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LINKING CONTINENTAL CLIMATE, LAND USE, AND LAND PATTERNS WITH GRASSLAND BIRD DISTRIBUTION ACROSS THE CONTERMINOUS UNITED STATES

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Abstract. Associations of the abundance and temporal incidence of 17 grassland bird species with climate, weather, farm crops, and landscape metrics were determined for the conterminous United States using hierarchical models. We developed statistical models using two versions of classification and regression tree analysis in which the variation of each species' response variable (both as number of individuals [1973–1989] and as temporal incidence [1981–1990] per Breeding Bird Survey route) was recursively partitioned into statistically distinct chains of environmental determinants or associations. The predictive power of these models was bimodal, yielding high R^2 values (above 38 percent) for one group of 12 species and low values (below 20 percent) for a second group of 5 (generally scarce or restricted-range) species. The fit of the models was strongly correlated with the size of each species' range. Climate variables—long-term annual precipitation, January temperature, and July temperature—appeared in many of the species models, often with strong effects (large R^2 values). January weather (annual deviation from long-term mean temperature) was also a consistent, though weaker, correlate. Sorghum (*Sorghum vulgare*) was the only strong crop correlate of most species abundances, but grain corn (*Zea mays*) and enrollment in the Conservation Reserve Program were consistent smaller contributors to most models. Wheat (*Triticum aestivum*) and durum wheat (*T. durum*) were other noteworthy variables, occurring in about half of the species models. The presence of soybeans (*Glycine max*) was a local modifier of abundance for almost all species. Considering only the leading variables for individual species, precipitation occurred in five species, grain corn in three, and durum wheat and sunflower (*Helianthus* sp.) in two each. The Conservation Reserve Program variable preempted grain corn for two species in the two years Conservation Reserve Program data were available. Other leading variables each appeared in only one species. A parallel analysis using remotely sensed land-use data to assess the relative roles of land-cover proportions and habitat patch attributes showed that grassland species were more strongly influenced by habitat patch variables, but less strongly influenced by land-cover proportions, than were nongrassland species. Grassland species' sensitivity to habitat patch variables appeared to be greater in wooded and cropland habitats than in habitats dominated by grass.

EL ENLACE ENTRE EL CLIMA CONTINENTAL, EL USO DE TERRENO Y LOS PATRONES DE TERRENO CON LA DISTRIBUCIÓN DE AVES DE PASTIZAL A TRÁVES DE LOS ESTADOS UNIDOS CONTÉRMINOS

Sinopsis. Se determinaron asociaciones de abundancia e incidencia temporal de 17 especies de aves de pastizal con el clima, el tiempo, las cosechas y las mediciones de paisaje para los Estados Unidos contérminos utilizando modelos jerárquicos. Elaboramos modelos estadísticos aplicando dos versiones diferentes de análisis de árboles de regresión y clasificación. En ellos, la variación de la variable respuesta de cada especie (tanto el número de individuos [1973–1989] como la incidencia temporal [1981–1990] por ruta del Breeding Bird Survey) se divide recursivamente en cadenas de determinantes ambientales o asociaciones que difieren estadísticamente. La capacidad de predicción de estos modelos fue bimodal, lo que produjo altos valores R^2 (más de un 38 por ciento) para un grupo de 12 especies y bajos valores (menos de un 20 por ciento) para un segundo grupo de 5 especies (generalmente escasas o con una extensión restringida). La conformidad de los modelos se correlacionó estrechamente con el tamaño de la extensión de cada especie. Las variables de clima—precipitación anual a largo plazo, temperatura en enero y temperatura en julio—aparecieron en muchos de los modelos de especie, a menudo con grandes efectos (altos valores de R^2). El tiempo en enero (la desviación anual de la temperatura promedio a largo plazo) fue también un correlativo congruente, aunque de menor importancia. El sorgo (*Sorghum vulgare*) fue el único correlativo de cosecha marcado para la abundancia de la mayoría de las especies, pero el maíz (*Zea mays*) y la inscripción en el Programa de Reservas de Conservación fueron factores menores siempre presentes que contribuyeron en la mayoría de los modelos. El trigo (*Triticum aestivum*) y el *Triticum durum* fueron otras variables que cabe mencionar, que aparecieron en aproximadamente la mitad de los modelos de especie. La presencia de soya (*Glycine max*) fue un modificador local de abundancia para casi todas las especies. Tomando en cuenta solamente las variables principales para las especies individuales, hubo precipitación en cinco especies, maíz en tres, y *Triticum durum* y girasol (*Helianthus* sp.) en dos cada uno. La variable del Programa de Reservas de Conservación reemplazó la variable de maíz para dos especies durante los dos años en que había datos disponibles del Programa de Reservas de Conservación. Otras variables principales aparecieron en sólo una especie cada una. Un análisis paralelo utilizando datos de usos del territorio obtenidos por detección remota para evaluar los papeles relativos de las proporciones de cobertura de

terreno y las características de rodales de hábitat demostró que las especies de pastizal fueron influidas en mayor grado por las variables de rodales de hábitat, pero que fueron influidas en menor grado por las proporciones de cobertura de terreno, que las especies que no eran de pastizal. La sensibilidad de especies de pastizal a las variables de rodales de hábitat pareció ser más grande en hábitats de árboles y de cosechas que en hábitats dominados por la hierba.

Key Words: agriculture; area sensitivity; climate; grassland birds; landscape ecology; regression trees.

Grassland birds have generally declined in the United States because of intensification of agriculture in the Midwest (Askins 1993) and reforestation and increased urbanization in the East (Witham and Hunter 1992, Litvaitis 1993). These declines have been particularly severe where the prairie has been fragmented and disturbed by farming, as in Illinois (Warner 1994). Farmland intensification has been aided by the development of new mechanical and chemical means of treating cropland and by economic support systems promoting their use (O'Connor and Shrubb 1986). In the United States these trends have been reflected in intensified corn (*Zea mays*) and soybean (*Glycine max*) production and in reductions in small-grain and forage crops, livestock, and pasture. Additionally, most hayfields are now intensively cultivated alfalfa (*Medicago sativa*) monocultures rather than mixed-species grasslands. The shift from perennial grassland to annually cultivated cropland is thought to be a major factor in the decline of several formerly common grassland bird species (Johnson and Schwartz 1993).

Much of the information available on the habitat requirements of grassland birds originates in site-intensive studies and focuses on microhabitat features. More spatially extensive studies, such as those by Johnson and Schwartz (1993), have used a regional set of sites and mesoscale habitat variables to characterize the correlates of favorable and unfavorable sites, and With (1994) has taken an explicitly landscape approach in studying the requirements of McCown's Longspur (*Calcarius mccownii*). Another approach is that of Whitmore (1981), who compared his results with those of Wiens (1973) to demonstrate that the habitat requirements of Grasshopper Sparrows (*Ammodramus savannarum*) are similar in different parts of the country.

