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Research article

Factors associated with grassland bird species richness: the relative roles of grassland area, landscape structure, and prey

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Abstract

The factors responsible for widespread declines of grassland birds in the United States are not well understood. This study, conducted in the short-grass prairie of eastern Wyoming, was designed to investigate the relationship between variation in habitat amount, landscape heterogeneity, prey resources, and spatial variation in grassland bird species richness. We estimated bird richness over a 5-year period (1994–1998) from 29 Breeding Bird Survey locations. Estimated bird richness was modeled as a function of landscape structure surrounding survey routes using satellite-based imagery (1996) and grasshopper density and richness, a potentially important prey of grassland birds. Model specification progressed from simple to complex explanations for spatial variation in bird richness. An information-theoretic approach was used to rank and select candidate models. Our best model included measurements of habitat amount, habitat arrangement, landscape matrix, and prey diversity. Grassland bird richness was positively associated with grassland habitat; was negatively associated with habitat dispersion; positively associated with edge habitats; negatively associated with landscape matrix attributes that may restrict movement of grassland bird; and positively related to grasshopper richness. Collectively, 62% of the spatial variation in grassland bird richness was accounted for by the model (adj-R^2 = 0.514). These results suggest that the distribution of grassland bird species is influenced by a complex mixture of factors that include habitat area affects, landscape pattern and composition, and the availability of prey.

Introduction

Over the past three decades, grassland birds breeding in North America have undergone substantial population declines (Knopf 1994; Herkert 1995; Peterjohn and Sauer 1999). All other things being equal, smaller populations have an increased chance of local extinction (Pimm et al. 1988). Thus, widespread declines in grassland bird abundance would be expected to manifest as declines in species richness as local populations wink out across a landscape. Because a general sign of ecosystem stress is a reduction in the variety of organisms (Rapport et al. 1985), species counts have a long history of use in assessing ecosystem well-being (Magurran 1988). Identifying those

environmental factors affecting changes in grassland bird richness will be important in recommending actions to conserve grassland bird communities.

A number of factors are thought to have played a role in declines in grassland bird populations. Herkert et al. (1996) hypothesized that the most likely factors associated with population declines are loss and degradation of native prairie. The conversion of formerly extensive tracts of grassland–shrubsteppe vegetation to agricultural land, and to urban and exurban development has reduced the amount of grassland habitat available for breeding (Herkert 1994; Best et al. 1995). Furthermore, habitat loss is often accompanied by reduced sizes and increased isolation of remnant patches (Fahrig 2003), and land use intensification in the intervening landscape matrix (Dunford and Freemark 2005). Landscape changes can also expose a higher proportion of individuals to nest predation and brood parasitism (Robinson et al. 1995; Blouin-Demers and Weatherhead 2001) and limit the movement of individuals among habitat units (Bélisle et al. 2001; Ricketts 2001) – all of which may result in higher local extinction rates (Boulinier et al. 2001), leading ultimately to an erosion of species richness (Rapport et al. 1985; Bascompte and Rodrígues 2001). However, edge habitats associated with land conversion may offset some declines in species richness by providing habitats that would otherwise be absent (Campi and Mac Nally 2001). Consequently, the overall impact of habitat conversion on biodiversity can be difficult to predict *a priori*.

In addition to landscape heterogeneity, the diversity of predators relies, in part, on variation in their primary prey species (Pimm 1991). The density of prey resources may affect the expression of competitive exclusion such that a high abundance of prey permits the coexistence of more species. A diversity of prey items may also serve to support coexistence through niche separation with different species specializing on distinct prey items. Grasshoppers (Orthoptera: Acrididae) are an important diet component of many grassland birds (Ehrlich et al. 1988) and their overall abundance and diversity may provide additional insights into the spatial variation in grassland bird richness. Wiens and Rotenberry (1979) found that 29% of the diet biomass of birds in four grassland/shrubsteppe habitats in North America consisted of orthopterans. However, grassland birds seem to exhibit opportunistic flexibility in their use of grasshoppers as a food resource with the diet percentage varying widely (0.4–58.6% horned larks; 5.4–53.1% western meadowlarks; 3.9–14.6% eastern meadowlarks; 14.1–77.1% grasshopper sparrows) between species and among individuals within species (Wiens 1973; Wiens and Rotenberry 1979). Because of this food resource plasticity it is unknown whether information on grasshopper abundance and diversity will explain additional spatial variation in grassland bird community structure beyond that explained by landscape structure and composition.

There is no consensus on the relative importance of landscape composition, landscape structure, and prey availability in explaining variation in species richness patterns. In this study we explore the degree to which the observed pattern of grassland bird richness in eastern Wyoming is explained by grassland habitat amount, grassland habitat configuration, landscape matrix effects, and prey availability. By quantifying the respective contribution of each factor, we hope to provide wildlife managers with insights on how to conserve avian diversity within an ecosystem type that has undergone widespread conversion to human-dominated land uses (Sieg et al. 1999; Hodgson et al. 2005).

Methods

Study area

The dry steppe landscape of eastern Wyoming covers approximately 200,000 km^2 (Figure 1) and is characterized by rolling plains of generally flat relief with occasional escarpments, canyons, valleys, mesas and buttes (Bailey 1995). This region has a semiarid climate, due to its location in the rain shadow of the Rocky Mountains (Borchert 1950; Stubbendieck 1988). The vegetation is generally classified as shortgrass/mixedgrass prairie and is characterized by a mixture of short and intermediate height grasses that are usually bunched and sparsely distributed across the landscape (Weaver 1954; Bailey 1995). Brushlands and scattered inclusions of forest vegetation associated with riparian and higher elevation sites are also present. Common grasses include blue grama

