramus bairdii*, in native prairie and introduced vegetation. Ecoscience 2:344–348.

Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 1999. Shrub-steppe bird response to habitat and landscape variables in eastern Washington, U.S.A. Conservation Biology 14:1145–1160.

Vickery, P. D., and J. R. Herkert. 2001. Recent advances in grassland bird research: where do we go from here? Auk 118:11–15.

Vickery, P. D., M. L. Hunter, and J. V. Wells. 1999*a*. Effects of fire and herbicide treatment on habitat selection in grassland birds in southern Maine. Studies in Avian Biology 19:149–159.

Vickery, P. D., P. L. Tubaro, J. M. Cardoso da Silva, B. G. Peterjohn, J. R. Herkert, and R. B. Cavalcanti. 1999*b*. Conservation of grassland birds in the western hemisphere. Studies in Avian Biology 19:2–26.

Warren, K. A., and J. T. Anderson. 2005. Grassland songbird nest-site selection and response to mowing in West Virginia. Wildlife Society Bulletin 33:285–292.

Whitmore, R. C. 1981. Structural characteristics of grasshopper sparrow habitat. Journal of Wildlife Management 45:811–814.

Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs 8:1–93.

Wiens, J. A. 1973. Interterritorial habitat variation in grasshopper and Savannah sparrows. Ecology 54:877–884.

Wilson, S. D., and J. W. Belcher. 1989. Plant and bird communities of native prairie and introduced Eurasian vegetation in Manitoba, Canada. Conservation Biology 3:39–44.

Winter, M. 1999. Relationship of fire history to territory size, breeding density, and habitat of Baird's sparrow in North Dakota. Studies in Avian Biology 19:171–177.

Winter, M., and J. Faaborg. 1999. Patterns of area sensitivity in grassland-nesting birds. Conservation Biology 13:1424–1436.

Winter, M., D. H. Johnson, and J. A. Shaffer. 2005*a*. Variability in vegetation effects on density and nesting success of grassland birds. Journal of Wildlife Management 69:185–197.

Winter, M., J. A. Shaffer, D. H. Johnson, T. M. Donovan, W. D. Svedarsky, P. W. Jones, and B. R. Euliss. 2005*b*. Habitat and nesting of Le Conte's sparrows in the northern tallgrass prairie. Journal of Field Ornithology 76:61–71.

Zimmerman, J. L. 1988. Breeding season habitat selection by the Henslow's sparrow (*Ammodramus henslowii*) in Kansas. Wilson Bulletin 100:17–24.

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Appendix A. We reviewed previously published literature (1969–2007) examining grassland-bird habitat selection. Presented are studies included in the literature review along with the number of vegetation variables examined (variables), the number of species-habitat models (models), the avian response variable(s) studied (response), and the major habitat type where the study took place (grassland type).