Much less is known about the correlates of these species' distributions over large spatial extents; the assumption is that the effects of microhabitat or mesoscale correlates determine the larger distribution (Brown 1984). Distributions, and particularly continental distributions, are more likely to be controlled by hierarchies of controlling or constraining factors (Krebs 1985). Before effective conservation programs for grassland species can be developed, we need to identify controlling factors at spatial scales other than that of the microscale of the local habitat patch (Wiens 1981). In this paper we take a macroecological approach (Brown 1995) to assess the pattern of environmental correlates for 17 species of grassland birds in the conterminous United States (Table 1). We used a class of statistical models known as classification and regression tree (CART) analysis that can handle hierarchical effects (see Rodenhouse et al. 1993).

METHODS

Bird Data

The bird data we analyzed were from the Breeding Bird Survey (BBS) for the conterminous United States. The BBS is based on 40-km roadside surveys, each containing 50 stops at 0.8-km intervals. Approximately 2,000 BBS routes are distributed randomly in the conterminous United States in 1-degree blocks of latitude and longitude by state. The number of routes per 1-degree block of latitude and longitude varies among states but is held constant in a state (Bystrak 1981). We used only "type one" routes (routes passing all quality-assurance checks) for the period 1973 through 1990. We used the total count (i.e., number of individuals) for each species and the incidence (i.e., proportion of years observed) for each species on each route. For crop analyses, we assigned each route to the county in which its starting coordinates lay, and in a spatial tessellation of a remotely sensed land-use analysis we assigned each route to the corresponding hexagon (see below). A variety of spatial autocorrelation analyses

TABLE 1. Total variance accounted for by the decision-tree models for individual species

Species	% variance
Western Meadowlark	76.1
Dickcissel	71.8
Horned Lark	64.8
Eastern Meadowlark	64.6
Ring-necked Pheasant	62.5
Bobolink	62.3
Savannah Sparrow	59.6
Vesper Sparrow	59.0
Grasshopper Sparrow	52.1
Lark Bunting	51.6
Upland Sandpiper	41.3
Chestnut-collared Longspur	38.9
Baird's Sparrow	15.3
Gray Partridge	11.7
Long-billed Curlew	11.1
Henslow's Sparrow	3.7
McCown's Longspur	3.3

indicated that these assignments retained adequate spatial resolution for the purposes of our study. Data for 17 species were extracted for analysis on the basis of adequate data in our time period (Table 1).

Range estimates were derived from maps of breeding densities prepared by the Patuxent Wildlife Research Center from BBS data (Sauer et al. 1997). Images of each species' range were converted to raster coverages using a Geographic Information System. The proportion of North America sampled by the BBS that was occupied by the species was used as the range estimate for each species. Although this approach may underestimate the total range of some species, by excluding the southern- and northernmost extents, it is spatially consistent with the abundance data for each species, and in our analyses an underestimate of range for a widespread species would be a conservative error.

Agriculture Data

Agriculture data for each county came from the periodic Censuses of Agriculture (U.S. Department of Commerce, Bureau of the Census) and the annual National Agricultural Statistics Service (NASS) estimates (U.S. Department of Agriculture). We used the Censuses of Agriculture for 1974, 1978, 1982, and 1987 that contained summary statistics for thousands of agriculture variables for each county in the United States. Censuses of Agriculture include acreages of common crops (e.g., corn, cotton [*Gossypium* sp.], and hay) as well as of uncommon crops (e.g., mint [*Mentha* spp.] for oil, hops [*Humulus lupulus*], and kale [*Brassica oleracea*]). The NASS compiles annual estimates of agriculture for each county in the conterminous United States. Counties are grouped into crop-reporting districts by state and according to climate, cropping practices, and other variables (U.S. Department of Agriculture 1987). The NASS agricultural statistics include annual estimates of common crops, with total acreage planted, seeded, and harvested. Estimates of crops sown and harvested from 1972 to 1989 were included in our database. Thus, the NASS agricultural statistics provide data for years without direct Census of Agriculture information. Data on the county acreage of land enrolled in the Conservation Reserve Program (CRP), a federal program initiated in 1986 which retires cropland from production, were obtained from the Natural Resources Conservation Service and were included as an additional cropping variable.

Weather and Climate Data

The primary weather and climate data used in the crop analyses were the Climatic Division Data from World WeatherDisc, a commercial product from WeatherDisc Associates, Inc. (Seattle, Washington). The WeatherDisc data we used covered the period 1961 through 1988; data from mid-1988 through 1990 came from the National Climatic Data Center. We used mean January and July temperatures and mean annual precipitation as parsimonious representatives of bird-relevant weather. We computed 30-yr averages for 1961–1990 to index long-term weather (i.e., climatic conditions) and computed the deviations of the annual values from these means as measures of short-term weather conditions. Thus, we had six climate or weather variables for each spatial unit in our analyses.

Remotely Sensed Data

For a subsidiary analysis, we used data from O'Connor et al.'s (1996) regression tree analysis of bird distribution in relation to remotely sensed data. O'Connor et al. (1996) used data from the Loveland et al. (1991) land-cover prototype, supplemented with an urban layer from the Digital Chart of the World (Danko 1992). This chart classifies each 1-km^2 pixel in the United States in 1990 in one of 159 (160 with the urban class) land-cover classes, doing so on the basis of the seasonal Advanced Very High Resolution Radiometry (AVHRR) profile for that point. O'Connor et al. (1996) adopted the U.S. Environmental Protection Agency's (EPA) Environmental Monitoring and Assessment Program hexagonal grid (Overton et al. 1990, White et al. 1992) as a spatial framework for this analysis. Each hexagon is approximately 635 km^2, with a point-to-point (center-to-center) spacing of approximately 27 km. All environmental correlates were determined as values typifying each hexagon, using only the 1,198 hexagons with BBS data satisfying our data quality criteria. Although this hexagon-based sampling averages the environmental data over a fixed area, the point-to-point spacing of 27 km across hexagons is acceptable given the length of each BBS route (40 km).

O'Connor et al.'s (1996) approach captured spatial variation in landscape structure that might reflect habitat fragmentation and other land-use "stressors," doing so by calculating various metrics of spatial pattern developed under the rubric of "landscape ecology" (Turner and Gardner 1990). In this context, stressors were regarded as any measures, or metrics, reflecting negative impacts on species richness. Various landscape metrics were calculated from the landscape pattern delineated with AVHRR imagery. The distribution of pixels in each hexagon was analyzed by treating contiguous pixels as "patches" for which metrics such as dominance, contagion, fractal dimensions, connectivity, and patch and edge characteristics could be calculated (O'Neill et al. 1988). Three metrics were determined for each land-cover class in each hexagon: the average size of patches of that class, the size of the largest patch of that class, and the largest value of the patch perimeter calculated for all patches of that class. Where a land-cover class was absent from the hexagon, the corresponding metric was set to zero. In addition, the average patch size in each hexagon, irrespective of land-cover class, was computed. Four climatic variables were available from the analyses: long-term averages of January mean temperature, July mean temperature, and annual precipitation and an index of seasonality, which was computed as the within-pixel change between the January and July temperature values (for further details see O'Connor et al. 1996).