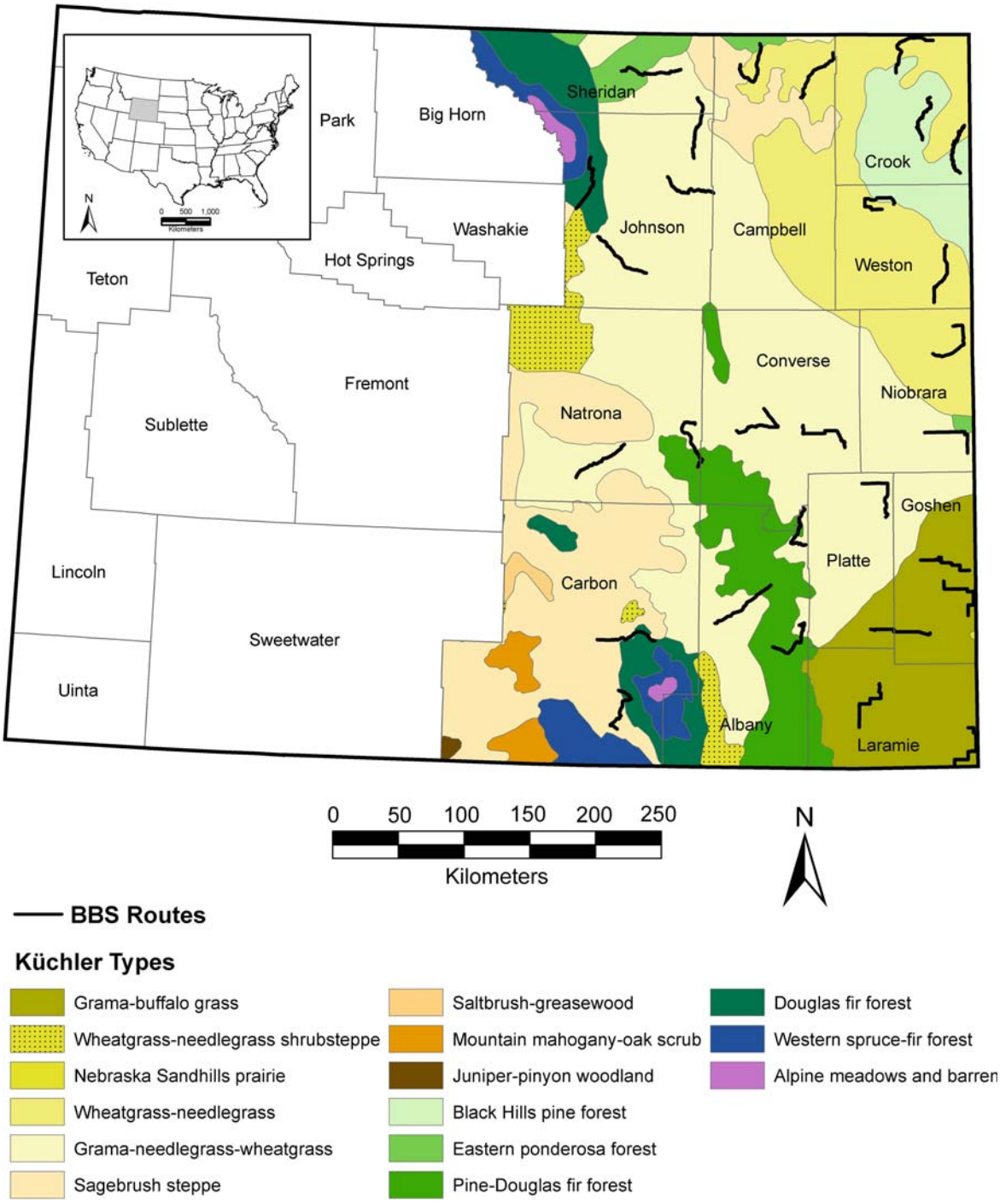

Figure 1. Study area, Küchler Potential Natural Vegetation types (Küchler 1993), and distribution of 29 breeding bird survey routes in eastern Wyoming, USA.

(*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), western wheatgrass (*Pascopyrum smithii*), sand dropseed (*Sporobolus cryptandrus*), needleandthread (*Hesperostipa comata*) and ring muhly (*Muhlenbergia torreyi*) (Sims 1988, p. 278). Shrubs generally found in the study area include

sagebrush (*Artemisia* spp.) and rabbitbrush (*Chrysothamnus* spp.) In pre-settlement times, drought, fire, and grazing were the major landscape disturbances (Sims 1988; Lauenroth et al. 1999). Following settlement, much of this region had been used as rangeland or converted into dry land or irrigated cropland (Burke et al. 1994; Sieg et al. 1999). Common crop types in this area are hay, wheat, barley, sugar beets, dry beans, and corn (Wyoming Agricultural Statistics Service 2002). The conversion of grassland and shrub-steppe communities to cultivated fields in eastern Wyoming has resulted in various degrees of land-use intensification.

Landscape characterization

We used 1996 Landsat 5 Thematic Mapper (TM) data from seven scenes to develop land cover classes (30 × 30 m resolution). Landsat scenes were acquired for late August–October of 1996, during senescence of shrubs and deciduous trees, but prior to snowfall. All seven bands were used for land cover classification including the blue (0.45–0.52 μm), green (0.52–0.60 μm), red (0.63–0.70 μm), near infrared (0.76–0.90 μm), mid-infrared (1.55–1.75 μm), thermal infrared (10.40–12.50 μm) and a second mid-infrared band (2.08–2.35 μm). The processing and classification of the satellite images was done using ERDAS Imagine 8.4 image processing software on a SUN SPARC 10 workstation. Using high-resolution color-infrared aerial photography (NAPP 1:24000, USGS-EROS Data Center, Sioux Fall, SD) as reference data, cover types were assigned to spectrally similar clusters of pixels using an unsupervised classification technique (ISODATA program, ERDAS Imagine 8.4). A modified Anderson classification (Anderson et al. 1976) was used to assign clusters to one of seven broad, Level I, land cover classes and to one of 15 more detailed, Level II, land cover categories (Table 1). Once each cluster was assigned to a land cover class, a supervised classification using a maximum likelihood classifier algorithm as the decision rule was implemented. The output thematic land cover images were imported into ARC/INFO (ESRI, Redlands, CA, USA) to facilitate spatial analyses. An accuracy assessment on the output thematic map was conducted using a stratified random sample of 500 pixels allocated proportionately across Level II categories. The random sample of pixels were compared with truth, where the "true" cover type was determined using an independent set of high-resolution reference aerial photography (NAPP 1:24000, USGS-EROS Data Center, Sioux Fall, SD). Classification errors by individual land cover classes and overall classification accuracy were computed. We used Kappa analysis (Congalton and Green 1999, p. 49) to assess whether the observed level of agreement between our classified image and reference data was significantly better than that expected by chance.

