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UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

A MULTISCALE ANALYSIS OF FACTORS INFLUENCING
THE DISTRIBUTIONS OF BIRDS IN THE SOUTHERN GREAT PLAINS

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

Doctor of Philosophy

By

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Norman, Oklahoma
1998

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A MULTISCALE ANALYSIS OF FACTORS INFLUENCING
THE DISTRIBUTIONS OF BIRDS IN THE SOUTHERN GREAT PLAINS

A Dissertation approved for the
DEPARTMENT OF ZOOLOGY

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PREFACE

This dissertation is presented as three chapters. Each chapter has been submitted to a refereed journal and is formatted accordingly. The first chapter has been submitted to *Landscape Ecology*, the second to *Conservation Biology*, and the third to the *Wilson Bulletin*.

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ABSTRACT

Songbird populations in North American prairies have exhibited the most widespread and steepest declines of any group. According to the North American Breeding Bird Survey, only 10% of grassland birds have shown positive growth. Of particular concern are prairie birds that are sensitive both to local habitat and area characteristics of the landscape. I studied the influence of local- and landscape-level habitat factors on breeding-bird communities in a prairie landscape in southwestern Oklahoma, U.S.A. Local habitat characteristics were sampled at study plot transects, and landscape measures were computed from a land-cover map digitized from aerial photography. Landscape variables within 100 m × 1500 m belt transects were computed from digitized aerial photography. Multiscale ordination revealed that landscape characteristics were most pronounced at a spatial scale of 8 ha (*i.e.*, 100 m × 800 m). General trends of landscape structure were summarized on principal components, resulting in the delineation of orthogonal gradients of heterogeneity and fragmentation. Grassland bird species were associated with large homogeneous habitat patches, while woodland species occurred in small heterogeneous patches. Bird species categorized on the basis of migratory status showed considerable variation along gradients reflecting the degree of heterogeneity and fragmentation. Mean patch size was an important factor in discriminating among groups of bird species classified on the basis of habitat, nesting height, and nest type.

Habitat regression models using local and landscape habitat components explained 79% of the variation in bird species richness and 41% of the variation in

abundance. Bird species richness was best explained by landscape habitat variables, while overall bird abundance was related to a combination of local and landscape variables. Abundance of woodland and grassland/savanna species was accounted for by local habitat variables representing vegetation and a slope gradient. Models for typical woodland species—Tufted Titmice (*Parus bicolor*), Red-eyed Vireos (*Vireo olivaceus*), Great Crested Flycatchers (*Myiarchus crinitus*), and Northern Cardinals (*Cardinalis cardinalis*)—were explained primarily by local vegetation characteristics ($r^2=0.52-0.74$). A combination of local and landscape habitat features accounted for the variation (local, 42-100%; landscape, 0-60%) in abundance of four typical grassland/savanna species—the Field Sparrow (*Spizella pusilla*), Eastern Meadowlark (*Sturnella magna*), Grasshopper Sparrow (*Ammodramus savannarum*), and Dickcissel (*Spiza americana*). In general, avian-community indices were related both to landscape and local habitat characteristics. Ecological groups of birds and individual species were accounted for primarily by local habitat characteristics.

I evaluated the degree of fragmentation of habitats used by grassland and savanna bird species in a prairie landscape. Habitat fragmentation was estimated using perimeter-area fractal dimension computed at 13 spatial scales ranging from 10 to 1,000 ha. Fractal dimension measures of habitats used by grassland/savanna birds were compared with those of randomly-selected sites. Habitat fragmentation, measured by fractal dimension, is not a scale-independent feature of the landscape. Habitats occupied by grassland/savanna birds were significantly different from randomly-chosen sites at spatial scales of 50 and 75 ha. Mourning Doves (*Zenaida macroura*), Dickcissels (*Spiza*

americana), Field Sparrows (*Spizella pusilla*), and Eastern Meadowlarks (*Sturnella magna*) occurred in habitats that exhibited a higher level of fragmentation than random sites. The spatial configuration of habitat patches is an important factor for determining the appropriate spatial scale to evaluate habitat fragmentation. Natural fragmentation of the grasslands by woodlands associated with intermittent streams has a strong influence on the distribution of grassland/savanna birds.

Conservation strategies for prairie birds should take into consideration that particular species respond differently to local- and landscape-level habitat characteristics and that broad-scale conservation recommendations are likely to be ineffective across a variety of landscapes.

**Landscape-level influences on the distribution of birds in the southern
Great Plains**

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Abstract

I studied the influence of landscape-level factors within bird communities in the southern Great Plains, USA. Landscape variables (mean habitat patch size, number of patches, habitat richness, corrected perimeter/area, related circumscribing circle, contagion, angular second moment, and contrast) within 100 m × 1500 m belt transects were computed from digitized aerial photography. Multiscale ordination revealed that landscape characteristics were most pronounced at a spatial scale of 8 ha (*i.e.*, 100 m × 800 m). General trends of landscape structure were summarized on principal components, resulting in the delineation of orthogonal gradients of heterogeneity and fragmentation. Grassland bird species were associated with large homogeneous habitat patches, while woodland species occurred in small heterogeneous patches, which reflects the fact that in southwestern Oklahoma, grassland patches are more extensive than woodland tracts. Bird species categorized on the basis of migratory status showed considerable variation along gradients reflecting the degree of heterogeneity and fragmentation. Mean patch size was an important factor in discriminating among groups of bird species classified on the basis of habitat, nesting height, and nest type.

Keywords: bird distributions, Oklahoma, multiscale ordination, principal-components analysis, discriminant analysis, Great Plains

1. Introduction

A landscape can be defined as a heterogeneous land area composed of an interacting mosaic of patches (McGarigal and Marks 1995). The importance of spatial and temporal patterns of heterogeneity in landscapes has been well documented (*e.g.*, Danielson 1991; Hardt and Forman 1989; Milne *et al.* 1989; Pulliam *et al.* 1992). Such patterns of heterogeneity are known or hypothesized to affect many ecological phenomena including population dynamics, life histories, dispersal patterns, species diversity, predation, and patterns of natural selection (Wiens 1994; Addicott *et al.* 1987).

The dynamics of a local population may be influenced not only by the characteristics of the local environment, but also by the surrounding landscape (Turner *et al.* 1995). For example, Pearson (1993) examined the relative influence of local- and landscape-level factors on wintering bird populations and found that landscape characteristics were important factors influencing bird species richness and diversity. In fragmented shrubsteppe habitats, Knick and Rotenberry (1995) found that some breeding passerine birds depended on local vegetation cover and landscape features, such as patch size of shrub habitats and the similarity of sites.

Although broad-scale landscape patterns influence the ecological relationships of organisms, using the same spatial scale to examine spatial heterogeneity in two different landscapes may not be the most effective approach (Wiens 1976, 1989; Addicott *et al.* 1987). For example, a semi-arid grassland typical of the Edwards Plateau region in Texas is composed of a mosaic of juniper and oak clusters interspersed within a matrix of grasslands (Smeins and Merrill 1988). Spatial heterogeneity in a semi-arid landscape is

not readily comparable with that of habitats of northern Minnesota that are composed of deciduous hardwood and mixed deciduous-coniferous forests with scattered clearcuts. Therefore, it is necessary to determine the appropriate scale of heterogeneity of the landscape prior to evaluating the ecological relationships of the organisms or populations.

I examined the landscape characteristics of an area in the southern Great Plains and determined the spatial scale at which landscape patterns are most pronounced. Additionally, I evaluated the influence of landscape factors on the distribution of birds and determined the landscape features that show the greatest efficacy for distinguishing among groups of bird species.

2. Methods

2.1. Study area

The study area (160,535 ha) is located in southwestern Oklahoma, USA (Fig. 1). It is centered on the Fort Sill Military Reservation (38,292 ha) and includes approximately 80% of the Wichita Mountains National Wildlife Refuge. Several small communities are included in the study area.

The area is transitional, containing vegetation communities typical of both mesic and xeric environments. The native vegetation at Fort Sill and the surrounding area represents communities found in both moist eastern deciduous forests and dry, rocky grasslands. Typical habitats found in the study area include: (1) grasslands of short, mixed and tall grasses; (2) rangeland, which is a grassland that has been grazed or cut for hay; (3) agricultural fields of cultivated crops; (4) mesquite savanna composed of mixed

grasses with scattered mesquite (*Prosopis glandulosa*); (5) oak savanna that is intermediate between grassland and upland deciduous forest; (6) bottomland forest; (7) riparian vegetation; (8) woody-vegetation patches, which are small patches of planted trees; and (9) small woodland patches associated with disturbed areas. Descriptions of these vegetation types are provided in Appendix A.

2.2. Sampling techniques

Remotely-sensed data were collected for the study area to develop a land-cover classification. After classifying the landscape, I computed landscape indices at a variety of spatial scales. Plots were established to sample bird communities.

2.2.1 Remote sensing

A land-cover map of the study area was produced from 1990 National High Altitude Photography (NHAP) panchromatic aerial photographs. I obtained 172 61 cm × 61 cm photographs (scale 1:7920) from the U.S. Agricultural Stabilization and Conservation Service, Salt Lake City, Utah. Photographs were taken 24 November to 9 December 1990. Each photograph was georeferenced using 7.5-minute topographic maps (1:24000) obtained from the U.S. Geological Survey. Land-cover categories, including 12 vegetation and 3 land-use types (15 total; see descriptions in Appendix A), were identified by visual interpretation. Polygons defining land-cover boundaries were manually delineated using the Geographic Resources Analysis Support System (GRASS), a geographic information system (GIS; CERL 1989). After completing a digitized vector

map for each photograph, the individual vector maps were coalesced to create a single vector map of the study area. Each polygon (ca. 9,000 total) representing a defined land-cover patch was labeled appropriately. The labeled vector map was rasterized at 1-m resolution to produce the final land-cover classification map of the study area. The land-cover map was checked for accuracy by ground-truthing. Steps involved in the process of producing the rasterized land-cover map are summarized in Figure 2. The final land-cover classification map of the study area is shown in Figure 3.