Analytical Approach

We programmed a Fortran version of the decision-tree algorithm of Sonquist et al. (1973; Knowledge Seeker, version 2.0) to assess the association of our independent variable, the count of species on a BBS route, with a set of independent variables spanning climate and cropping information. Counts of zero were fairly frequent, and consequently bird counts were first normalized by use of the random normal scores trans-

formation (Bradley 1968). The decision-tree algorithm sorted the bird counts in the region on each independent variable in turn and determined the best threshold along this gradient that maximized the difference between the dependent variable values in the two subsets. For example, in evaluating wheat (*Triticum aestivum*) as a splitting variable, the BBS routes were ordered from those in the area with the lowest wheat acreage to those in the area with the highest wheat acreage. The data set was split at the median wheat value into a low-wheat group and a high-wheat group, and the normalized bird counts in the two groups were tested for significant difference ($P < 0.01$) by means of a t-test. The remaining explanatory variables were then analyzed and similarly tested. If more than one variable resulted in a significant difference between species counts in high and low groups, the variable explaining the greatest percentage of the variance in the set of routes was chosen and the routes were split into two subsamples at the threshold for that variable. The splitting process was repeated for each of the two groups, leading to the identification of four subsamples. The process was again repeated until no division of a group across any of the available variables resulted in a significant difference in average bird counts between subsamples. The final output was represented as a decision tree with a series of end-nodes whose values for species abundance were set by the chain of environmental conditions along the path back to the root node. This method identified the extent and pattern of correlation between dependent and independent variables, and in particular allowed for the occurrence of constraints and of contingent effects (Breiman et al. 1984).

We summarized the output of the algorithm by computing the proportion of variance accounted for by a given model and by dividing this variance among the individual explanatory variables present in the final model (Clark and Pregibon 1992). To incorporate sampling variance in our estimates, we used a bootstrapping approach (Efron 1982) to select repeated random samples of the data set for analysis and reported the median percentage of variance in the data set explained by each variable over all bootstrap replicates. Preliminary analysis suggested that 60-plus bootstrap replicates were needed to stabilize the variance of these medians. Our final analyses were based on 100 bootstrap replicates.

We analyzed data for each odd-numbered year from 1973 through 1989. Differences in results between years arose for two reasons: because some variables were mutually correlated and varied from year to year, or because the true association of a species with a variable changed substantially from year to year because of changes in cropping practices, weather, or other variables.

Because of the computational complexity of the method, not every explanatory variable was considered in the tree construction for every species. An abbreviated screening analysis, based on 10 bootstrap samples of the data set, was performed first for each species for 1973, 1979, 1985, and 1989. This analysis was used to determine which variables were likely to be statistically significant in the final analysis. A full analysis, based on 100 bootstrap samples, was then performed on data from every other year using variables that had been identified in the initial screening analysis. The final results considered 30 variables that could potentially explain the BBS counts in each year examined (Table 2). Twenty-two variables measured land use (percent of county land planted in a crop and CRP acreage); three measured climate (30-yr averages of annual precipitation and January and July temperatures); three measured weather (deviation from 30-yr averages of annual precipitation and January and July temperatures); and two were geographic variables (latitude and longitude). Measurements of most explanatory variables were available from 1973 through 1989, but occasionally a variable had to be omitted for a year in which its value was unreported.

We also examined the environmental correlates, derived from the remotely sensed data, of temporal incidence for each grassland species using the regression tree modules of the S-plus statistical package (MathSoft Inc., Seattle, Washington). We used cross-validation techniques to optimize the fit of each regression tree (Clark and Pregibon 1992), an approach preferable to the bootstrap sampling we used in the crop analyses (Breiman et al. 1984). For these analyses incorporating landscape metrics, we report the percent mean deviance explained as a measure of the goodness-of-fit equivalent to an R^2 value (S. Urquhart, pers. comm.).

RESULTS

Goodness-of-fit of Models

The percentage of variance explained by each species model ranged from 76.1% for Western Meadowlark (*Sturnella neglecta*) to 3.3% for McCown's Longspur (Table 1). The models fell into two groups: 12 species whose models accounted for 38% or more of the variance in abundance and 5 species whose models accounted for less than 20% of the variance (Table 1).

We were interested in determining whether the range in the variance explained by each of these 17 models might be a scale phenomenon (Table 1). Given the spatially extensive nature of variables such as climate and common crop acreages, a wide-ranging species might be expected to adapt to one or more of these variables, whereas a restricted-range species might simply incorporate the variation in these same variables across its range as a constant (Allen and Starr 1982). If this were the case, one would expect model fit to be correlated with range size across species. We tested this hypothesis by computing the Spearman rank correlation of model fit (as percent variance explained) with the proportion of the North American BBS area occupied by the species and found a strong correlation to support this explanation (Spearman rho = 0.733, $P < 0.002$).

Predictor Variables

The variables that appeared in most species models were mean annual precipitation (15 spe-

TABLE 2. NUMBER OF SPECIES SHOWING CORRELATION WITH INDIVIDUAL VARIABLES AND SUMMARY STATISTICS FOR CORRESPONDING SPECIES VARIANCES FOR EACH VARIABLE