Table 1. Land classification used to characterize landscape structure (modified from Anderson et al. 1976).

Level I	Level II
1.0 Urban	1.1 Residential
	1.2 Commercial, Industrial, Transportation (Roads)
2.0 Agricultural	2.1 Pasture, Alfalfa, Hay – irrigated
	2.2 Row Crops
	2.3 Small grains
	2.4 Fallow
3.0 Natural/Semi-natural Rangeland	3.1 Herbaceous Grassland
	3.2 Shrub and Brushland
4.0 Forestland	4.1 Deciduous Forest
	4.2 Evergreen Forest
5.0 Open Water	5.1 Open Water
6.0 Wetland	6.1 Herbaceous Wetland
	6.2 Wooded Wetland
7.0 Barren Land	7.1 Bare Ground, Rocks, Clay
	7.2 Strip Mines, Gravel Pits

Grasshopper abundance and richness estimates

Grasshopper (Orthoptera: Acrididae) surveys have been conducted since the late 1940's across much of the western United States. Surveys organized by the USDA Animal and Plant Health Inspection Service (APHIS) are conducted along roadsides (Berry et al. 1996) over a 3–4 week period starting around 15 July. Therefore, grasshoppers are counted in the late nymphal and early adult stages. Surveys count all grasshoppers within a ~930 cm^2(1 ft^2) sampling grid. At each stop along the roadside transect, 18 repeated counts are used to estimate mean grasshopper density. We

converted these densities to a per m^2 estimate as in Schell and Lockwood (1997). Since 1988, sweep-net surveys have been conducted to identify grasshopper species composition. Both grasshopper density and species richness were used as potential covariates of grassland bird species richness.

Grasshopper data were obtained from the Wyoming Grasshopper Information System (WGIS) (Zimmerman 1998). To coincide with the landscape structure data set, the total number of grasshoppers per m^2 and the list of grasshopper species collected at each survey site across eastern Wyoming were extracted for the period 1994–1997. These data were brought into a GIS (Geographical Information System) to create a point coverage of mean annual grasshopper density and species richness. The grasshopper survey coverage was used as a base map to spatially interpolate grasshopper density and richness to a 30×30 m grid across the eastern half of Wyoming using inversed distance weighting (IDW; Haining 1990, p. 294). Interpolation was necessary because grasshopper survey points were not co-located with bird survey sites.

Breeding bird richness estimation

The North American Breeding Bird Survey (BBS) is comprised of approximately 3700 survey routes randomly located along secondary roads across the United States and southern Canada. Each year a competent observer drives a 39.4-km route, stopping every 0.8 km (a total of 50 stops/route) to record all birds seen and heard within a 0.4-km radius for a 3-min period [see (Droege 1990) for details].

The set of BBS routes selected for this study was based on BBS administrator defined criteria for acceptability, broad habitat characteristics along the route, and adequacy of survey effort. Route acceptability is based on the competency of the observer, weather conditions at the time of survey, and survey date which must occur within the peak breeding season window for a particular location (for eastern Wyoming this is the month of June). We only included routes that traversed some grassland habitat, which was defined as approximately 5% of the landscape route-buffer in grassland cover. Using a minimal amount of grassland area as the cut-off for inclusion provided a set of BBS routes that had high variability in the proportion of grassland habitat for this study. Finally, routes needed to have been surveyed a minimum of 3 years within a 5-year window centered on 1996 (year of land cover imagery). Using 3 years of survey data to characterize the bird community was selected to increase the detection of rare species and to reduce the temporal variability characteristic of single-year survey data (Wiens 1981). Given these selection criteria, a total of 29 routes qualified for our study (Figure 1).

We focused our analysis on species associated with grassland habitats using a two-step process. First we defined a comprehensive list of grassland species occurring in the United States by combining species lists from three published sources (Johnsgard 1979, p. xliii, Table 3; Peterjohn and Sauer 1993; Samson and Knopf 1996). Second, we edited the list to include only those species that had the potential of being observed in the study area. The edited list included only those species that were actually observed along any of the 29 selected BBS survey routes at any time during the preceding 33-year period (1966–1998). The final grassland species pool included 28 species (Table 2).

Because species with low detection probabilities can be missed during the survey process (Nichols 1992), use of raw species counts as a measure of species richness is known to be biased low (Boulinier et al. 1998). For this reason we estimated grassland bird richness on each route using the Nichols et al. (1998) extension of capture-recapture theory to species richness estimation. Specifically, we used the software program COMDYN (Hines et al. 1999). This program uses a closed population model to derive richness estimates that account for heterogeneity in species. Species were substituted for individuals in the classic capture-recapture approach, and each species was identifiable as if they were a "marked" or "recaptured" individual based on a set of capture histories along each route (Hines et al. 1999). A capture occasion was defined as a 10-stop segment with a total of 5 segments (50 survey points) constituting one complete BBS route. The five adjacent segments along each BBS route were treated as discrete capture occasions, and the capture history of each species was used to estimate the detection probability as in Boulinier et al. (1998).

Table 2. Twenty-eight species comprising the grassland bird pool for eastern Wyoming.