2.2.2. Plot selection

The U.S. Army implemented the Land Condition Trend Analysis (LCTA; Tazik *et al.* 1992) program at Fort Sill to establish sample plots to inventory and monitor natural resources. The LCTA plots were selected by stratified-random sampling to provide an adequate representation of the various vegetation communities. For 98 LCTA plots, UTM coordinates for starting position and a randomly-chosen azimuth were determined to establish 100-m transects at each site. With the exception of artillery impact areas, the plots are relatively evenly distributed throughout the study area.

2.2.3. Bird sampling

Annual censuses of birds were made at the 98 plots from 1993-1995 using a modified point-count transect technique (Blondel *et al.* 1981). Each year the inventory was conducted within a two- to four-week span (falling within the period 15 April to 30 June) corresponding to the seasonal peak in breeding-bird activity. Each plot was censused

twice each year, once in the morning and once in the late afternoon. In total, each site was sampled six times (twice each year for three years). All morning censuses were conducted between 0.5 h before and 4 h after sunrise. Late-afternoon censuses were conducted during the 4 h prior to sunset. Plots were censused by slowly walking the length of a 100-m transect in 6 min and recording all birds seen or heard within 100 m of the transect line. I then stopped for 8 min and recorded any new birds seen or heard within 100 m. Finally, I walked back to the starting point over a period of 6 min, recording any new birds detected within 100 m.

The bird species (83 total; Appendix B) recorded in the study area were grouped (Peterjohn and Sauer 1993) by (a) habitat, (b) migratory status, (c) nesting height, and (d) nest type.

2.2.4. Landscape variables

Eight measures of landscape structure were computed for a series of contiguous quadrats (100 m × 100 m) in a belt transect 1,500 m long (Fig. 4). Belt transects were centered on each 100-m line transect. Landscape measures included: (1) mean habitat patch size; (2) number of patches; (3) habitat richness, the number of different habitats in the sampling area; (4) corrected perimeter/area, an index of patch shape; (5) related circumscribing circle, an index of patch shape that compares the average area of the smallest circles that can circumscribe individual habitat patches in the sampling area; (6) contagion, an index that quantifies the degree of aggregation or clumping; (7) angular second moment, a

measure of habitat homogeneity; and (8) contrast, a measure of the contrast or amount of local variation present in the landscape (see Appendix C for detailed descriptions).

In order to obtain an overview of the associations among the eight landscape variables, I used UPGMA (unweighted pair-group method using arithmetic averages; Sneath and Sokal 1973) cluster analysis to group them based on product-moment correlations. The cophenetic correlation coefficient was calculated for the resulting dendrogram, which provides an index as to how well the diagram summarizes the pairwise correlations among variables.

2.3. Statistical analysis

A series of multivariate analyses were used to evaluate the influence of landscape factors on the distribution of birds. Multiscale ordination was used to determine the spatial scale (*i.e.*, block size 8; see Results) at which landscape features are most pronounced.

Principal-components analysis was then used to characterize the general trends along gradients of landscape structure at this spatial scale. Central tendencies and homogeneity of variances of principal-component projections were evaluated for each grouping of bird species. Finally, stepwise discriminant function analysis was used to determine the landscape characteristics most important in distinguishing among groups of bird species.

2.3.1. Multiscale ordination

Conventional multivariate analyses of vegetation often are limited to examination of a single species at several spatial scales or several species at a single spatial scale.

However, associations of species in a community may be influenced by environmental and biological factors at various spatial scales. Thus, I have employed a multiscale ordination technique developed by Noy-Meir and Anderson (1971) and modified by Ver Hoef and Glenn-Lewin (1989) to examine landscape structure at multiple spatial scales for contiguous blocks along 1,500-m belt transects.

Covariance matrices for all landscape index pairs were calculated using Greig-Smith's (1983) two-term local covariance (TTLC) statistic, which computationally blocked the quadrats into increasing larger sizes (block size 1 = 100 m × 100 m, block size 2 = 100 m × 200 m, block size 3 = 100 m × 300 m, etc.). Block sizes beyond 15 could not be evaluated given the area of coverage of available aerial photography. Eigenvectors and eigenvalues were found for the total covariance matrix, which was computed by summing the covariance matrices for each block size. The eigenvalues were partitioned into the amounts that each block size contributed to that eigenvalue. These partitioned eigenvalues were plotted against block size, and the peak of such a curve revealed the scale at which the pattern was most pronounced (Ver Hoef and Glenn-Lewin 1989).

2.3.2. Principal-components analysis

I employed principal-components analysis to characterize general trends along orthogonal gradients reflecting landscape structure. Landscape variables were computed for the 98 sites at a single spatial scale (block size 8, determined from multiscale ordination analysis). Calculations were carried out with the computer package NTSYS-pc (Rohlf

1993) and starting with an 8-landscape-variable \times 98-sampling-plots matrix. From a matrix of correlations among eight landscape metrics, major trends were represented on principal-component axes (Sneath and Sokal 1973). I retained the first two components, which were the only ones with eigenvalues greater than 1.0. The first component explains the maximum amount of variance possible on a single axis. The second component accounts for the maximum amount possible of the remaining character variance. Correlations (*i.e.*, loadings) of original variables with principal components were generated, and component scores of each sample plot were projected onto the components. For projections, the landscape variables were standardized to a mean of 0 and standard deviation of 1 (Sneath and Sokal 1973). Values of each landscape variable were obtained for each bird species by averaging the values of that variable for each plot where the bird species occurred on at least one of the six censuses. Projections for bird species were computed using the loadings from the original analysis.

Kruskal-Wallis tests were used to compare the differences in central tendency of principal-component projections for bird species grouped on the basis of habitat and migratory status (Sokal and Rohlf 1995). Similarly, the Mann-Whitney *U*-test was employed to compare the differences in principal-component projections for species grouped by nesting height and nest type, which contain only two classes within each group. Also I examined projections with respect to homoscedasticity. Among groups of bird species categorized on the basis of habitat and migratory status, Bartlett's test for homogeneity of variances was employed (Sokal and Rohlf 1995). The Scheffé-Box test

was used to test for homoscedasticity for projections of bird species grouped on the basis of nesting height and nest type

2.3.3. Discriminant analysis

I used stepwise discriminant analysis (McLachlan 1992) to determine the subset of the eight landscape variables that, in combination, maximally discriminated among groups of birds species. I contrasted the following groups: (1) grassland species versus successional-scrub species versus woodland species; (2) permanent residents versus short-distance migrants versus Neotropical migrants; (3) ground- and low-nesting species versus midstory- and canopy-nesting species; and (4) cavity-nesting species and open-cup-nesting species. Values of each landscape variable were obtained for each bird species by averaging the values of that variable for each plot where the bird species occurred.

I used the computer package SYSTAT (SPSS Inc. 1996) for calculations. In the discriminant analysis, landscape variables selected tended to be those that exhibited relatively high variation among species and low variation within species. Forward and backward stepping was used (*i.e.*, variables were entered or removed from the classification function based on F -values). The F -to-enter a variable in the classification function was set at 4.0, while the F -to-remove was 3.9. Sample species were projected onto the resulting canonical axes.

Classification functions were derived to assign species to one of the groups, depending on the relative probability of group membership. A given species had an equal

probability of being assigned to any one of the groups; this does not mean that an equal number of species would be assigned to each group, but only that *a priori* I did not bias the possibility of a particular species being categorized as representing one group or another. In fact, because sample sizes for groups were unequal, more species were assigned to some groups than to others simply because plots had attributes that were characteristics of a particular group. Measurement values for the plot were multiplied by coefficients of the classification function, and the resulting products added to the constants of these function. The calculation was completed for all species and they were then assigned statistically to the appropriate group, depending on which of the resulting classification values was the greatest (Schnell *et al.* 1986). I also used a true-jackknifed classification procedure, which effectively leaves out the individual species being considered, recomputes coefficients of the function, and then evaluates the species. Typically, this procedure gives a better indication of the efficacy of functions to allocate or identify correctly new species (*i.e.*, those not used to compute the functions; Schnell *et al.* 1986).

As indicated by Morrison *et al.* (1992) and others, one must be judicious when interpreting discriminant analyses and other multivariate results where relatively small samples are involved for groups being evaluated, which is the case for some groups in my study. Use of the jackknife procedure does result in a conservative assessment of the degree of discrimination possible between groups.

3. Results

3.1. *Multiscale ordination*

As examples, the first partitioned eigenvalues for two sample plots are shown in Figure 5. For plot 42 (Fig. 5a), block size 8, corresponding to a patch size of 100 m × 800 m, contributed the most to the first eigenvalue. For plot 49 (Fig. 5b), there is a monotonic increase in the partitioned eigenvalue (*i.e.*, each block size contributed more than previous one).