Variable (+/− effect)	Number of species	Species effect (% variance explained)					Median rank
		Mean	SD	Minimum	Maximum	Years	
Mean annual precip. (−)	15	7.2	11.52	0.05	36.4	9	3.0
CRP (+)	10	6.1	6.05	0.80	19.6	2	4.5
January climate (−)	13	4.2	10.04	0.05	37.4	9	10.0
Sorghum (+)	12	4.0	8.23	0.05	29.9	9	7.0
Latitude (+)	13	3.9	7.06	0.05	26.0	9	7.0
July climate (m)	12	3.8	4.30	0.05	16.2	9	6.0
Longitude (+)	13	3.8	3.32	0.05	11.1	9	5.0
Durum wheat (+)	7	3.5	8.77	0.05	23.4	6	3.0
Grain corn (+)	11	2.9	2.90	0.05	8.4	9	5.0
Wheat (+)	8	2.9	3.56	0.05	9.4	4	4.5
Oats (+)	10	2.5	3.20	0.70	10.5	9	15.0
January weather (m)	11	1.7	1.32	0.05	5.4	9	5.0
All hay (+)	7	1.5	1.27	0.05	3.8	4	6.0
Soybeans (+)	13	1.5	1.61	0.05	5.1	9	10.0
Winter wheat (+)	12	1.4	1.29	0.05	4.0	9	9.0
Spring wheat (+)	8	1.4	3.06	0.05	8.9	5.5	6.0
Alfalfa (+)	7	1.3	0.56	0.70	2.3	4	11.0
Sunflowers (+)	5	1.2	1.29	0.05	3.2	5	14.0
Barley (m)	10	1.2	0.67	0.05	2.5	9	13.0
Other hay (m)	6	1.2	0.31	0.80	1.7	4	15.5
Deviation precip. (+)	10	1.0	0.42	0.05	1.7	9	10.5
July weather (+)	9	1.0	0.55	0.05	2.0	9	12.0
Tobacco (m)	1	0.9	0.90	0.90	0.9	9	23.0
Corn silage (+)	8	0.8	0.53	0.05	1.4	9	11.5
Cotton (−)	3	0.7	0.56	0.20	1.3	9	22.0
Beans (+)	1	0.6	0.60	0.60	0.6	8	17.0
Peanuts (−)	2	0.6	0.07	0.60	0.7	8.5	20.0
Potatoes (+)	4	0.5	0.32	0.05	0.8	4	17.5
Sugar beets (+)	3	0.3	0.49	0.05	0.9	2	9.0
Flaxseed (+)	5	0.2	0.42	0.05	1.0	2	10.0

Note: "Years" is the median of the number of years for which the variable was a correlate of the individual species (maximum 9 odd-numbered years, 1973–1989). Median rank was computed by ranking all variables in each species model as 1, 2, etc., by size and taking the median for each variable across species. Signs in parentheses indicate the dominant direction of the effect of the variable; "m" indicates mixed effects. "Climate" refers to 30-yr mean temperatures; "weather" refers to deviations about these means.

cies, accounting on average for 7.2% of the variance), mean January temperature (13 species, average effect 4.2%), latitude and longitude (13 species each, with average effects of 3.9 and 3.8%, respectively), soybeans (13 species, average effect 1.5%), and sorghum (*Sorghum vulgare*; 12 species, average effect 4.0%; Table 2). Note that these are highly summarized estimators. The effects of each variable considered were estimated in each of the nine annual models (alternate years from 1973 through 1989) computed for each species; the median of these annual effects for the variable was tabulated as a summary statistic for the species; and the species-specific medians were averaged across those species with non-zero medians as a summary statistic of the influence of that variable. In calculating these averages, species with no correlation with the variable were omitted rather than treated as zeros. We omitted these species because the magnitude of effect is of most interest for species correlated with that variable, whereas the proportion of species associated with the variable could be summarized separately. For individual species, both the median effects and the effects in individual years were often much higher (see below). It is important to remember that these effects are statistical correlates and may be directly responsible for the response or may have an indirect effect, the latter occurring in the case of variables that may be highly correlated with an unmeasured variable (in sensu "surrogacy" of Breiman et al. 1984).

The number of species correlated with a variable and the average size of the correlation effect were themselves broadly correlated, but there were a few exceptions (Table 2). Soybeans (13 species), winter wheat (*Triticum* sp.; 12 species), and perhaps barley (*Hordeum vulgare*; 10 species) all appeared in more of the species models than was typical for their mean effects

(Table 2). This was also true for the three weather variables—deviations from long-term mean January and July temperatures and from long-term annual precipitation—but this was likely due to correlated responses by all the species to regional weather in individual years. Conversely, some variables had atypically few species correlates (Table 2), most notably the level of CRP enrollment in the county, a variable with strong effects on certain species (Lauber 1991, Johnson and Schwartz 1993). CRP data were available in our analyses only for 1987 and 1989, and the low representation of the CRP enrollment variable surely reflects that fact. Durum wheat (*T. durum*; 7 species, average effect 3.5%), wheat (8 species, average effect 2.9%), and all hay (7 species, average effect 1.5%), however, were under-represented variables that lacked such obvious analysis bias by way of explanation. Some variables, such as tobacco (*Nicotiana tabacum*), beans (Leguminosae), and peanuts (*Arachis hypogea*), were only weakly correlated with just one or two species (Table 2).

As a measure of the consistency of these associations between species and crop or environmental variables, we tallied the number of years in which the correlation was significantly nonzero for each species (maximum of 9 odd-numbered years, 1973–1989). In most cases, strongly correlated variables had the most consistent results, occurring in all years for all species (acknowledging that the CRP variable could appear in at most 2 yr for each species). The exceptions were durum wheat, wheat, and all hay, all of which appeared only in four of the year-specific models and in fewer species models than might have been expected.

Conversely, some variables (e.g., cotton [*Gossypium*] and corn silage) had weak effects but appeared consistently in the annual species models (Table 2). The remaining cases with lower numbers of years with effects were all variables with weak overall effects and with eight or fewer species correlates. Most crops were positively associated with the abundance of the species with which they were correlated (Table 2); only peanuts and cotton, both minor influences, were consistently negative. January climate and mean annual precipitation had negative correlations with most species, but July climate had different effects with different species. Weather effects were likewise variable; warm summers and wet years favored most species, but January weather was more varied in its effects.

As previously noted, the distribution of the variance explained by all models was bimodal. It was possible that the importance of some variables in well-fitting models was diluted by weak associations of those same variables with species with poor-fitting models. We therefore addressed the question of whether certain variables might not be consistently the most important variable (largest variance explained) across many species, irrespective of the size of the variance explained by the variable. We ranked the variables in each species model based on the size of the contribution to explained variance to obtain the median ranks across all species (Table 2). This ranking revealed a consistent pattern: certain variables (e.g., mean annual precipitation and extent of durum wheat cultivation) were generally the strongest predictors in individual grassland bird species models; CRP, cultivation of wheat or grain corn, annual January temperature, and longitude were usually the five strongest predictor variables for individual species. Spring wheat (*Triticum* sp.), hay, and sorghum production, July climate, and latitude were also fairly high ranking variables. Other variables, notably beans, potatoes (*Solanum tuberosum*), peanuts, cotton, and tobacco, were typically low-ranking predictors for most species (Table 2). Most crop correlates were again positive and most weather and climate correlates negative (Table 2).