Common Name	Scientific Name	Common Name	Scientific Name
Mountain Plover	*Charadrius montanus*	Baird's Sparrow	*Ammodramus bairdii*
Long-billed Curlew	*Numenius americanus*	Vesper Sparrow	*Pooecetes gramineus*
Upland Sandpiper	*Bartramia longicauda*	Savannah Sparrow	*Passerculus sandwichensis*
Northern Harrier	*Circus cyaneus*	Lark Sparrow	*Chondestes grammacus*
Ferruginous Hawk	*Buteo regalis*	Cassin's Sparrow	*Aimophila cassinii*
Swainson's Hawk	*Buteo swainsoni*	Field Sparrow	*Spizella pusilla*
Prairie Falcon	*Falco mexicanus*	Clay-colored Sparrow	*Spizella pallida*
Ring-necked Pheasant	*Phasianus colchicus*	Chestnut-collared Longspur	*Calcarius ornatus*
Sharp-tailed Grouse	*Tympanuchus phasianellus*	McCown's Longspur	*Calcarius mccownii*
Short-eared Owl	*Asio flammeus*	Lark Bunting	*Calamospiza melanocorys*
Burrowing Owl	*Athene cunicularia*	Dickcissel	*Spiza americana*
Common Poorwill	*Phalaenoptilus nuttallii*	Bobolink	*Dolichonyx oryzivorus*
Horned Lark	*Eremophila alpestris*	Western Meadowlark	*Sturnella neglecta*
Grasshopper Sparrow	*Ammodramus savannarum*	Brewer's Blackbird	*Euphagus cyanocephalus*

Based on the capture histories of species among the route segments, COMDYN estimates species richness ($\hat{S}_{i,t}$) for route i and year t. Reported standard errors ($\pm$ SE) of the estimate are based on 200 bootstrap iterations. Mean species richness ($\bar{S}_i$) for route i was calculated as the arithmetic average of three annual richness estimates selected within the 5-year window. Our response variable for model development was the 3-year mean species richness for each BBS route in the study area. A noteworthy assumption of COMDYN is that each capture occasion (a route segment) is a replicate sample of the same bird community (Nichols et al. 1998). Changes in habitat along a route, therefore, may represent a violation of this assumption (Boulinier et al. 1998). However, the jackknife estimator used in COMDYN has been shown to be robust to assumption violations (Hines et al. 1999) and is recommended for landscape scale analysis of species richness with BBS data (Boulinier et al. 1998).

Linking bird richness with landscape structure and prey availability

Digital BBS route paths (National Atlas of the United States, data available at http://nationalatlas.gov/MLD/bbsrtsl.html) were overlaid on the 30×30 m resolution land cover and grasshopper coverages to extract 1.0 km (radius) buffers around each route. This buffer size was selected because it encompassed the entire breeding territory size of most grassland birds that could potentially be detected along a survey route in our study area (exceptions are Prairie Falcon [*Falco mexicanus*], Swainson's Hawk [*Buteo swainsoni*], Northern Harrier [*Circus cyaneus*], Ferruginous Hawk [*Buteo regalis*] and Short-eared Owl [*Asio flammeus*]).

Landscape structure metrics surrounding each route were estimated from FRAGSTATS, version 3.01 (McGarigal et al. 2002). Landscape metrics were of three general classes: primary habitat area, primary habitat arrangement, and matrix characteristics (Table 3). Primary habitat was defined as the total area of herbaceous natural/semi-natural grasslands (land cover class 3.1 in Table 1). Primary habitat arrangement was measured as the density of grassland patches, the density of edge associated with grassland habitats, and the dispersion of grassland habitats throughout the BBS-buffer as defined by the average nearest neighbor distance between grassland patches and the mean proximity (Table 3). Matrix characteristics focused on those land cover classes thought to affect the overall survivorship and movement of species between patches of primary grassland habitat. These matrix habitat classes included secondary breeding habitat (pasture, shrub and brushlands, and herbaceous wetlands), non-habitat (deciduous and evergreen forest, and wooded wetlands), and intensive anthropogenic dominated land cover (urban, cultivated lands including fallow, and strip mines). Any landscape metric where patch size was critical to its estimation (examples include mean patch size, perimeter to area ratio) were excluded because patches often extended beyond the 1.0 km linear landscape buffers.

Table 3. Landscape and grasshopper variables used in modeling estimated grassland bird species richness.

Variables	Definition	Units	Metric type
GA	Proportion of herbaceous grassland (3.1).	unitless	Primary habitat area
NP	Density of herbaceous grassland (3.1) patches. A patch was defined using the 8-neighbor rule.	#/ha	Primary habitat arrangement
TE	Total edge density between grassland (3.1) and non-grassland land cover.	m/ha	Primary habitat arrangement
ENN	Mean Euclidean nearest neighbor distance between grassland patches.	m	Primary habitat arrangement
PROX	Mean proximity within 500 m. Computed as the sum of patch area over all grassland patches, whose edges are within 500 m of the focal patch, of each patch size divided by the square of its distance from the focal patch.	unitless	Primary habitat arrangement
ILU	Proportion of intensive land uses (1.1, 1.2, 2.2, 2.3, 2.4, 7.2).	unitless	Matrix characteristic
SH	Proportion of secondary habitat (2.1, 3.2, 6.1).	unitless	Matrix characteristic
NNH	Proportion of natural non-habitat (4.1, 4.2, 6.2).	unitless	Matrix characteristic
Matrix_Edge	Edge density among matrix land cover classes (1.1, 1.2, 2.1, 2.2, 2.3, 2.4, 3.2, 4.1, 4.2, 6.1, 6.2, 7.2).	m/ha	Matrix characteristic
ILU_Edge	Edge density between grassland (3.1) and intensive land uses (1.1, 1.2, 2.2, 2.3, 2.4, 7.2).	m/ha	Matrix characteristic
PRD	Patch richness density measured as the number of land cover class patch types, divided by the total area of the landscape (Level II land classification).	#/ha	Matrix characteristic
IJI	Interspersion/juxtaposition measured as the total interspersion over the maximum possible interspersion for a given number of patch types. IJI approach zero when grassland patches are adjacent to only one other land cover class and approaches 100 when grassland patches are equally adjacent to all land cover classes (Level II land classification).	unitless	Matrix characteristic
GH/m^2	Grasshopper density	#/m^2	Prey availability
GHdiversity	Grasshopper species richness	count	Prey availability

Codes appearing parenthetically under the definition are defined in Table 1.