Results of multiscale ordination for each plot are summarized in a frequency distribution of block sizes that had the highest eigenvalues for the first eigenvector (Fig. 6). The block size with the largest number of sites having the highest eigenvalue for the first eigenvector occurred at block size 8, indicating that landscape structure is most pronounced at this spatial scale. A second peak also was found in the figure at block size 15. However, in general, sites exhibiting the highest eigenvalue at block size 15 showed a continual increase with each block size contributing more than the previous one (*e.g.*, Fig. 5b). Therefore, the peak eigenvalue for these sites is limited by the maximum block size evaluated, which suggests that the proportion of the eigenvalue contributed for many of these sites would continue to increase with block sizes larger than 15. Thus, the peak at block size 15 is most likely a cumulative effect for all sites with peak eigenvalues greater than or equal to block size 15. Overall, the data indicate that block size 8 represents the most appropriate scale.

3.2. Association of landscape variables

Given that selection of landscape variables for inclusion in this study was based in part on the premise that they should represent different aspects of landscape-level characteristics of the plots and should not be largely redundant, it is not surprising that, in general, the variables selected were not highly correlated (Table 1). Based on absolute correlations, the variables form two groups (Fig. 7), the first of which has corrected perimeter/area and related circumscribing circle, which are negatively associated (see Table 1); as corrected perimeter area increases, the related circumscribing circle decreases. In the second cluster, contagion and richness are the most closely related. These are grouped with mean patch size (Fig. 7), which decreases as contagion and richness increase (Table 1). The three are then sequentially joined by contrast, angular second moment, and number of patches (Fig. 7); contrast and number of patches are positively correlated with contagion and richness, while angular second moment is negatively associated (Table 1).

3.3. Principal-components analysis

Principal-components analysis can be helpful in summarizing landscape data and possibly identifying fundamental gradients, thus providing an overview of relationships among sample plots (Grzybowski *et al.* 1994). Based on data for block size 8, the first two components accounted for 77.6% of the total variance in the landscape variables (Table 2). Component I is a composite of landscape variables representing patch area, habitat richness, habitat homogeneity, and degree of clumping of patches (high positive loadings for mean habitat patch size and angular second moment; high negative loadings

for habitat richness, contagion, and number of patches). Thus, principal component I represents a gradient from areas with small heterogeneous patches to areas with large homogeneous patches. Component II has high positive loadings for corrected perimeter/area and contrast, which measures the degree of fragmentation and compaction. Related circumscribing circle, a measure of the extent of local variation in the habitat types, had a high negative association on component II. Thus, component II can be characterized as a gradient representing the degree of habitat patch fragmentation, ranging from compacted areas with little fragmentation (negative scores on component II) to fragmented areas with local variation in habitat patches (positive scores).

Projections of bird species onto principal components I and II are shown in Figure 8. The first grouping of species, categorized by habitat, includes grassland species, successional-scrub species, and woodland species (Fig. 8a). There were few occurrences of bird species such as great blue herons or mallards that were classified as being primarily wetland or open-water birds. Thus, these species were not included in this analysis. Projections for these groups on component I differ significantly in central tendency (Table 3). The six grassland species have relatively high values on principal component I, indicating an association with large homogeneous patches. Cassin's sparrow had the highest score on this component (lower right portion, Fig. 8a); this species occurs in large patches of short and mixed grassland. Differences among groups in variance on component II approached statistical significance (Table 3), with grassland species tending to be found on sites with an intermediate degree of fragmentation, as indicated by their intermediate scores on component II. Projections for successional-

scrub and woodland species were broadly distributed on this component. Some woodland species were found in highly compacted areas (*e.g.*, red-shouldered hawk; lower left, Fig. 8a), while others occupied highly fragmented sites (*e.g.*, white-eyed vireo; upper left, Fig. 8a) as indicated by component II.

Projections of bird species categorized on the basis of migratory status are shown in Figure 8b. Permanent residents, short-distance migrants, and Neotropical migrants are broadly distributed on components I and II, indicating that bird species in each of these groups are found on sites with a variety of landscape characteristics. Sites occupied by permanent residents, including northern cardinal and northern mockingbird, are more centrally distributed on component II than are short-distance or Neotropical migrants.

The third classification of bird species was based on nesting height and included mainly passerines (see Appendix B). Projections of ground- and low-nesting species, as well as midstory- and canopy-nesting species, are depicted in Figure 8c. No significant differences between these groups were found for central tendency or variance (Table 3).

Projections on components I and II for cavity-nesting and open-cup-nesting passerine species are shown in Figure 8d. A highly significant difference was found in group variances on component I (Table 3). Cavity-nesting species, including the Carolina chickadee and eastern bluebird, were narrowly distributed with intermediate values on component I, indicating their association with sites that are transitional between small heterogeneous and large homogeneous patches. Projections for open-cup-nesting species were broadly distributed on component I. Projections on component II were widely scattered for both cavity-nesting species and open-cup-nesting species, indicating that

species of both groups were found on sites that varied considerably from highly compacted to highly fragmented.

3.4. *Discriminant analysis*

Discriminant analyses highlight the combinations of landscape variables that best differentiate between specified groups of sites. Below I describe the habitat differences among groups of bird species based on habitat, migratory status, nest height, and nest type.

When evaluating the bird species grouped by habitat, the resulting discriminant function separating grassland, successional-scrub, and woodland species (Fig. 9a) included two variables (Table 4). Statistically, the most important variable was mean patch size. Grassland species often were found in areas with large habitat patches, while woodland species were found in those with smaller patches. The second variable entered was number of patches. Woodland species typically were associated with areas that are moderately heterogeneous, while grassland species occurred in large homogeneous grasslands. Classification functions correctly assigned 77% of woodland species and 67% of grassland species. However, less than one-half (47%) of successional-scrub species were correctly classified (plotted in Fig. 9a). In prairie landscapes, some successional-scrub species, such as the field sparrow and Bewick's wren, typically are associated with edge habitats that are transitional between woodlands and grasslands. Thus, it is not surprising that classification accuracy for successional-scrub species is lower than for woodland and grassland species.

In the analysis of bird species classified according to migratory status, the two variables selected for the discrimination function (Table 4) were notably different from those incorporated in the previous analysis. The first variable entered, angular second moment, reflects the amount of homogeneity in the landscape. The next variable, related circumscribing circle, measures the degree of compactness. These variables, in combination, were not effective in discriminating among bird species on the basis of migratory status. Fewer than one-half of permanent-resident species and short-distance-migrant species correctly classified (42 and 45%, respectively), and only 38% of Neotropical migrants were correctly classified (Fig. 9b). Thus, landscape characteristics alone are not sufficient for distinguishing among bird species based on migratory status.

For species categorized by nest height, mean patch size and corrected perimeter/area were the first two variables entered (Table 4). Mean patch size also was statistically important in the analysis of species grouped by habitat (see above). More than one-half of the ground- and low-nesting species (68%), as well as canopy-nesting species (59%), were correctly assigned by the classification functions derived from the discriminant analysis (Fig. 9c). Ground- and low-nesting species, such as the dickcissel and Bell's vireo, are common throughout the grassland areas, which are characterized by large habitat patches. Summer tanagers and blue-gray gnatcatchers are midstory- and canopy-nesting species that are associated with upland forest vegetation, which generally occurs as small fragmented patches in this region of the continent.

The variables selected in the discriminant analysis for bird species grouped by nest type were the same as those entered in the analysis of bird species categorized by

habitat (Table 4). Mean patch size was entered first, followed by number of patches. Classification functions derived from the analysis were successful in correctly assigning 75% of cavity-nesting species and 67% of open-cup-nesting species (plotted in Fig. 9d). Cavity-nesting species, including white-breasted nuthatches and red-bellied woodpeckers, typically are found in the forested areas, while open-cup-nesting species are found both in woodlands and open grasslands. Thus, classification accuracy was relatively high, which is similar to the efficacy of discriminant analysis for bird species categorized by habitat.

4. Discussion

The field of landscape ecology has emerged in response to environmental problems—such as habitat fragmentation, global climate change, and loss of biodiversity—that require an expansion of the scope and scale of study (Turner *et al.* 1995). A fundamental issue in landscape ecology is the determination of the appropriate ecological scale, which varies with both the organism and the questions of interest (Wiens 1989; Levin 1992).

Landscapes throughout North America may differ markedly with regard to the spatial arrangement of habitats; therefore, the appropriate spatial scale for examination of patterns of heterogeneity may vary among landscapes. For example, the spatial configuration of habitats in a prairie landscape, which is characterized by large patches of grasslands interspersed with relatively small patches of upland and bottomland deciduous forests, is conspicuously different than a landscape composed of a shrub-steppe vegetation. Thus, the ecological relationships of organisms should be evaluated at a spatial scale or scales appropriate for a particular landscape.

In a study of wintering bird communities in the Piedmont region of Georgia, USA, Pearson (1993) examined the influence of local and landscape-level factors by interpreting aerial photographs. He concluded that the distribution of some species may depend not only on the characteristics of the local habitat, but also on those of surrounding habitat patches. Thus, the occurrence of some species can only be explained with the inclusion of habitats characteristics at a broader scale.

In my study, landscape characteristics derived from quantified aerial photography were examined over a range of scales. Results from multiscale ordination revealed that landscape characteristics were most pronounced at a spatial scale at block size 8, represented by a 100 m × 800 m belt transect equivalent to an 8-ha area.