Examination of the major correlates (i.e., variables accounting for > 5% of the median variance explained) for each species showed clear patterns when summarized across species. Agriculture and climate variables had substantial effects in the breeding distribution of all 17 species, whereas geographic and weather variables had substantial effects in only 11 and 6 species, respectively (Table 3). Similar patterns were observed after grouping all predictor variables into three categories (agricultural, climatic, and geographic [latitude/longitude]) and ranking them by total variance explained for each species (Table 4). Agriculture variables were dominant for eight species (Gray Partridge [*Perdix perdix*], Ring-necked Pheasant [*Phasianus colchicus*], Upland Sandpiper [*Bartramia longicauda*], Grasshopper Sparrow, Baird's Sparrow [*Ammodramus bairdii*], Henslow's Sparrow [*A. henslowii*], Chestnut-collared Longspur [*Calcarius ornatus*], and Dickcissel [*Spiza americana*]); climate variables for six species (Long-billed Curlew [*Numenius americanus*], Horned Lark [*Eremophila alpestris*], Lark Bunting [*Calamospiza melanocorys*], McCown's Longspur, Bobolink [*Dolichonyx oryzivorous*], and Western Meadowlark); and geographic variables for only one species (Savannah Sparrow [*Ammodramus savannarum*]). Two species (Vesper Sparrow [*Pooecetes gramineus*] and Eastern Meadowlark [*Sturnella magna*]) had models in which agriculture and climatic variables accounted for sim-

TABLE 3. VARIABLES ACCOUNTING FOR AT LEAST 5% OF THE MEDIAN VARIANCE EXPLAINED FOR EACH SPECIES

Species	Predictor variables
Gray Partridge	sunflower (+), CRP (+), durum wheat (+), January climate (−), all hay
Ring-necked Pheasant	CRP (+), grain corn (+), wheat (+), latitude (+), mean annual precipitation
Upland Sandpiper	sunflower (+), durum wheat (+), mean annual precipitation, sorghum, flaxseed, January weather, CRP, longitude
Long-billed Curlew	mean annual precipitation (−), January climate (−), longitude (+), winter wheat (+), soybeans, spring wheat
Horned Lark	mean annual precipitation (−), CRP (+), wheat, soybeans, grain corn, winter wheat
Vesper Sparrow	spring wheat (+), January climate (−), latitude (+), mean annual precipitation, oats
Lark Bunting	mean annual precipitation (−), longitude (m), July climate, January climate, spring wheat, January weather
Savannah Sparrow	latitude (+), oats (+), January climate, sorghum, July climate
Grasshopper Sparrow	CRP (+), grain corn (+), wheat, all hay, January weather, cotton, July weather, sorghum, mean annual precipitation
Baird's Sparrow	durum wheat (+), latitude (+), mean annual precipitation (−), soybeans, wheat
Henslow's Sparrow	grain corn (+), July climate (−), potatoes (+)
McCown's Longspur	mean annual precipitation (−), corn silage (−)
Chestnut-collared Longspur	durum wheat (+), longitude (+), mean annual precipitation (−), spring wheat, flaxseed, soybeans
Dickcissel	sorghum (+), longitude (+), July climate, January weather, soybeans, all hay
Bobolink	January climate (−), longitude (−), oats
Eastern Meadowlark	July climate (+), January weather (m), grain corn, longitude, latitude, all hay, sorghum, mean annual precipitation
Western Meadowlark	mean annual precipitation (−), CRP (+), January weather (m)

Note: Variables accounting for at least 10% of the median variance show direction of effect in parentheses; effects are positive (+), negative (−), or mixed (m). Data on the Conservation Reserve Program (CRP) were available only for 1987 and 1989. "Climate" refers to 30-yr mean temperatures; "weather" refers to deviations about these means.

TABLE 4. RELATIVE IMPORTANCE OF VARIABLE GROUPINGS (AGRICULTURE, CLIMATE, AND GEOGRAPHIC) FOR EACH SPECIES

	Rank of category based on mean % variance explained					
Species	1	N	2	N	3	N
Dickcissel	Agriculture (42.2%)	10	Climate (18.8%)	6	LatLong (10.8%)	2
Ring-necked Pheasant	Agriculture (40.3%)	15	Climate (13.4%)	5	LatLong (8.9%)	2
Vesper Sparrow	Agriculture (26.3%)	12	Climate (22.8%)	6	LatLong (9.9%)	2
Grasshopper Sparrow	Agriculture (33.1%)	16	Climate (14.7%)	6	LatLong (4.0%)	2
Upland Sandpiper	Agriculture (27.0%)	12	Climate (11.4%)	6	LatLong (2.9%)	2
Chestnut-collared Longspur	Agriculture (28.4%)	7	LatLong (6.9%)	1	Climate (3.7%)	1
Baird's Sparrow	Agriculture (11.9%)	3	LatLong (1.9%)	1	Climate (1.5%)	1
Gray Partridge	Agriculture (9.8%)	9	Climate (1.8%)	1	LatLong (0.14%)	1
Henslow's Sparrow	Agriculture (2.2%)	2	Climate (1.5%)	1	—	–
Western Meadowlark	Climate (50.3%)	6	Agriculture (17.6%)	9	LatLong (8.2%)	2
Horned Lark	Climate (35.9%)	6	Agriculture (24.9%)	12	LatLong (4.1%)	2
Eastern Meadowlark	Climate (29.9%)	7	Agriculture (27.1%)	17	LatLong (7.6%)	2
Bobolink	Climate (42.4%)	5	Agriculture (11.2%)	8	LatLong (8.6%)	2
Lark Bunting	Climate (29.1%)	5	LatLong (13.5%)	1	Agriculture (8.8%)	7
Long-billed Curlew	Climate (6.0%)	2	Agriculture (2.9%)	5	LatLong (2.1%)	2
McCown's Longspur	Climate (2.9%)	1	Agriculture (0.4%)	1	—	–
Savannah Sparrow	LatLong (26.7%)	2	Agriculture (19.3%)	9	Climate (13.7%)	6

Note: Total variance explained for each category, in parentheses, was calculated by summing across each category's variables. The number of variables that contributed to each category is given as N.

TABLE 5. RELATIVE IMPORTANCE OF LAND-COVER AND PATCH VARIABLES IN DIFFERENT HABITATS

Anderson land covers		Frequency of correlations (negative)			
Class	Type	Land-cover variables	Patch variables	Total variables	% patch variables
4	grass-dominated	7(1)	6(1)	13	46
1	cropland and pasture	4	8(1)	12	67
3	woodland/cropland	3	7(2)	10	70
9	mixed (decid./conif.) forest	3	4(2)	7	57
6	mixed grass/shrub rangeland	2(1)	2	4	50
7	deciduous forest	3	1	4	25
5	shrub-dominated rangeland	1	0	1	0
8	coniferous forest	0	1	1	100
14	urban	1	0	1	0
2	grassland/cropland	1	0	1	0
Totals		25(2)	29(6)	54	54

ilar amounts of the explained variation (Table 4). Of these three categories, geographic variables typically (11 of 17 species) accounted for the least amount of explained variation (Table 4).