Grasshopper density was used as an overall measure of prey availability to the grassland bird community and grasshopper species richness as an indication of prey diversity (e.g., size, phenology, behavior) that could provide an axis for resource partitioning among different grassland bird species. The interpolated density and richness estimates for grasshoppers in each 30×30 m grid within the 1-km BBS buffer were used to estimate an overall route-level mean for each prey metric (Table 3).

Statistical analysis

Prior to selecting an appropriate modeling approach, we evaluated the distribution properties of the dependent variable. We found no evidence that mean grassland bird richness departed from a normal distribution [$W = 0.98$, $p < 0.76$; Shapiro and Wilk (1965)] suggesting ordinary least squares (OLS) regression was an appropriate statistical model. An evaluation of spatial autocorrelation in mean species richness with Moran's I coefficient (Moran 1950) at various distance lags k and the resulting correlogram (Bailey and Gatrell 1995, p. 269) showed no evidence of spatial dependence among observations ($I = -0.008$, $p = 0.435$) suggesting that autoregressive approaches (see Lichstein et al. 2002) were unnecessary and that OLS remained an appropriate modeling approach.

Our model specification process followed the principle of parsimony (Burnham and Anderson 2002, p. 31) and progressed from simple to complex explanations for variation in grassland bird species richness. We modeled variation in mean species richness ($\bar{S}$) in a step-down fashion regressing $\bar{S}$ on a single variable, or variable set, in sequential order retaining residuals after each step. We ordered our evaluation of predictor variables to reflect the hierarchical process of habitat selection by individuals (sensu, Johnson 1980) and its effect on species richness patterns. Existing theoretical and empirical studies suggest that habitat selection

often proceeds in a hierarchical fashion with broad-scale requirements acting as a filter or constraint for more local-scale requirements (e.g., Poff 1997). Invoking this logic, we proposed that grassland birds would initiate habitat selection by first evaluating suitability in terms of grassland habitat extent, followed by evaluations of how grassland habitat is arranged, the characteristics of the landscape matrix within which habitat is embedded, and finally by the availability of prey resources.

Applying this logic, we first regressed $\bar{S}$ against grassland habitat area. The simplest explanation for variation in species richness is the amount of habitat available – the species-area relationship (Rosenzweig 1995). The two most commonly used functional forms (for review see Tjørve 2003) for this relationship are the power model (Arrhenius 1921) and the exponential model (Gleason 1922). We considered a third functional form – a linear relationship between richness and area – to acknowledge the possibility that our particular data do not support a nonlinear model specification. All three model forms were considered candidate models to capture the species-area effect.

Once we accounted for the species-area effect, we considered the marginal contribution that grassland habitat arrangement had in further explaining variation in $\bar{S}$. We considered all possible regressions based on four arrangement variables (Table 3) as candidate models. Because it is known that habitat area constrains arrangement on the landscape (Gustafson and Parker 1992), we statistically removed the confounding covariation between grassland area and grassland arrangement metrics using the methods of partial correlation analysis (Draper and Smith 1981, p. 265). We fit either *n*th-order polynomials or nonlinear models, selecting that model that resulted in the maximum R^2 and a symmetric distribution of residuals about 0 as in Flather and Bevers (2002). This process transformed our habitat arrangement variables into a set that was now independent of habitat amount in the 1-km buffer about each route.

The third step in our model selection process involved the evaluation of variables characterizing the landscape matrix. It has been shown by simulation (Gustafson and Gardner 1996; Fahrig 2001) and observation (Ricketts 2001; Dunford and Freemark 2005) that matrix characteristics can affect the movement and survivorship of individuals across a landscape. These processes ultimately affect species persistence and therefore observed species richness levels. All possible combinations of the seven matrix variables (Table 3) were considered candidate models.

Because biotic interactions have been considered a locally scaled constraint on species occurrence (Poff 1997, p. 401), we considered last whether prey availability explained any residual variability in grassland bird richness. We considered two measures of prey availability – grasshoppers density and richness. Grasshopper density may affect the expression of competitive exclusion such that high prey abundance could permit the coexistence of more species (Wiens and Rotenberry 1979). Furthermore, high prey diversity may permit higher levels of coexistence through resource partitioning (Pulliam 1986). A total of four candidate models of prey availability were considered.

At each model specification step we selected the "best" model from amongst the candidates using Akaike's Information Criterion (AIC; Burnham and Anderson 2002, p. 60). We used AIC_c, the bias corrected version of AIC, for small sample sizes. The model with the minimum AIC_c has the most support given the data and competing models were identified as those with AIC_c values within 2 units of the best model (i.e., $\Delta\ AIC_c < 2$; Burnham and Anderson 2002, p. 70). All statistical analyses were completed using SAS (SAS Institute 1990).