The distribution of bird species on principal component I, which represents a gradient from small heterogeneous patches to large homogeneous patches, showed substantial variation. However, if we consider species grouped by habitat association, there are observable distinctions. For example, grassland species were predominately found in areas characterized by large homogeneous habitat patches. This pattern also has been observed by Vickery *et al.* (1994) in a study of grassland and early-successional bird species in the northeastern United States. They found that only grasslands 200 ha or larger are likely to support a diverse grassland bird fauna. Vickery *et al.* (1994) found that grasshopper sparrows, which also occurred in my study, reached 50% incidence in grasslands approximately 100 ha in area. Woodland species in my study were associated with small heterogeneous habitat patches. Forests, which comprise only 35% of the total cover in the study area, are generally associated with intermittent and perennial drainages

that tend naturally to have convoluted boundaries. Combined with the artificial habitat alteration, forests typically were smaller and more fragmented relative to grassland areas. Thus, woodland bird species were found primarily in relatively small forest patches. The influence of habitat area on woodland species has been well documented (*e.g.*, Hinsley *et al.* 1995; McGarigal and McComb 1995); however, Blake and Karr (1987) found that bird communities supported by small forest patches typically are dominated by ecological generalists.

Avian species grouped by migratory status were found in areas with a broad range of landscape characteristics. Permanent residents, short-distance migrants, and Neotropical migrants did not show a clear association with landscape characteristics summarized on principal component I or II. Results from discriminant analysis indicate that landscape variables associated with the degree of habitat fragmentation were the best predictors of group membership; however, classification functions did not efficiently distinguish among bird species grouped by migratory status. This finding is different from conclusions based on landscape studies of bird communities associated with eastern deciduous forests of North America. Neotropical migrants in landscapes dominated by forests generally do not occur in small forest patches (Freemark and Collins 1992). However, the composition of Neotropical migrants in forest-dominated landscapes of eastern North America is markedly different than that in prairie landscapes of the southern Great Plains. Many Neotropical migrants of eastern forest landscapes are forest-interior wood-warblers, which are not common in prairie landscapes; many of these wood-warblers are area sensitive and not found in small-sized forest patches.

Bird species classified by nesting height did not as a group exhibit a distinct preference for areas with particular landscape characteristics. Ground- and low-nesting species were located in areas that varied considerably with regard to habitat heterogeneity and fragmentation. Similarly, midstory- and canopy-nesting species occurred in areas all along the gradients summarized by principal components. The most effective landscape variables for discriminating ground and low nesters from midstory and canopy nesters were mean habitat patch size combined with corrected perimeter/area. Since many of the ground- and low-nesting species are grassland species, it is not surprising that habitat patch area is an important characteristic. Also, the midstory- and canopy-nesting species are edge and forest species, which are associated with relatively small woodland patches. In a study of bird assemblages in an agricultural landscape in Canada, Freemark and Merriam (1986) found that occurrences of ground-nesting birds almost exclusively explained habitat heterogeneity, whereas the incidence of canopy-nesting species was explained by habitat patch area. The results from the Canadian study are opposite those in my study. However, the difference may be the result of a difference between the two regions in species composition of the ground- and canopy-nesting groups. In the Canadian study, the ground-nesting species were primarily forest-interior and edge species. In the southern Great Plains, the ground-nesting species generally are sparrows associated with grasslands.

Landscape variables (mean habitat patch size, number of patches) were most effective in distinguishing between cavity- and open-cup-nesting species. Most cavity-nesting species in the southern Great Plains occur in forest or edge habitats (Pogue and

Schnell 1994). Thus, cavity-nesting species were predominately associated with small heterogeneous habitat patches, as indicated from principal-components analysis. Hawrot and Niemi (1996) found that the distribution and abundance of secondary cavity-nesting species in a mixed conifer-hardwood forest in Wisconsin were explained by landscape characteristics of the forest edge and fractal dimension, the latter of which measures the complexity of patch shape. In contrast, the abundance of open-cup-nesting species was correlated with edge and area characteristics. I found that open-cup-nesting species in the southern Great Plains could not be characterized by particular landscape variables, which is most likely because open-cup-nesting species occurred both in forest and grassland habitats.

In summary, landscape characteristics are effective in explaining the occurrence of bird species in the southern Great Plains. However, bird-species composition in prairie landscapes differs considerably from landscape studies from other regions of North America. Thus, it is important to consider species composition before making blanket predictions regarding groups of bird species. For example, suggesting that habitat area requirements are the most important landscape characteristics for Neotropical migratory birds may not be appropriate in landscapes where forest is not the dominant vegetation type.

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Appendix A: Description of land-cover types

Following are descriptions of the land-cover types distinguishable on the 1990 panchromatic aerial photographs. With minor modifications, names of land-cover types correspond to those in the floral inventory of Fort Sill (Johnson *et al.* 1992).

Bottomland forest.—Tall forest with closed, coarse textured canopy located close to major perennial drainages on deep soils. May have as many as 15 tree species, but usually dominated by sugarberry (*Celtis laevigata*) or American elm (*Ulmus americana*). Other important species include bur oak (*Quercus macrocarpa*), soapberry (*Sapindus saponaria*), and box elder (*Acer negundo*). Often a dense understory of shrubs, vines, and herbaceous plants.

Residential/urban.—Residential area containing paved roads, houses, and other man-made buildings.

Cross-timbers.—Closed canopy or somewhat open, low forest composed mostly of post oak (*Q. stellata*) and blackjack oak (*Q. marilandica*) in uplands and along intermittent drainages. Understory is sparse in closed-canopy sites and moderately dense in more open sites.

Disturbed area.—Clearly distinguishable areas on aerial photographs that are regularly maintained or disturbed. Includes buildings, ranges, parade fields, airfields, and firing points.

Agriculture.—Cultivated lands that have defined boundaries. Often appear as dark areas with parallel linear features on aerial photographs, indicative of planted or tilled rows.

Mesquite savanna.—Mixed grass with scattered mesquite (*Prosopis glandulosa*).

Occurs on level areas with deep soils.

Mixed grass.—Usually reaches a height of 0.5 to 1.0 m and usually dominated by little bluestem (*Schizocyrium scoparium*). Big bluestem (*Andropogon gerardia*), sideoats grama (*Bouteloua curtipendula*), and switchgrass (*Panicum virgatum*) often important.

Has few or no trees, and most is on level on gently sloping areas with deep soils.

Oak savanna.—Scattered trees in mixed grass. Transitional between cross-timbers and mixed grass.

Osage-orange/locust/elm.—Small patches of native, early successional tree species including osage-orange (*Maclura pomifera*), black locust (*Robinia pseudoacacia*), winged elm (*U. alata*), and American elm. Often associated with overgrazed or disturbed grassland communities.

Rangeland.—Predominately mixed grasses dominated by little bluestem and big bluestem. Sideoates grama and switchgrass often are important. Does not reach height of typical mixed grasslands due to grazing and cutting.

Riparian.—Vegetation close to ponds and drainages. Strongly influenced by water-saturated soil and/or mechanical action of floodwater. Sometimes located adjacent to bottomland forest or cross-timbers, and distinguished from them on aerial photographs by crown color and texture.

Short grass.—Occurs on shallow, rocky soils on hillsides and ridges, usually with visibly bare rock. Often dominated by grama grasses (*B. gracilis* and *B. hirsuta*).

Tall grass.—Occurs on areas of deep, level fertile soils and dominated by big bluestem. Switchgrass and little bluestem usually important. Tall-grass type is similar to mixed grass, but former grows to height of 2 m or more and has more biomass.

Woody-vegetation patch.—Small plots of planted trees and shrubs on grassland areas. Observable on aerial photographs as round, square or rectangular patches with striated appearance due to rows of planted vegetation. Dominant tree species include black locust and osage-orange. Dominant shrub species include members of the Rosaceae family.

Water.—Ponds, perennial and intermittent streams.

Appendix B: Bird-species composition of each group.

I. HABITAT.

Grassland species.—Northern harrier (*Circus cyaneus*), ring-necked pheasant (*Phasianus colchicus*), dickcissel (*Spiza americana*), Cassin's sparrow (*Aimophila cassinii*), grasshopper sparrow (*Ammodramus savannarum*), eastern meadowlark (*Sturnella magna*).

Successional-scrub species.—Northern bobwhite (*Colinus virginianus*), ash-throated flycatcher (*Myiarchus cinerascens*), Carolina wren (*Thryothorus ludovicianus*), Bewick's wren (*Thryomanes bewickii*), gray catbird (*Dumetella carolinensis*), brown thrasher (*Toxostoma rufum*), white-eyed vireo (*Vireo griseus*), Bell's vireo (*V. bellii*), yellow warbler (*Dendroica petechia*), northern cardinal (*Cardinalis cardinalis*), blue grosbeak (*Guiraca caerulea*), indigo bunting (*Passerina cyanea*), painted bunting (*P. ciris*), rufous-crowned sparrow (*Aimophila ruficeps*), field sparrow (*Spizella pusilla*), lark sparrow (*Chondestes grammacus*), American goldfinch (*Carduelis tristis*).

Woodland species.—Red-shouldered hawk (*Buteo lineatus*), wild turkey (*Meleagris gallopavo*), yellow-billed cuckoo (*Coccyzus americanus*), barred owl (*Strix varia*), chuck-will's-widow (*Caprimulgus carolinensis*), ruby-throated hummingbird (*Archilochus colubris*), red-bellied woodpecker (*Melanerpes carlinus*), ladder-backed woodpecker (*Picoides scalaris*), downy woodpecker (*P. pubescens*), hairy woodpecker (*P. villosus*), pileated woodpecker (*Dryocopus pileatus*), eastern wood-pewee (*Contopus virens*), great crested flycatcher (*M. crinitus*), Carolina chickadee (*Parus carolinensis*), tufted titmouse (*P. bicolor*), white-breasted nuthatch (*Sitta carolinensis*), blue-gray

gnatcatcher (*Polioptila caerulea*), Swainson's thrush (*Catharus ustulatus*), red-eyed vireo (*V. olivaceus*), black-and-white warbler (*Mniotilta varia*), Kentucky warbler (*Oporornis formosa*), summer tanager (*Piranga rubra*).