Among climate variables, it is interesting to note the lower median ranking of January weather (annual deviation from long-term mean temperature) than of January climate (mean temperature) values (median rank of 5 versus 10; Table 2). This was the result of a markedly bimodal distribution of ranks for January climate. For six species (Gray Partridge, Long-billed Curlew, Vesper Sparrow, Lark Bunting, Savannah Sparrow, and Bobolink), January climate was among the top four most significant variables (Table 3). For another group of seven species (Ring-necked Pheasant, Upland Sandpiper, Horned Lark, Grasshopper Sparrow, Dickcissel, and Eastern and Western meadowlarks), January climate appeared only at rank 10 or higher, indicating that the variable had only a peripheral or local effect in the decision trees involved. For all 13 of these species except Gray Partridge and Long-billed Curlew, however, January weather also appeared in the species models, as a subsidiary modifier to climate effects for four of the species above (Vesper Sparrow, Lark Bunting, Savannah Sparrow, and Bobolink) and as a variable dominant to climate for the last seven species. For species wintering in Central and South America, these correlations must be due to indirect effects.

When considering other weather and climate variables, annual precipitation had the strongest effects. For Horned Lark, Lark Bunting, and Western Meadowlark, long-term annual precipitation was far more important (R^2 = 29.3, 15.0, and 32.0%, respectively) than January climate. July climate had a large effect only for Eastern Meadowlark (R^2 = 14.3%), though Horned Lark, Lark Bunting, and Western Meadowlark all had high-ranking contributions (range 4–6%). Annual variation in July temperature had its strongest link with Grasshopper Sparrow (but only at R^2 = 3.2%), and variation in annual precipitation was weakly linked (approximately 2%) with Upland Sandpiper, Dickcissel, and Eastern and Western meadowlarks.

An analysis of satellite-derived land-use and land-pattern variables yielded regression tree models of the incidence of each species over a set of 1,198 BBS routes in the conterminous United States (Table 5). Incidence is the proportion of surveys on each BBS route in which a species was recorded between 1981 and 1990. For most species, incidence and abundance were well correlated (Wright 1991). The independent variables considered were climatic data, proportions of each land-cover class (of 160 classes) around each route, and various pattern metrics of patch size and edge characteristics of the landscape around each route. The data set is described in more detail in O'Connor et al. 1996. The frequency of occurrence of land-use and land-pattern variables that occurred in the regression tree models is summarized across all 17 species (Table 5). To avoid excessive detail, the summary collapses the 160 land-cover classes used in the analyses to the 14 classes of an Anderson et al. (1976) Level II classification. Thus, the incidence of seven species was correlated with the extent of one of the grass-dominated habitats that comprise the Anderson land-cover Class 4 (Table 5). Of these correlates, only one was negative. Similarly, six species models contained a statistical dependence on one of the patch attributes of habitat in land-cover Class 4, with five species more abundant and one less abundant in areas with larger patches of this cover type (Table 5).

Some evidence suggests that habitat patch features may be significant in certain land clas-

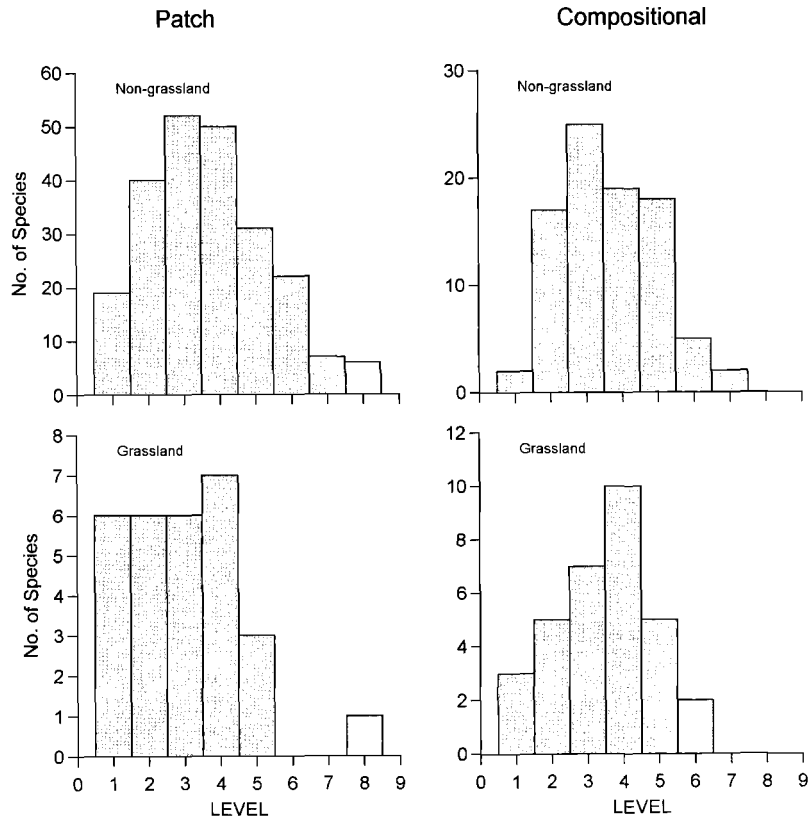

FIGURE 1. Frequency distributions of the level (e.g., level 1 is the root node) in decision-tree models at which patch variables and proportion of land-class (i.e., compositional) variables act. Grassland bird species show a significant skew to the left for patch variables and a significant skew to the right for compositional variables.

ses (Table 5). Overall, patch variables occurred more frequently in the models (53.7%) than did land-cover variables (Table 5). However, these patch correlates were more frequently influential in the Anderson Level II land classes not dominated by grass or rangeland, and particularly so in those classes with five or more correlations in total (Classes 1, 3, and 9). As expected, Class 4 (grass dominated) had the most correlations for grassland species; in this and the two rangeland classes, patch variables provided about half the predictors of species incidence (8 of 18 correlates). Patch variables were in the minority (1 of 4, or 25%) in Class 7 (deciduous forest). Among the four classes with most correlations, 46% of the correlations were patch related in Class 4, but 66% (19 of 29) were patch related in Classes 1, 3, and 9. The sample sizes were too small to obtain significant results even with the marked imbalance between land classes.

We analyzed the significance of patch variables for grassland species further, by comparing the relative influence of patch and land-proportion (compositional) variables in models for grassland and for all other species in the BBS (R. J. O'Connor, unpubl. data). We considered only those species with models involving either of these variable types. We plotted the frequency with which patch variables had their effect at the root level (level 1) of their trees, at the next level down (level 2), and so on (Fig. 1). Variables acting nearer the root of a regression tree have a more widespread, and usually stronger, influence than do variables acting deeper in the tree. A comparison of patch variables for nongrassland and grassland species showed a significant skew to the left for grassland species (Wilcoxon test, P = 0.012; Fig. 1). Similarly, a comparison of the location of action of associations involving the proportion of land class present in the hexagon showed the reverse: grassland species had compositional variables acting farther away from the tree root than did other species (Wilcoxon test, P = 0.028; Fig. 1). These results con-

firm the idea that patch variables were more critical, and compositional variables less critical, in the distribution of grassland species than of other species.