Results

Landscape characterization

The classification of each BBS route into habitat cover types resulted in a thematic map representative of the land cover classes identifiable using Landsat TM satellite imagery (Figure 2). The overall amount of grassland habitat within the 1-km landscape buffers surrounding each survey route varied from a minimum of 342.9 ha (4.2% of the landscape) to 6728.5 ha (83.3% of the landscape). The overall agreement between the classified image and the reference photography was 78.2% – a level of agreement exceeding that expected with a random classifier (Kappa = 72.2). Classification accuracy was greatest for residential, commercial (industrial and transportation), water, evergreen forest, row crops, and fallow cover types (> 80% accuracy). Primary grassland habitat was

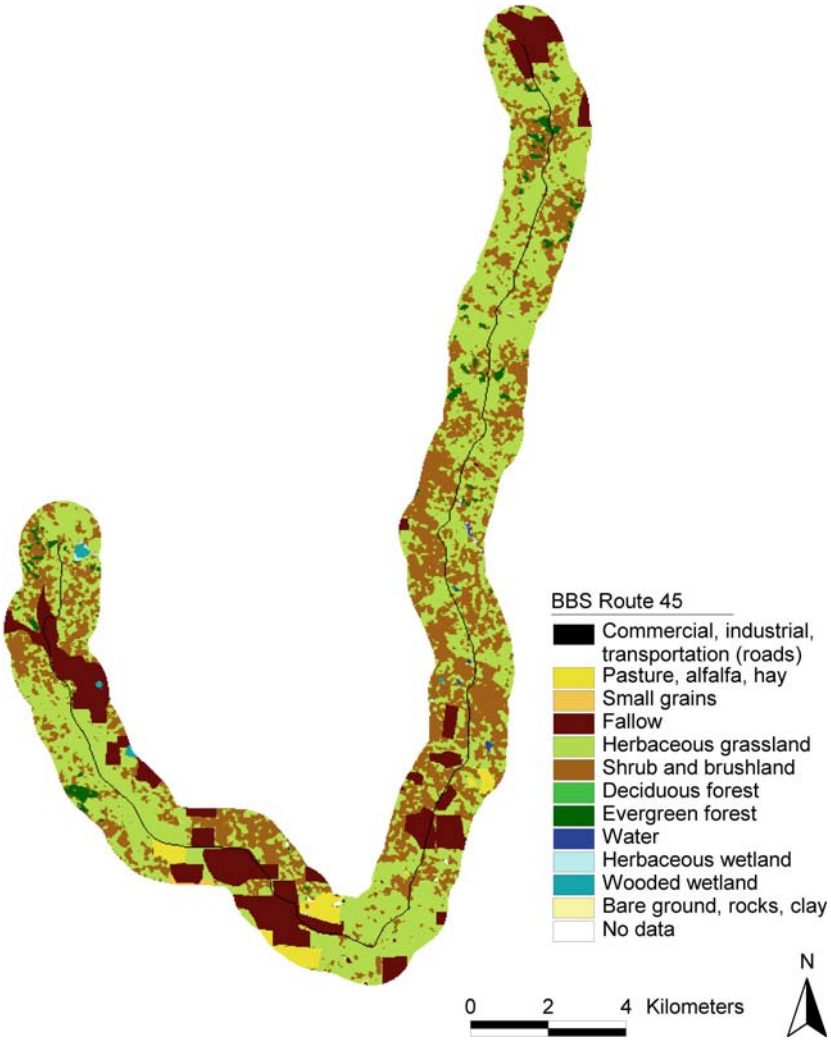

Figure 2. Example breeding bird survey route (# 45, Campbell County, NE Wyoming) classified into land cover classes defined in Table 1 within a 1-km buffer.

correctly classified 71.1% of the time. Grassland was misclassified as shrubland 25.6% of the time, and agriculture or urban 3.3% of the time. The least accurately classified land class was deciduous forest (61.8%) that was frequently misclassified as woody wetland – errors that likely had little impact on our analysis given the similarity of riparian and forested wetland habitats.

Grassland bird richness

Twenty-eight species were included in the pool of grassland birds for which route-level richness estimates were generated (Table 2). For the 1994–1998 time period, 3-year mean estimates of grassland bird richness ($\bar{S}$) from COMDYN ranged from 3 to 17 among the 29 routes (Figure 3). Across all 29 routes, mean grassland bird species richness was $8.57 \pm$ SD 3.01, CV = 35%. $\bar{S}$ was greater than or equal to the observed species richness on all routes, as would be expected when detection probabilities are < 1.0, but the two quantities were highly correlated ($r = 0.95$, $p < 0.0001$).

Modeling

The exponential model best explained the relationship between bird species richness and grassland

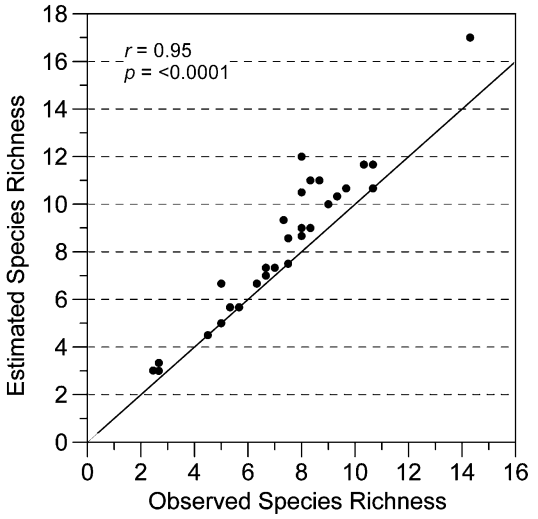

Figure 3. Estimated and unadjusted bird species richness (1994–1998) for breeding bird survey routes from eastern Wyoming. The 45° line is a reference for equality of observed and estimated species richness. The Pearson product moment correlation (r) between observed and estimated richness is reported.

habitat amount (GA), although both the power and linear model were highly competitive (Table 4). The exponential model explained 16.8% of the variation in species richness indicating that the amount of primary habitat available to birds in the 1-km buffer is important in explaining bird species richness ($p = 0.027$). Because habitat amount is represented as a proportion of the 1-km buffer area, the intercept term estimates the maximum richness expected (~10 species) on a route comprised entirely of grassland habitat.