II. NEST TYPE.

Cavity-nesting species.—American kestrel (*Falco sparverius*), barred owl, red-bellied woodpecker, ladder-backed woodpecker, downy woodpecker, hairy woodpecker, pileated woodpecker, ash-throated flycatcher, great crested flycatcher, purple martin (*Progne subis*), Carolina chickadee, tufted titmouse, white-breasted nuthatch, Bewick's wren, eastern bluebird (*Sialia sialis*), European starling (*Sturnus vulgaris*).

Open-cup-nesting passerine species.—Yellow-billed cuckoo, eastern wood-pewee, eastern phoebe (*Sayornis phoebe*), western kingbird (*Tyrannus verticalis*), eastern kingbird (*T. tyrannus*), scissor-tailed flycatcher (*T. forficatus*), barn swallow (*Hirundo rustica*), canyon wren (*Catherpes mexicanus*), Carolina wren, blue-gray gnatcatcher, Swainson's thrush, American robin (*Turdus migratorius*), gray catbird, northern mockingbird (*Mimus polyglottus*), brown thrasher, loggerhead shrike (*Lanius ludovicianus*), white-eyed vireo, Bell's vireo, red-eyed vireo, yellow warbler, black-and-white warbler, Kentucky warbler, summer tanager, northern cardinal, blue grosbeak, indigo bunting, painted bunting, dickcissel, Cassin's sparrow, rufous-crowned sparrow, field sparrow, lark sparrow, grasshopper sparrow, red-winged blackbird (*Agelaius phoeniceus*), eastern meadowlark, common grackle (*Quiscalus quiscula*), American goldfinch.

III. MIGRATORY STATUS.

Short-distance migrant species.—Green heron (*Butorides striatus*), little blue heron (*Egretta caerulea*), cattle egret (*Bubulcus ibis*), great egret (*Casmerodius albus*), turkey vulture (*Carthartes aura*), northern harrier, red-shouldered hawk, red-tailed hawk (*Buteo jamaicensis*), American kestrel, killdeer (*Charadrius vociferus*), mourning dove (*Zenaida macroura*), belted kingfisher (*Ceryle alcyon*), eastern phoebe, Bewick's wren, American crow (*Corvus brachyrhynchos*), eastern bluebird, American robin, brown thrasher, loggerhead shrike, European starling, Cassin's sparrow, field sparrow, red-winged blackbird, eastern meadowlark, common grackle, brown-headed cowbird (*Molothrus ater*), American goldfinch.

Permanent residents.—Great blue heron (*Ardea herodias*), Canada goose (*Branta canadensis*), ring-necked pheasant, wild turkey, northern bobwhite, great horned owl (*Bubo virginianus*), barred owl, red-bellied woodpecker, ladder-backed woodpecker, downy woodpecker, hairy woodpecker, pileated woodpecker, Carolina chickadee, tufted titmouse, white-breasted nuthatch, canyon wren, Carolina wren, northern mockingbird, northern cardinal, rufous-crowned sparrow, house sparrow (*Passer domesticus*).

Neotropical migrant species.—Mississippi kite (*Ictinia mississippiensis*), Swainson's hawk (*Buteo swainsoni*), common nighthawk (*Chordeiles minor*), chuck-will's-widow, chimney swift (*Chaetura pelagica*), ruby-throated hummingbird, eastern wood-pewee, ash-throated flycatcher, great crested flycatcher, western kingbird, eastern kingbird, scissor-tailed flycatcher, purple martin, northern rough-winged swallow (*Stelgidopteryx serripennis*), cliff swallow (*Hirundo pyrrhonota*), barn swallow, blue-

gray gnatcatcher, Swainson's thrush, gray catbird, white-eyed vireo, Bell's vireo, red-eyed vireo, yellow warbler, black-and-white warbler, Kentucky warbler, summer tanager, blue grosbeak, indigo bunting, painted bunting, dickcissel, lark sparrow, grasshopper sparrow, orchard oriole (*Icterus spurius*), northern oriole (*I. galbula*).

IV. NESTING HEIGHT.

Ground- and low-nesting species.—Yellow-billed cuckoo, ash-throated flycatcher, canyon wren, Carolina wren, Bewick's wren, Swainson's thrush, gray catbird, northern mockingbird, brown thrasher, white-eyed vireo, Bell's vireo, black-and-white warbler, Kentucky warbler, northern cardinal, blue grosbeak, indigo bunting, painted bunting, dickcissel, Cassin's sparrow, rufous-crowned sparrow, field sparrow, lark sparrow, grasshopper sparrow, eastern meadowlark, red-winged blackbird.

Midstory- and canopy-nesting species.—Eastern wood-pewee, eastern phoebe, great crested flycatcher, western kingbird, eastern kingbird, scissor-tailed flycatcher, purple martin, northern rough-winged swallow, cliff swallow, barn swallow, American crow, Carolina chickadee, tufted titmouse, white-breasted nuthatch, blue-gray gnatcatcher, eastern bluebird, American robin, loggerhead shrike, European starling, red-eyed vireo, yellow warbler, summer tanager, common grackle, orchard oriole, northern oriole, American goldfinch, house sparrow.

Appendix C: Description of landscape indices

Variables and indices used in evaluation of landscape features. Descriptions of variables taken in part from Baker (1992,1994), O'Neill *et al.* (1988), and Riitters *et al.* (1995).

Average patch size.—Mean patch size of all patches within sampling area (m²).

Number of patches.—Total number of patches within sampling area.

Habitat richness.—Total number of land-cover types present within sampling area.

Corrected perimeter/area.—Mean values calculated for all land-cover patches in sampling area:

$$CPA = 0.282 n^{-1} \sum_{k=1}^n (B_k A_k^{-0.5}), \quad (1)$$

where n is number of land-cover patches within circle, B_k is perimeter of patch k (in meters) and A_k is area of patch k (m²). For individual patch, value can range from 0.0 for circle and to infinity for infinitely long and very narrow patch. Value for a square is 1.12.

Related circumscribing circle.—Mean values calculated for all habitat patches within sampling area:

$$RCC = 2 \pi^{-0.5} n^{-1} \sum_{k=1}^n (A_k^{0.5} L_k^{-1}), \quad (2)$$

where L_k is longest axis of patch k (in meters) and other variables are as above.

Compares area of patch to area of smallest circle that can circumscribe patch, thus providing measure of compaction. For a given patch, index varies from 0.0 to 1.0 as compactness approaches that of a circle. A square has value of 0.798.

Contagion.—Quantifies degree of clumping:

$$C = 2 \ln(m) \sum_{i=1}^m \sum_{j=1}^m P_{ij} \ln(P_{ij}), \quad (3)$$

where m is the number of land-cover types and P_{ij} refers to the proportion of times where a pixel of land-cover type i occurs next to one of land-cover type j . Pixel size was 1 m².

A measure of texture that quantifies adjacency of similar land-cover types (Baker 1994).

In a sense is simply local measure of diversity. A grey-level co-occurrence matrix

(GLCM; $m \times m$) is calculated. A GLCM entry indicates total number of times habitat

type i is adjacent to habitat type j . Total number of adjacencies calculated by moving

through sampling area pixel-by-pixel. Values can range from 1.16 to 3.38.

Angular second moment.—Measure of homogeneity:

$$ASM = \sum_{i=1}^m \sum_{j=1}^m (P_{ij})^2, \quad (4)$$

where m is total number of land-cover types in sampling area, P_{ij} is total number of times land-cover type i is adjacent to land-cover type j (Musick and Grover 1990).

Contrast.—Measure of contrast or amount of local variation present in the sampling area:

$$CON = \sum_{i=1}^m \sum_{j=1}^m [(i-j)^2 P_{ij}], \quad (5)$$

where m is the total number of land-cover types in the sampling area, P_{ij} is the total number of times that land-cover type i is adjacent to land-cover type j (Musick and Grover 1990).

Table 1. Pearson product-moment correlation coefficients for eight landscape variables based on 98 plots at block size 8.

Variable	Variable						
	1	2	3	4	5	6	7
1 Corrected perimeter/area							
2 Related circumscribing circle	-0.78						
3 Contagion	-0.31	0.45					
4 Angular second moment	0.38	-0.50	-0.45				
5 Contrast	0.05	0.10	0.64	-0.53			
6 Number of patches	-0.26	0.40	0.57	-0.41	0.48		
7 Richness	-0.26	0.35	0.90	-0.61	0.79	0.57	
8 Mean patch size	0.45	-0.63	-0.79	0.71	-0.50	-0.66	-0.72

Table 2. Principal-component loadings based on analysis of eight landscape variables.

numbers indicated highest absolute loadings.

Variable	Component	
	I	II
1 Corrected perimeter/area	0.512	0.769
2 Related circumscribing circle	-0.664	-0.663
3 Contagion	-0.870	0.198
4 Angular second moment	0.760	0.053
5 Contrast	-0.685	0.604
6 Number of patches	-0.722	0.090
7 Richness	-0.884	0.334
8 Mean patch size	0.912	0.079
Eigenvalue	4.64	1.56
Percent variance explained	58.1	19.5

Table 3. Comparisons of central tendency (Kruskal-Wallis test for groups based on habitat and migratory status; Mann-Whitney U -test for those based on nesting height and nest type) and homogeneity of variance (Bartlett's test for habitat and migratory status; Scheffé-Box test for nesting height and nest type) of principal-component projections for bird groups. Probability levels (p) indicated in parentheses, with statistically significant values highlighted in bold.