DISCUSSION

Grassland bird distributions at the spatially extensive scale of our analyses were markedly influenced first by crop distribution, second by climate, and third by habitat patch size and shape (Tables 2 and 4).

Crop Correlates

Areas of extensive cultivation of sorghum, wheat, and grain corn were generally favorable to grassland bird species. Correlations with these crops were among the largest contributors of variance explained in many species models and, for at least some species, explained much of the variance. Several other crops, either more regional in distribution or only locally grown, were likewise positively associated with the abundance of grassland species but contributed less to the overall variance explained and had low ranking in the individual regression trees. This last feature can be summarized as reflecting local modification of predictions, with these variables having only local effects in regions where abundance was set by constraints imposed by other crop or climate variables.

Our results suggest that farmers' choices about cropping practices have implications for grassland species at several levels. First, it is clear that high enrollment in the CRP has major benefits for grassland birds. Despite our having only 2 yr of CRP data, many species were more abundant in CRP areas than in non-CRP areas, and several species, notably Gray Partridge and Ring-necked Pheasant, showed strong positive associations with CRP enrollment, which were consistent with previous analysis of BBS data with respect to the CRP (Lauber 1991). Lauber found that many species showed spatial associations of density with CRP enrollment but that many of these correlations were apparent even prior to the advent of the CRP. However, he was able to show that for several species, including Ring-necked Pheasant and Western Meadowlark, densities increased differentially in these areas with the advent of the CRP. A possible explanation for high densities in what later proved to be areas of high CRP enrollment may well be that these have long been areas of high soil erosion; enrollment by farmers in earlier "set-aside" programs to reduce erosion could have favored grassland species by the cessation of tillage operations inimical to the birds' success (Lauber 1991). Lauber's analyses of temporal trends are supported by the results of detailed studies of use of CRP fields in particular regions. Johnson and Schwartz (1993) found that several prairie species with restricted ranges (particularly Lark Bunting, Grasshopper and Baird's sparrows, Dickcissel, and Bobolink) were less abundant on annually tilled cropland than on CRP lands and that many of these species had previously been declining in the central United States. The only grassland species they found to be less abundant on CRP than on non-CRP lands were Vesper Sparrow and Chestnut-collared Longspur, both of which prefer sparse vegetation.

A second conclusion to be drawn from our findings in relation to cropping is that the spatially extensive cultivation of certain crops, notably sorghum, grain corn, and wheat, may create agricultural environments conducive to breeding for grassland birds. We do not claim that these crops are necessarily favorable through cause and effect; instead, they may share with grassland birds environmental requirements we did not directly measure (e.g., topography, soil type). Alternatively, the cultivation practices and associated land-management patterns may create conditions favorable to these birds. Long-billed Curlews apparently do well in wheat fields in Oklahoma that are subjected only to spraying (Shackford 1994), and Horned Larks have long been known to thrive in cultivated fields (Graber and Graber 1963). The benefits of particular crops need not accrue solely to breeding birds; certain crops modify the effects of snow cover in winter, permitting foraging to continue in fields where other vegetation would trap the snow in an impenetrable mass (Larsen et al. 1994). For some grassland birds, small grains may approximate a natural grassland, as shown by Warner (1994) for Ring-necked Pheasants; only Horned Larks, however, appear capable of persisting in a monoculture of cereal crops (Owens and Myres 1973). It is also possible that cultivation maintains ephemeral conditions that some species prefer. Grasshopper Sparrows favor open grasslands providing openings and gaps through which the birds can move while foraging (Whitmore 1981), and open-planted crops may provide an adequate substitute. Chestnut-collared Longspurs, however, though needing open vegetation in which to forage, will not nest in cultivated fields (Owens and Myres 1973).

The third point to be drawn from our crop analyses is that some crops—among them soybeans, oats (*Avena*), alfalfa, sunflowers (*Helianthus* spp.), and barley—appeared only as local modifiers of species distributions already largely constrained by other factors. Some of these may be chance correlations; sunflowers, for example,

are grown mainly in the Dakotas, and their correlations with species with ranges centered in this region may be due to confounding effects. Barley and soybeans, however, consistently displayed the same correlations from year to year (Table 2), so they may have a more ecological basis. Some of these small correlations probably reflect use of the crop as an adequate substitute for native habitat; thus the correlation of durum wheat with Baird's Sparrow (Table 3) may result from the species using this crop as a source of vegetative cover in what is otherwise an agricultural waste (Owens and Myres 1973).

Influence of Climate

The pattern of influence of climate variables in our analysis is of considerable interest given Root's (1988a) demonstration of the power of climatic limits to constrain winter bird distribution. We found that in most grassland bird species there were significant associations between climate and weather variables and local breeding abundance. Breeding-season analyses of climate influences on bird populations are more likely to be mediated indirectly (e.g., by climate influence on productivity; Rotenberry et al. 1995). Currie (1991) hypothesized that the latitudinal gradient in breeding-species richness was set largely by the corresponding productivity gradient. In contrast, wintering-distribution limits appear to be very close to those set by a model of physiological limits to maximum daily metabolic rates for resident species (Root 1988a). Among the seven species for which a climate variable was the largest correlate of breeding distribution, only that for the Bobolink involved winter climate (Table 3). Because Bobolinks winter in South America, however, winter temperatures in the United States cannot be directly related to their abundance; whatever effects winter temperatures have on Bobolinks must therefore be indirect. Price (1995) reached the same conclusion from his model of the climate envelope of the Bobolink.

Our other major climate effects largely differ from those reported by Price (1995). Our results implied that Eastern Meadowlarks were more abundant in hot summer areas (Table 3), but Price (1995) found a complex pattern of responses to temperature for this species, with quadratic functions of mixed sign describing dependencies on temperatures in summer and in the wettest month of the year. Where we found negative effects of annual precipitation for Horned Lark, Lark Bunting, and Western Meadowlark, Price (1995) reported generally negative effects only for Lark Bunting. For Horned Lark he found positive effects of precipitation in spring and in the coldest month, and for Western Meadowlark his largest terms were positive contributions from precipitation in winter and in the hottest and driest month but with negative terms for other seasonal components of precipitation. Thus, the overall effect of precipitation on Western Meadowlarks depends on the distribution of seasonality of that precipitation. It is also worth noting here how different methods yield different answers to what is apparently the same general question of climate correlates. Price (1995) derived a single climate envelope for the entire range of each species, producing rules applicable over the entire range but expressed in strongly seasonal aspects of climate. Our study modeled regional abundance in terms of less seasonal climate variables using CART. Walker (1990) has previously shown how the climate envelope and CART approaches yield complementary perspectives on the environmental correlates of species distribution and has pioneered their integration into a common model.