Because many routes had <40% grassland habitat within the 1-km buffer, grassland habitat arrangement varied extensively from route to route. Patch density of grassland habitat (NP), and grassland edge density (TE) were related to habitat amount as a simple quadratic relationship. The mean proximity of grassland habitat patches (PROX) and mean nearest neighbor distance among grassland patches (ENN) were related to habitat amount as an exponential relationship. The most parsimonious predictors of bird richness were the nearest neighbor distances among grassland patches (ENN) and the total edge density involving grassland habitat (TE) ($F = 3.97$, $p = 0.03$, $R^2 = 0.234$). As the distance among grassland habitat patches ($p = 0.015$) and the density of grassland edge ($p = 0.032$) increased, bird richness declined (Table 4). No competing models were considered strong alternatives to our

Table 4. Model selection results using information theoretic criteria applied in a hierarchical step-down fashion that first accounts for habitat area effects, followed by habitat arrangement effects, landscape matrix effects, and finally prey availability effects.

Model specification step	Model	K	AIC_c	ΔAIC_c	R^2	Incremental R^2
Step 1: Area effect						
Best	$\bar{S} = 10.58 + 1.36*\ln(GA)$	3	74.000	0.000	0.168	0.168
Competing	$\bar{S} = 10.67*GA^{0.155}$	3	74.380	0.380	0.162	
	$\bar{S} = 7.35 + 3.90*GA$	3	75.072	1.072	0.115	
Step 2: Arrangement effect						
Best	$R_1 = 0.004 - 0.08*ENN - 0.07*TE$	4	57.340	0.000	0.234	0.195
Competing	None					
Step 3: Matrix effect						
Best	$R_2 = 2.236 - 5.46*NNH - 0.148*ILU_Edge$	4	46.499	0.000	0.312	0.199
Competing	$R_2 = 2.328 + 2.73*ILU - 5.44*NNH - 0.19*ILU_Edge$	5	48.276	1.777	0.339	
Step 4: Prey availability						
Best	$R_3 = -2.280 + 0.45*Ghdiversity$	3	39.994	0.000	0.097	0.041
Competing	None					
Full Model	$\bar{S} = 10.75 + 1.35*\ln(GA) - 0.07*ENN - 0.10*TE$ $-5.94*NNH + 0.48*Ghdiversity$	8	39.994	0.000	0.618	

The best (minimum AIC_c) and competing ($\Delta AIC_c < 2.0$) models at each step are identified. The number of parameters estimated (K) include the intercept, regression coefficients, and the residual variance (Burnham and Anderson 2002, p. 12). The incremental R^2 is the proportion of corrected total sum of squares and provides a comparable statistic (reported for "best" models only) of explanatory power across model specification steps. Dependent variables in Steps 2 – 4 are designated as R_i and represent the residual variance (R) from Step i.

best model ($\Delta AIC_c > 2$). Incorporating habitat arrangement into the model explained slightly more (19.5%) of the overall variation in bird richness than habitat amount alone (see incremental R^2 in Table 4).

The marginal contribution of landscape matrix characteristics to explaining bird richness was based on an evaluation of a relatively large number of predictor variables (Table 3). However, the minimum AIC_c model included only two matrix variables – the amount of natural non-habitat (NNH) and the density of edge associated with intensive land uses (ILU_Edge). Increases in NNH ($p = 0.003$) and ILU_Edge ($p = 0.029$) tended to reduce grassland bird richness and their combined effect explained 31% of the remaining variation (19.9% additional variance explained) in richness (Table 4). The ΔAIC_c values indicated one competing model that accounted for slightly more of the remaining variation in grassland bird richness (nearly 34%) but was penalized for being more complex. This model also was characterized by interpretation difficulties as the proportion of the 1-km buffer that was in intensive land uses (ILU) had an unexpected positive coefficient, although it was not significantly different from 0 ($p = 0.32$).

The final step in fitting the hierarchical model evaluated the effects of grasshopper density and diversity. From the set of candidate models (a model for each prey variable individually and a model including their combined effect), grasshopper diversity (GHdiversity) was the only prey model with any empirical support (Table 4). Areas of eastern Wyoming that supported higher grasshopper diversity also tended to support higher bird richness. This model accounted for an additional 9.8% (adding 4.1% of incremental explanatory power) of the variation in bird richness, although the strength of the relationship ($p = 0.0996$) was weaker than for previous model building steps.

The full model accounted for nearly 62% of the total variation (adj-$R^2 = 0.514$) in bird richness across eastern Wyoming (Table 4). The standard error of the estimate, a measure of prediction precision (Draper and Smith 1981, p. 207), was just over 2 species ($s_{y.x} = 2.09$), or ~15% of the range of estimated species richness (Figure 3). Portions of the study area with greater amounts of grassland habitat and grasshopper diversity tended to be associated with higher bird richness. All selected grassland habitat arrangement and landscape matrix variables were negatively associated with bird richness. The importance of each variable, as reflected in the standardized regression coefficients (β'_i), did not depend on the particular step that a variable was considered in our hierarchical model specification process. The most important variable was edge density associated with grassland habitat ($\beta'_{TE} = -0.56$), followed by the proportion of natural non-habitat ($\beta'_{NNH} = -0.50$), and the nearest neighbor distance between grassland patches ($\beta'_{ENN} = -0.45$). The amount of primary habitat ranked fourth in overall importance ($\beta'_{GA} = 0.41$), followed by land use within the landscape matrix ($\beta'_{ILU_Edge} = -0.39$) and prey availability ($\beta'_{GHdiversity} = 0.22$).

Discussion

Studies at broad spatial scales are needed for a complete understanding of the effects of human-induced landscape change on biodiversity Brown 1995). Describing species distribution patterns and uncovering possible mechanisms underlying these patterns are critical because intensified human uses of land continues to alter the availability, quality, and distribution of habitats supporting native species. The research reported here, based on a hierarchial modeling process that incorporated landscape to local scale explanations of bird species richness, yielded a 6-variable model explaining 62% of the variability in our data (adj-$R^2 = 0.514$). This model included variables measuring grassland habitat amount and arrangement, land cover matrix characteristics, and prey.