Statistics	Principal component	
	I	II
Habitat		
Central tendency (H)	9.01 (0.011)	0.11 (0.944)
Homogeneity of variance (X^2)	2.74 (0.254)	5.89 (0.053)
Migratory status		
Central tendency (H)	1.73 (0.422)	0.93 (0.627)
Homogeneity of variance (X^2)	4.14 (0.127)	8.87 (0.012)
Nesting height		
Central tendency (U_s)	419.50 (0.133)	270.50 (0.220)
Homogeneity of variance (F_s)	1.38 (0.273)	0.14 (0.718)
Nest type		
Central tendency (U_s)	240.50 (0.168)	302.50 (0.823)
Homogeneity of variance (F_s)	22.16 (0.002)	0.09 (0.772)

Table 4. Statistics for stepwise discriminant analyses of bird groups.

Variable	Order of entry	Standardized canonical variable coefficients		Classification function ^a		
		1	2			
Habitat						
				Grassland	Successional-	Woodland
Mean patch size	1	1.768	-0.073	3.988	0.102	-1.886
Number of patches	2	1.500	0.939	3.154	0.058	-1.962
Constant		0.177	0.168	-2.977	-1.100	-1.551
Migratory status						
				Permanent	Short-distance	Neotropical
Angular second moment	1	-0.661	-0.511	-0.115	0.205	-0.137
Related circumscribing circle	2	1.257	-1.010	0.010	0.072	0.310
Constant		-0.037	0.001	-1.105	-1.118	-1.148

Table 4. Continued.

Variable	Order of entry	Standardized canonical variable coefficients		Classification function ^a		
		1	2			
Nesting height						
				Ground- &	Midstory- &	
Mean patch size	1	-0.875	—	0.406	-0.348	—
Corrected perimeter/area	2	0.533	—	-0.499	-0.008	—
Constant		0.113	—	-0.844	-0.744	—
Nest type						
				Cavity-nesting	Open-cup-	
Mean patch size	1	1.777	—	-1.743	0.287	—
Number of patches	2	1.641	—	-1.995	0.124	—
Constant		0.188	—	-1.114	-0.710	—

^a Used with original measurements. Add products of measurements and corresponding function values to constant; classify into group depending on which classification function results in the higher numerical value.

FIGURE CAPTIONS

Fig. 1. Location in USA of study area in (A) Oklahoma and (B) southwestern portion of state. Detailed map (C) of study area (indicated by dashed rectangle) including Fort Sill Military Reservation, a portion of Wichita Mountains National Wildlife Refuge, and surrounding communities. Dotted lines indicate county boundaries and heavy solid lines indicate major highways.

Fig. 2. Flow diagram showing steps required to produce rasterized land-cover map from original aerial photographs.

Fig. 3. Land-cover classification of study area (dashed rectangle in Fig.1).

Fig. 4. Belt transect showing contiguous block sizes used to compute landscape indices for multiscale ordination analysis.

Fig. 5. Partitioned eigenvalues for block sizes 1 to 15 on composite axis 1 for sample plots (a) plot 42 and (b) plot 49.

Fig. 6. Frequency distribution of block sizes for all plots that had highest eigenvalues for composite axis 1.

Fig. 7. UPGMA cluster analysis based on absolute correlations of landscape variables for 98 plots at block size 8. Cophenetic correlation coefficient is 0.80.

Fig. 8. Projections of birds on principal components I and II for species classified by (a) habitat, (b) migratory status, (c) nest height, and (d) nest type. Ellipses represent 95% confidence intervals.

Fig. 9. Projections of bird species on canonical variables determined from stepwise discriminant analysis. Bird species classified by (a) habitat, (b) migratory status, (c) nest height, and (d) nest type.