Root's (1988a, b) work focused on the correlation of wintering limits with midwinter climate conditions. She has elsewhere identified the lack of knowledge about breeding limits as a critical gap in our understanding of environmental constraints on birds (Root 1993). We found that, for several species, breeding densities were also correlated with midwinter climates, with fewer breeding pairs where winters are cold (Table 2); however, winter climate was a major predictor only for the Bobolink, a neotropical migrant (Table 3). Whereas climatic constraint by January temperatures was clearly widespread across species (Table 2), year-to-year variation in January temperatures also appeared regularly and at some strength in species models. The bimodal distribution of ranks for January climate, in combination with consistent effects for January weather, revealed the existence of one group of species with breeding distributions sensitive to midwinter climate conditions (Gray Partridge, Long-billed Curlew, Vesper Sparrow, Lark Bunting, Savannah Sparrow, and Bobolink) and a second group (Ring-necked Pheasant, Upland Sandpiper, Horned Lark, Grasshopper Sparrow, Dickcissel, and Eastern and Western meadowlarks) more sensitive to year-to-year variation in conditions. Dickcissels have long been known to be sensitive to annual variations in winter conditions, largely because poor winters may constrain the rate of progression of the spring migration northward (Fretwell 1986). Our findings suggest that other grassland bird species may share a similar sensitivity. For resident species such as Gray Partridge and Ring-necked Pheasant, however, winter conditions can have direct effects; heavy precipitation

as snow covers the ground, and food resources for overwintering become limiting (Riley 1995).

Our results suggest that summer temperature limits are not as important for grassland birds as studies suggest they are for other groups of birds (Blake et al. 1992, O'Connor 1992). Similarly, Price (1995) found only 7 of 23 species to be correlated either with summer temperatures or with temperatures in the hottest month, generally with negative effects evident. The link with drought identified by Blake et al. (1992) is congruent with the importance of precipitation associations found here. July temperatures typically may be associated with drought, such that our analyses attribute variations in density to variations in precipitation rather than to temperature. Drought effects appear to be rather short-lived in grassland birds, with most species recovering within 1 yr (George et al. 1992). It is tempting to suggest that the absence of summer temperature links is because grassland birds redistribute themselves each year in line with the prevailing distribution of weather-controlled resources, as argued previously of Dickcissels by Fretwell (1986). If this were the case, one might expect a pattern of strong correlations with the weather variables considered here instead of the lack of correlations we found (Table 2). Therefore, we consider whether breeding distributions might not instead be constrained in a climate envelope by the distribution of habitat.

Influence of Patch Variables

Our analyses lend considerable support to earlier research that suggested that grassland birds are particularly sensitive to habitat fragmentation. Area sensitivity is well established. Samson (1980) and Johnson and Temple (1986) concluded that small fragments of grasslands cannot support species that need interior habitats, and Vickery et al. (1994) and Herkert (1994) have shown through site-specific studies that grassland birds are more likely to occur on large patches of grassland habitat than on small ones. Vickery et al. (1994) demonstrated area sensitivity for Upland Sandpipers, Vesper, Savannah, and Grasshopper sparrows, Bobolinks, and Eastern Meadowlarks. Our results expand these studies in two significant ways. First, we found that grassland bird species as a class are more influenced by habitat patch variables, and less influenced by land-use proportions in an area, than are other bird species (Fig. 1). Patch variables are present significantly higher in the regression tree models for grassland species than for other species, thus ensuring that they affect proportionately more of the survey area and that they constrain distributions more than does landscape composition. Thus, grassland species are differentially susceptible to habitat fragmentation.

Second, we raise the possibility that patch variables are more influential in habitats less dominated by grass (Table 5). A differential toward stronger association of incidence and patch variables in nongrassland habitats implies that patch configuration or size issues have become more important in the cropland and wooded areas that have replaced native prairies. To our knowledge, no one has previously suggested that species might be more acutely selective in less favored habitats than in preferred habitats, though it is a logical outcome of more general phenomena such as the habitat hierarchies of Brown (1969) and Fretwell and Lucas (1969). One might expect that birds using secondary habitats would be more selective as to which parts of these habitats they use if they are unable to settle in their preferred habitats. In their study in Maine, Vickery et al. (1994) noted that the grassland species they studied may have favored grassland-barrens rather than hayfields and pastures simply because grassland-barrens were the principal source of large expanses of grassland habitat.

If grassland habitats are generally becoming scarcer in North America, and particularly in agricultural areas (Askins 1993, Warner 1994), birds are likely to use near-equivalent patches of cropland and other nonnatural habitat (Litvaitis 1993, Vickery et al. 1994) but to require larger areas of such before settling there. Thus, With (1994) suggests that the natural habitat of McCown's Longspur in native short-grass prairies has now become a mosaic of pastures variably grazed by cattle and fragmented by agricultural activities and human development, and that the species may treat heavily grazed pastures as near approximations of the original habitat. In cropland-pasture, one would expect larger patches to be favored over smaller ones. Similarly, Warner (1994) found that the diversity of grassland species was highest on those study sites closest to grassland. Warner also demonstrated that Ring-necked Pheasant nests hatched more successfully the greater the amount of grassland (whether strip cover, forage crops, or small grains) surrounding the nest. These studies indicate how the increased influence of patch variables in secondary habitats might arise, under the assumption that these habitats are being used by populations displaced from preferred grassland habitats.

A more alarmist interpretation is also possible: some of the scarcer grassland species may display greater apparent selectivity simply because there are now so few individuals remaining that they fill only the better components of

the available habitats (O'Connor 1981, Vickery et al. 1994). Whatever the processes underlying the pattern, our findings endorse the need to preserve remaining large plots of grassland habitats and to consolidate smaller patches in management efforts. The role of the CRP may be critical in this regard.

A Cautionary Note

An important reservation about the findings here, not only for crop variables but for climate and habitat patch analyses, is that the CART models we used, despite their sophistication, return only estimates of correlations. Therefore, our conclusions are subject to the normal caveats of correlation analysis, in particular that correlation does not ensure causation. Some conclusions are likely to be stronger than first apparent with a correlation analysis. Our emphasis on patch variables and on CRP effects are each based on analyses with very different biases than in the site-specific studies of Vickery et al. (1994) and Herkert (1994) for area sensitivity and of Johnson and Schwartz (1993) for the CRP. Hence, our arrival at a similar assessment of the importance of these variables for grassland bird species lends strength to all the studies; different sources of bias are unlikely to yield similar conclusions in the absence of a real ecological effect. The broad spatial extent of our analyses and their replication across multiple years provide a robust overview of the correlates of grassland bird distribution that has hitherto been unavailable. Our results highlight particular patterns of correlation as deserving of further attention and raise some important new questions about constraints on the distribution of grassland bird species.

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PETER D. VICKERY AND JAMES R. HERKERT, EDITORS

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Peter D. Vickery and James R. Herkert
Editors

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