Study	Variables[a]	Models[b]	Response[c]	Grassland type
Ahlering and Faaborg (2006)	4	1	D	Mixed native
Bajema et al. (2001)	15	1	O	Reclaimed mine
Bakker et al. (2002)	5	18	O	Mixed native
Bollinger (1995)	12	5	A	Planted[d]
Bossenbroek et al. (2005)	4	8	A	Tall, mixed, and short native
Bryan and Best (1994)	4	5	NS	Waterways
Camp and Best (1994)	5	1	NS	Roadsides
Chapman et al. (2004)	3	1	A	Mixed native
Cunningham (2005)	3	7	O, A	CRP[e]
Davis (2005)	6	5	NS	Mixed native
Davis and Duncan (1999)	17	9	O	Mixed native and planted
Davis et al. (1999)	8	3	O	Mixed native
Delisle and Savidge (1997)	12	8	A	CRP
Dieni and Jones (2003)	13	6	NS	Mixed native
Fletcher and Koford (2002)	5	8	D	Tall native and restored
Fondell and Ball (2004)	6	2	NS	Planted pasture
Fritcher et al. (2004)	4	6	D	Mixed native
Giuliano and Daves (2002)	3	1	A, NS	Planted
Granfors et al. (1996)	5	2	NS	CRP
Grant et al. (2004)	3	14	O	Mixed native
Greer and Anderson (1989)	12	1	NS	Mixed native
Herkert (1994)	8	12	O	Restored native
Herkert and Glass (1999)	2	1	A	Tall native
Jones and Bock (2005)	2	9	NS, F, T	Tall native, planted, and sacaton
Kelly et al. (2006)	4	4	A	Short and Chihuahuan desert transition zone
Kershner and Bollinger (1996)	3	1	NS	Airport grasslands
Knick and Rotenberry (1999)	8	5	O	Sagebrush
Koper and Schmiegelow (2006*a*)	4	11	D, Rich	Mixed native
Koper and Schmiegelow (2006*b*)	4	10	D, A, Rich	Mixed native
Koper and Schmiegelow (2007)	4	1	NS	Mixed native
Lusk et al. (2003)	8	1	NS	Mixed native
Madden et al. (2000)	9	10	O	Mixed native
Martin and Forsyth (2003)	11	4	O, NS	Cropland
Maurer (1996)	8	6	D	Mesquite
McMaster and Davis (2001)	10	10	O, Rich, E	Planted and cropland
Nocera et al. (2007)	5	11	O, A, Rep	Agricultural
Norment et al. (1999)	6	5	A, Rich	Cool- and warm-season, pasture, fallow, forb-dominated, and old field
Patterson and Best (1996)	6	8	D, NS	CRP
Prescott and Murphy (1999)	2	2	A, Rich	Planted and cropland
Reed (1986)	6	1	T	Mixed native
Rotenberry and Wiens (1980)	22	16	A	Tall, mixed, and short native
Scott et al. (2002)	10	7	O, A	Reclaimed mine
Sutter (1997)	20	1	NS	Mixed native
Sutter and Brigham (1998)	10	8	A	Planted
Sutter and Ritchison (2005)	12	3	NS	Grazed
Sutter et al. (1995)	5	2	A	Mixed native and planted
Vander Haegen et al. (1999)	14	7	O	Shrub-steppe
Vickery et al. (1999*a*)	9	12	O	Sand-plain
Warren and Anderson (2005)	10	3	NS	Planted
Whitmore (1981)	11	1	T	Reclaimed mine
Wiens (1969)	18	7	O, NS	Planted
Wilson and Belcher (1989)	10	7	A	Mixed native and planted pastures
Winter (1999)	3	1	D	Mixed native
Winter and Faaborg (1999)	9	4	D	Tall native
Winter et al. (2005*a*)	8	2	D, NS	Tall native
Winter et al. (2005*b*)	4	3	D	Tall native
Zimmerman (1988)	7	2	T	Tall native

[a] Includes only small-scale vegetation variables. Does not include variables such as distances to edges or large-scale evaluations of plant cover type (e.g., using Geographic Information Systems or remote sensing). This number only includes variables that were retained by original authors for statistical analyses, not all vegetation factors that were measured.

[b] Includes only those species that fit our criteria of a breeding grassland songbird.

[c] A = abundance, D = density, O = occurrence (presence or absence), NS = nest-site selection, F = postfledgling habitat selection, T = territory selection, Rich = species richness, E = species evenness, Rep = Reproductive activity.

[d] Planted grassland included hay fields and pastures planted with exotic species.

[e] Land enrolled in the United States Department of Agriculture, Conservation Reserve Program.

Appendix B. We reviewed previously published literature (1969–2007) examining grassland-bird habitat selection. Presented are the avian species studied in 57 published articles (Appendix A) that we included in our vote-counting analysis.

Common name	Scientific name	Breeding habitat[a]
Horned lark	*Eremophila alpestris*	Grassland
Sedge wren	*Cistothorus platensis*	Grassland
Sage thrasher	*Oreoscoptes montanus*	Successional or scrub
Sprague's pipit	*Anthus spragueii*	Grassland
Common yellowthroat	*Geothlypis trichas*	Successional or scrub
Botteri's sparrow	*Aimophila botterii*	Grassland
Cassin's sparrow	*Aimophila cassinii*	Grassland
Clay-colored sparrow	*Spizella pallida*	Successional or scrub
Brewer's sparrow	*Spizella breweri*	Successional or scrub
Field sparrow	*Spizella pusilla*	Successional or scrub
Chestnut-collared longspur	*Calcarius ornatus*	Grassland
McCown's longspur	*Calcarius mccownii*	Grassland
Baird's sparrow	*Ammodramus bairdii*	Grassland
Grasshopper sparrow	*Ammodramus savannarum*	Grassland
Henslow's sparrow	*Ammodramus henslowii*	Grassland
Leconte's sparrow	*Ammodramus leconteii*	Grassland
Nelson's sharp-tailed sparrow	*Ammodramus nelsoni subvirgatus*	Wetland[b]
Vesper sparrow	*Pooecetes gramineus*	Grassland
Savannah sparrow	*Passerculus sandwichensis*	Grassland
Sage sparrow	*Amphispiza belli*	Successional or scrub
Black-throated sparrow	*Amphispiza bilineata*	Successional or scrub
White-crowned sparrow	*Zonotrichia leucophrys*	Successional or scrub
Song sparrow	*Melospiza melodia*	Successional or scrub
Lark sparrow	*Chondestes grammacus*	Successional or scrub
Lark bunting	*Calamospiza melanocorys*	Grassland
Dickcissel	*Spiza americana*	Grassland
Bobolink	*Dolochonyx oryzivorus*	Grassland
Western meadowlark	*Sturnella neglecta*	Grassland
Eastern meadowlark	*Sturnella magna*	Grassland
Brown-headed cowbird	*Molothrus ater*	Grassland
American goldfinch	*Carduelis tristis*	Successional or scrub

[a] Breeding Bird Survey breeding habitat designation (Sauer et al. 2007).
[b] But see Nocera et al. (2007).