Fig. 1

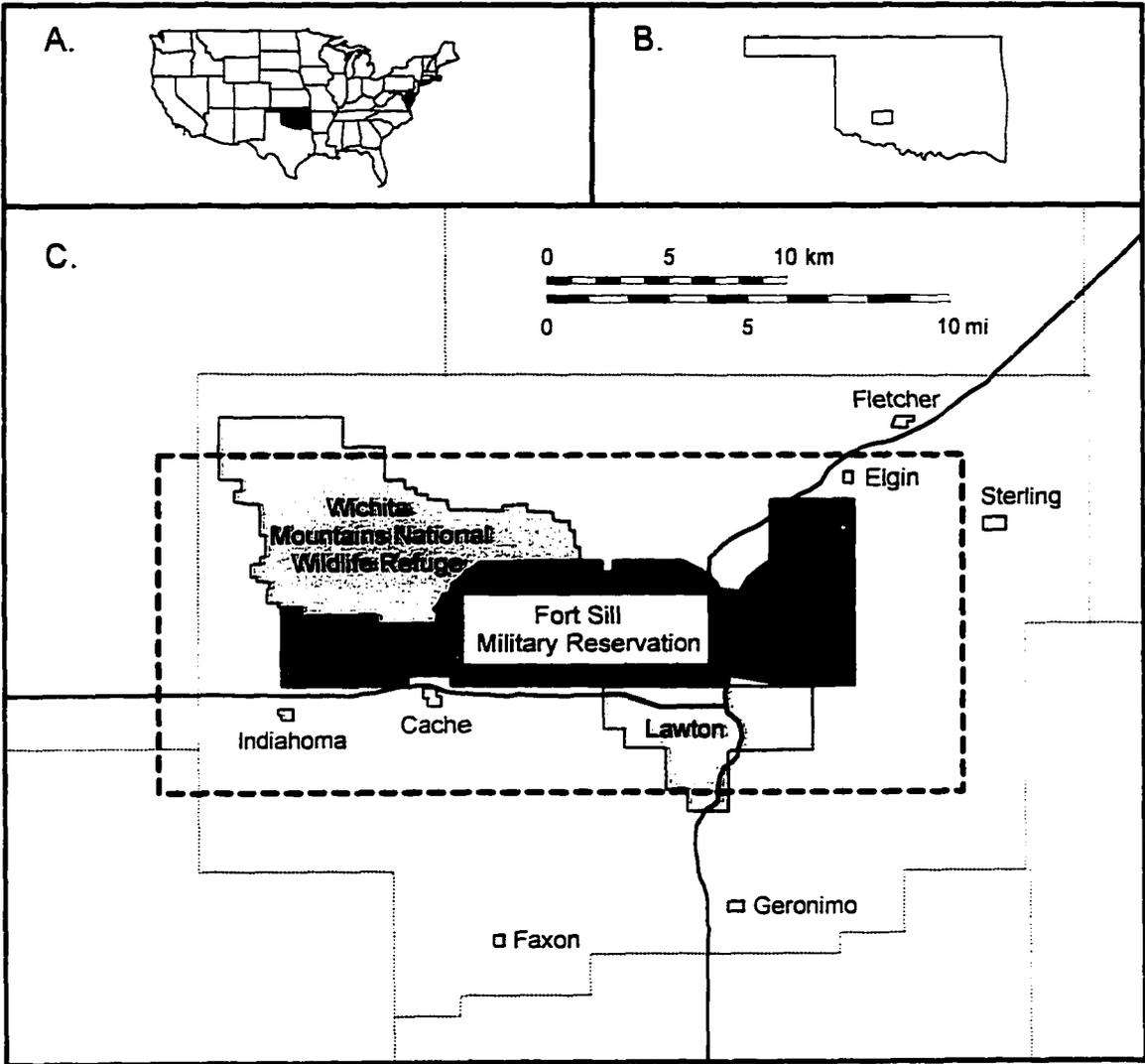


Fig. 2

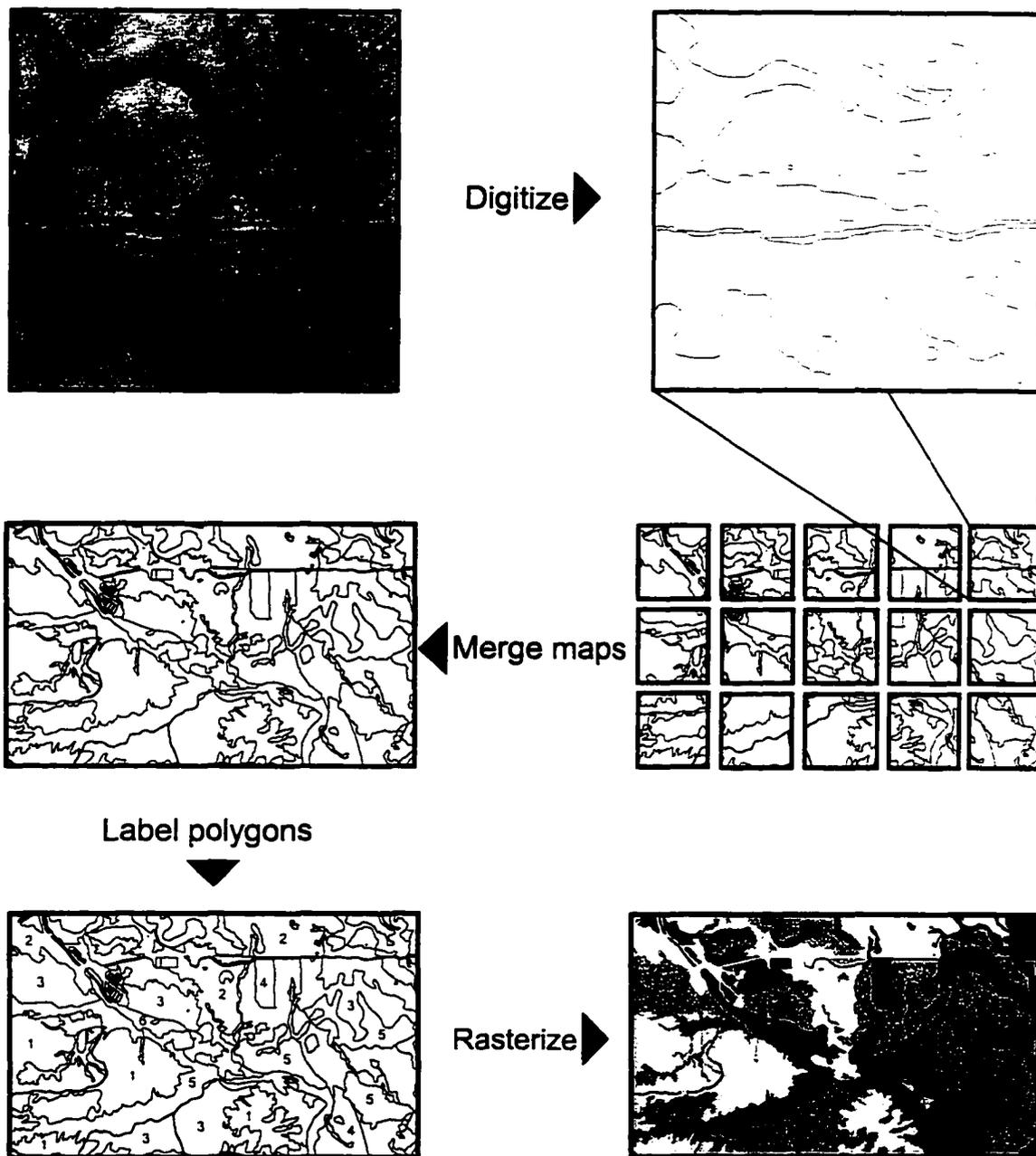
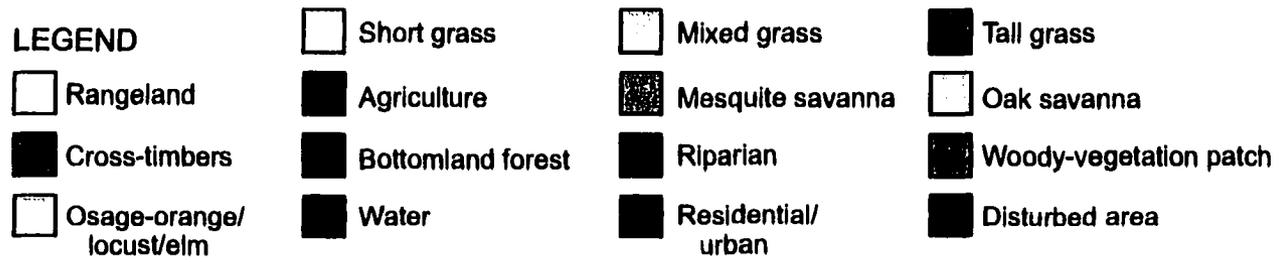




Fig. 3



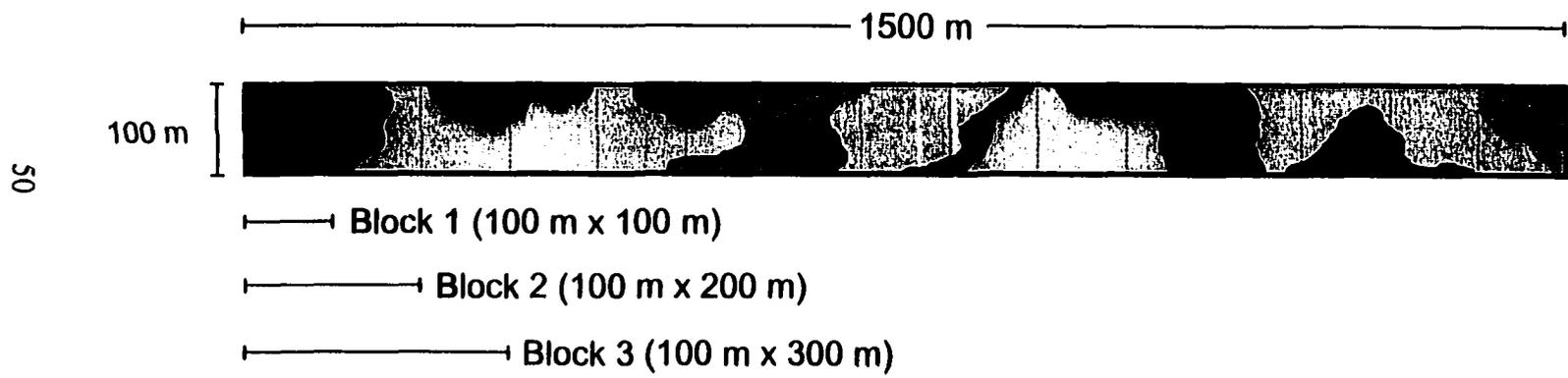


Fig. 4

Fig. 5

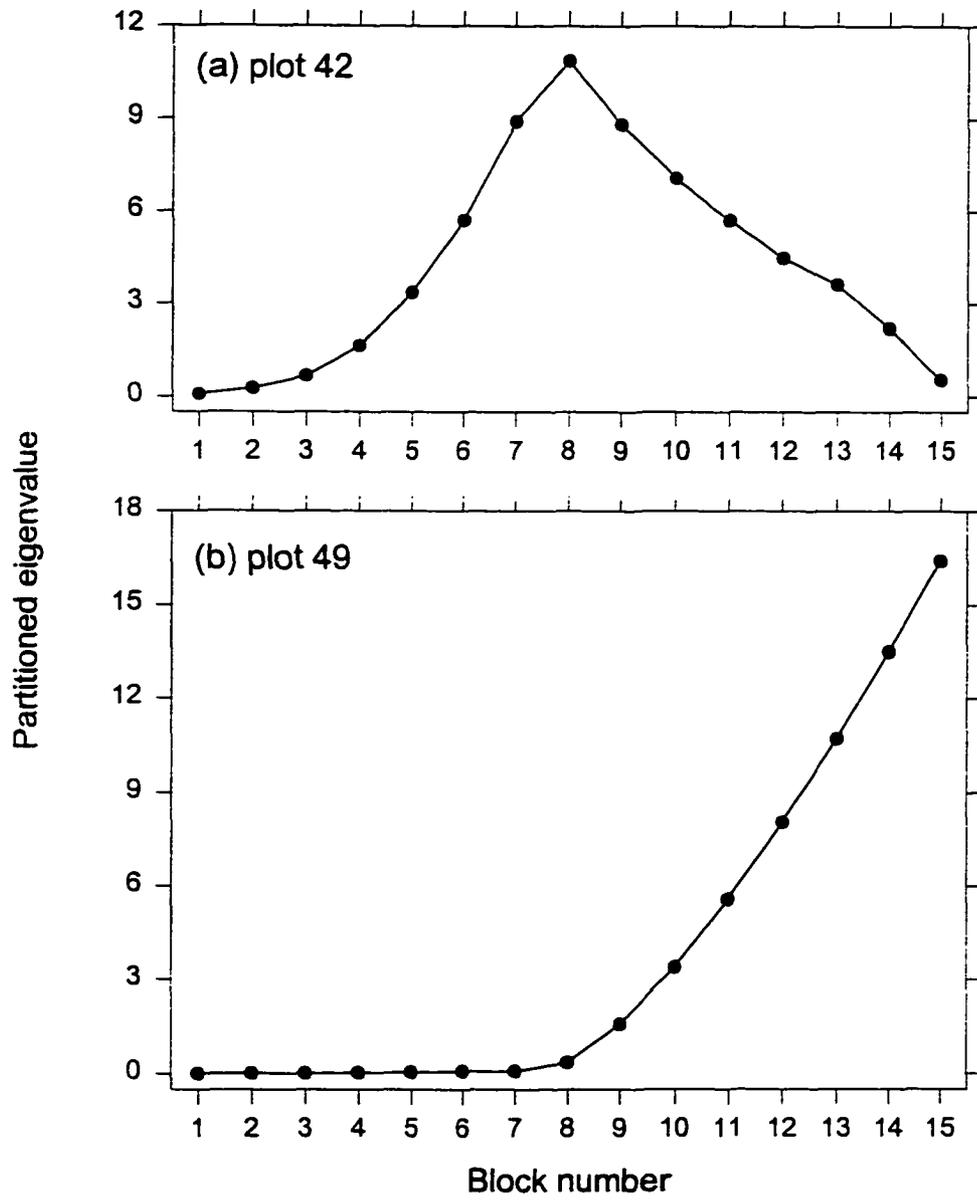
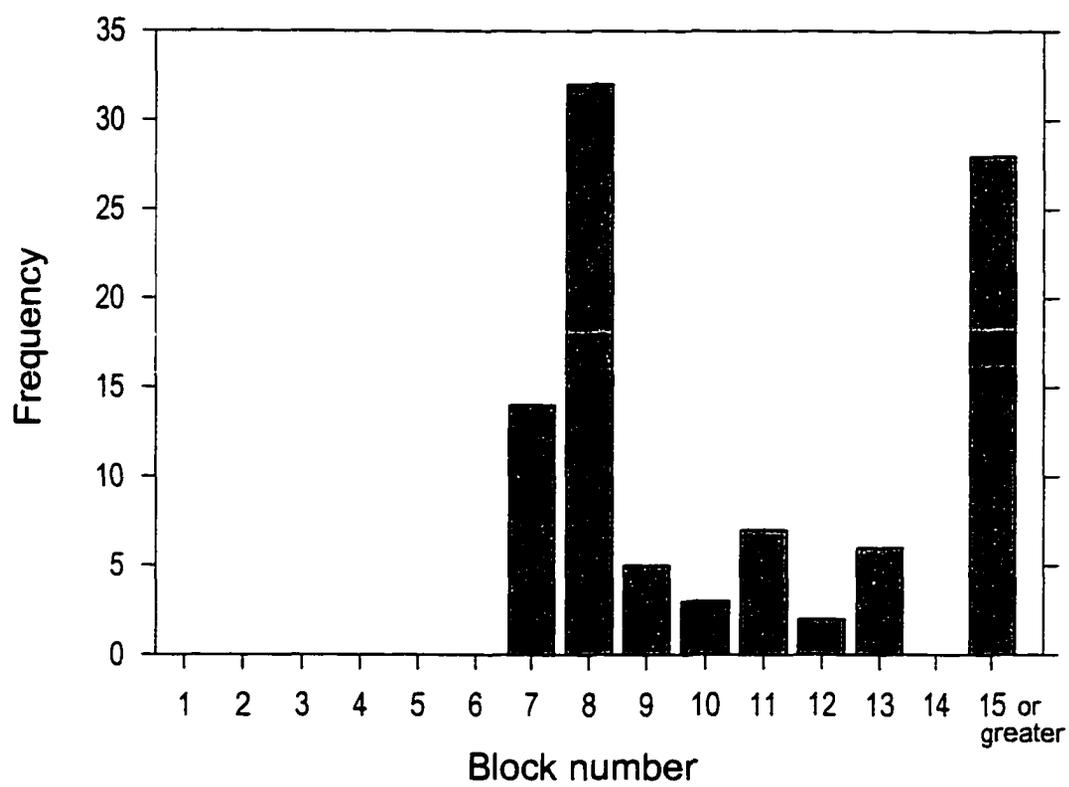