When analyzed over multiple landscapes that varied in the amount and arrangement of grassland habitat, our results demonstrated that grassland habitat amount was a strong predictor of bird species richness. Habitat area alone accounted for nearly 17% of the variation in grassland bird richness, an amount that is $3-7x$ the mean explanatory power of recently reported main effects in the ecology literature (Møller and Jennions 2002). In addition to area effects, 19.5% of the variation in grassland bird species richness was explained by habitat arrangement and shape measurements. This finding is atypical of much previous research that reports weak habitat

arrangement effects on biodiversity when compared to habitat amount effects (Fahrig 2003, p. 499). We found that proximity of habitat patches and amount of edge habitat were important predictors of bird species richness. This study demonstrates that more aggregated grassland patches are associated with increased bird species richness. Large, continuous patches of grassland habitat may higher resource density and while minimizing the risk of movement to exploit those resources. The importance of large patches of grassland with less edge habitat supports the species-area theory with the addition of habitat arrangement and patch shape. Edges may be ecological traps or population sinks as predator density is often higher in edges (Flaspohler et al. 2001) and predators may use edges as travel corridors (Small and Hunter 1988). Therefore, over the long-term, edges may be detrimental to the viability of grassland birds. This is supported by the negative relationship between species richness and edges found in this study.

The matrix in which habitat is embedded was also an important predictors of bird species richness. The amount of natural/semi-natural non-habitat habitat (NNP) and the amount of edge between intensive land uses and grassland habitat (ILU_Edge) were both negatively correlated with species richness. Surrounding landscape features are important predictors of bird occurrence and previous research has documented the importance of the matrix on bird distributions (Hanson and Urban 1992; McGarigal and McComb 1995). Our results support the importance of the matrix on species richness of grassland avifauna.

We found a positive relationship between grasshopper prey diversity and grassland bird species richness. The diversity of grasshoppers provides a highly variable and nutritious prey source. Breeding grassland/shrubsteppe avian species have been found to consume a varied diet that shifted between years at any single location with extensive variation in diet among individuals within a local population (Wiens and Rotenberry 1979). Wiens and Rotenberry (1979) theorized that grassland birds exhibit behavioral plasticity in food resource selection, perhaps a highly evolved strategy for exploiting resources in a dynamic system such as grasslands of eastern Wyoming. Our results support this theory as indicated in the positive relationship between bird species richness and grasshopper diversity.

Broad-scale studies have several methodological limitations. Because it is often infeasible to conduct controlled, replicated experiments at this scale, inferences about the relationships between pattern and process are often based on correlations. Consequently, researchers are frequently forced to rely on integrating existing data sets collected for unrelated purposes to search for broad-scale patterns and trends. Such is the case with our study. Nevertheless, broad scale, correlative studies have the potential to provide useful insights into the relationships between landscape patterns, environmental variables, and variation in avian community structure so long as efforts are made to control for factors that may render inferences spurious.

We took a number of steps to minimize the risk of incorporating spurious relationships into our model. To control for known biases in the BBS data, we estimated species richness using capture-recapture theory to account for demonstrated heterogeneity in detection probabilities among bird species (see Nichols et al. 1998; Boulinier et al. 1998; Hines et al. 1999). When the model selection process was based on the raw species counts, the best model was a complex 7-variable model. This model which accounted for 76.8% of the variation in grassland bird richness (adj-$R^2 = 0.69$), included the proportion of the landscape in intensive land uses (ILU) and the grassland edge density with intensive land uses (ILU_Edge) as additional predictor variables,. However, model interpretation is more problematic since the coefficient on ILU is positive (a counterintuitive result), and the estimated coefficients on ILU and grasshopper diversity (GHdiversity) are not different from 0 ($p > 0.56$). ILU includes a diverse grouping of cover types that characterize urban and agricultural lands. Thus, the positive association with ILU may be an artifact of the underlying heterogeneity of this land cover class in our study area.

Another factor that could affect our inferences, particularly given our small sample size ($n = 29$), is the presence of outliers. Observation 28 (BBS route 112) had the maximum "studentized" residual (3.3) that was due to its unusually high estimate of species richness (Figure 3). This route is located in extreme southeastern corner of

Wyoming in Laramie County (Figure 1). However, our model specification process was robust to the exclusion of this observation from the analysis.

A final step to minimize the chance of erroneous inferences was the model specification process itself. We constructed models *a priori* based on hypothesized theoretical and empirical relationships between habitat and birds. The scale of our observation unit was not arbitrarily defined, but was based on species territory sizes to avoid the modifiable areal unit problems (Jelinski and Wu 1996). Furthermore, we implemented a hierarchical model specification method that proceeded from simple to complex explanations of grassland bird species richness based on our current understanding of the processes controlling the spatial distribution of species (e.g., Johnson 1980; Poff 1997). That is, observed distribution patterns are believed to be expressions of a multi-stage process proceeding from broad to specific attributes of the environment. Environmental factors operating early in the process are viewed as necessary but not sufficient for species presence. If we instead had used a stepwise selection algorithm (Draper and Smith 1981, p. 307), we would have estimated a very different model that accounted for only 35.6% of the total variation in bird richness based on the proportion of natural non-habitat (NNH) within the landscape buffer. Although this model was simpler, it failed to capture the importance of other habitat and prey variables. In our view, the deliberate hierarchical process we implemented will yield a model with greater generality to other applications than simply fitting a model that did not reflect the biological processes believed to control species distribution patterns.

This study was a broad-scale study examining relationships between the spatial patterns of bird species richness and landscape and prey covariates. Because of the nature of this study, no direct cause–effect relationships can be inferred. However, the results of observational studies allow tenable hypothesis to be put forth. This study found that in eastern Wyoming, a combination of habitat amount, habitat arrangement, attributes of the landscape matrix and prey were predictors of grassland bird species richness. As such, the amount and context in which habitat it embedded, the surrounding matrix and food resources are important to consider for management of grassland birds.

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