Appendix C. We reviewed previously published literature (1969–2007) examining grassland-bird habitat selection. Presented are the vegetation variables used to predict grassland-bird habitat use in 57 studies (Appendix A) grouped into 8 broad categories.

Abiotic horizontal coverage
- Bare ground
- Dung
- Rock

Biotic horizontal coverage
- Alfalfa (*Medicago* spp.)
- Annual forbs
- Annual grass
- *Artemisia* spp.
- *Atriplex* spp.
- Big sagebrush (*Artemisia tridentata*)
- Bitterbrush (*Purshia tridentata*)
- Black-grama (*Bouteloua eriopoda*)
- Blue-grama (*Bouteloua gracilis*)
- Brome (*Bromus* spp.)
- Broomsedge (*Andropogon virginicus*)
- Cactus
- Clover (*Trifolium* spp.)
- Common yarrow (*Achillea millefolium*)
- *Cornus* spp.
- Creeping juniper (*Juniperus horzontalis*)
- Dandelion (*Taraxacum* spp.)
- Dead grass
- Dead vegetation
- False indigo (*Amorpha* spp.)
- Fescue (*Festuca* spp.)
- Forbs
- Grass (all types)
- Green rabbit brush (*Ericameria teretifolia*)
- Grey rabbit brush (*Chrysothamnus nauseosus*)
- Herbs
- Japanese brome (*Bromus japonicus*)
- June grass (*Koeleria macrantha*)
- Kentucky blue grass (*Poa pratensis*)
- Leafy spurge (*Euphorbia esula*)
- Lichen
- Litter
- Little bluestem (*Andropogon scoparius*)
- Live grass
- Live vegetation
- Mid-grass
- Moss
- Moss phlox (*Phlox hoodii*)
- Northern wheatgrass (*Elymus lanceolatus*)
- Obtuse sedge (*Carex obtusata*)
- Orchard grass (*Dactylis glomerata*)
- Perennial forbs
- Perennial grass
- Porcupine grass (*Stipa spartea*)
- *Rhus aromatica*
- *Rhus glauca*
- *Rosa* spp.
- Rothrock grama (*Bouteloua rothrockii*)
- Russian thistle (*Salsola kali*)
- Sedge
- Shadscale (*Atriplex confertifolia*)
- Short-grass
- Shrub
- Spruce-top grama (*Bouteloua chondrosioides*)
- Stiff sagebrush (*Artemisia rigida*)
- Stout-stemmed grasses
- Stubble
- Three awns (*Aristida* spp.)
- Three-tip sagebrush (*Artemisia tripartite*)
- Tree
- Vegetation (all types)
- Weeds

Appendix C. Continued.

- Western wheatgrass (*Pascopyrum smithii*)
- Wheat (*Triticum* spp.)
- Winterfat (*Krascheninnikovia lanata*)
- Woody
- *Yucca* spp.

Density
- Broad-leaf grass
- Clumped grasses
- Dead vegetation
- Dwarf shrub
- Exotic grass
- Forb
- Grass (all types)
- Horizontal density (board or pole)
- Litter
- Live vegetation
- Narrow-leaf grass
- Native grass
- Shrub
- Vegetation (all types)
- Vertical density (board or pole)
- Woody vegetation

Litter depth

Patchiness
- CV Robel pole
- CV % grass coverage
- CV % live vegetation coverage
- CV % vegetation coverage
- CV forb ht
- CV litter depth
- CV max. − min. forb or shrub ht
- CV vegetation density
- CV vegetation ht
- Heterogeneity index (HI) vegetation density[a]
- HI litter depth
- Point to plant distance HI
- SD of vegetation ht

Richness; evenness; diversity
- Forb richness
- Forb species diversity
- Grass richness
- Grass species diversity
- Herb richness
- Plant richness
- Vegetation (general) diversity
- Vegetation diversity (horizontal plane)
- Vegetation diversity (vertical plane)
- Vegetation evenness

Vegetation ht
- Effective leaf ht
- Forb ht
- Max. grass ht
- Shrub ht
- Vegetation ht

Vegetation volume
- Horizontal screening cover (board or pole)
- Robel pole
- Vertical screening cover (board or pole)

[a] Rotenberry and Wiens (1980).