Fig. 6



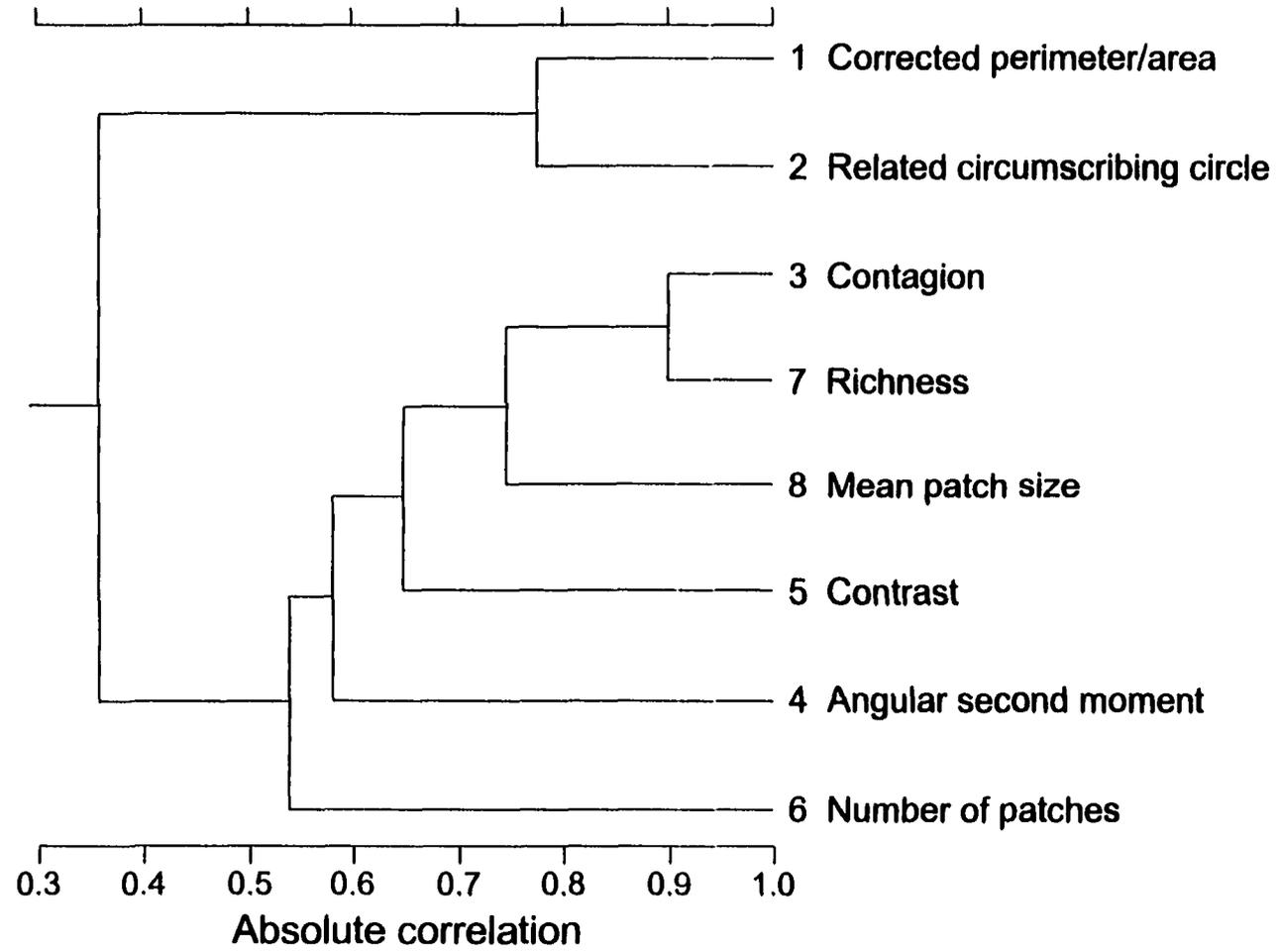


Fig. 7

Fig. 8

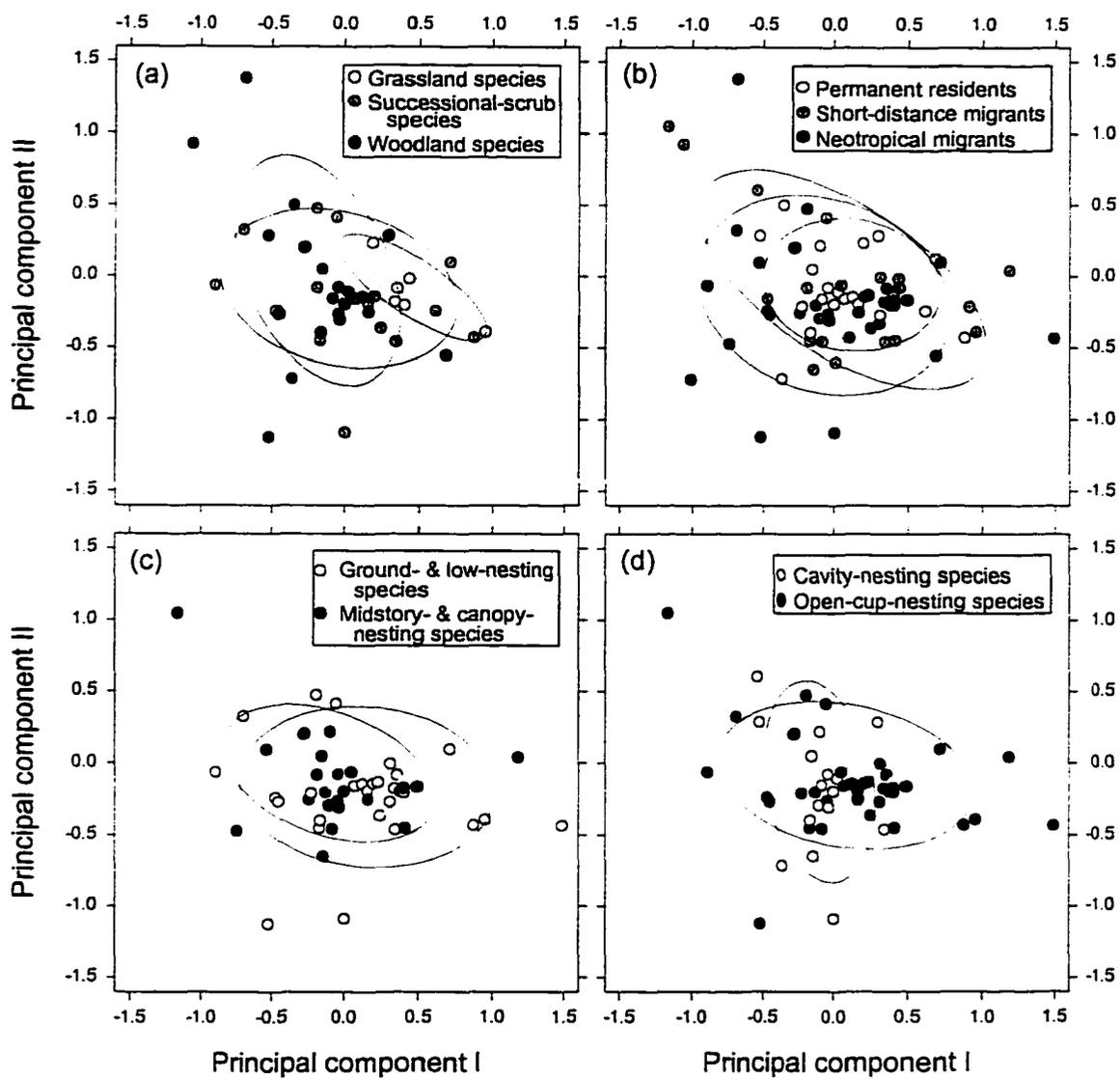
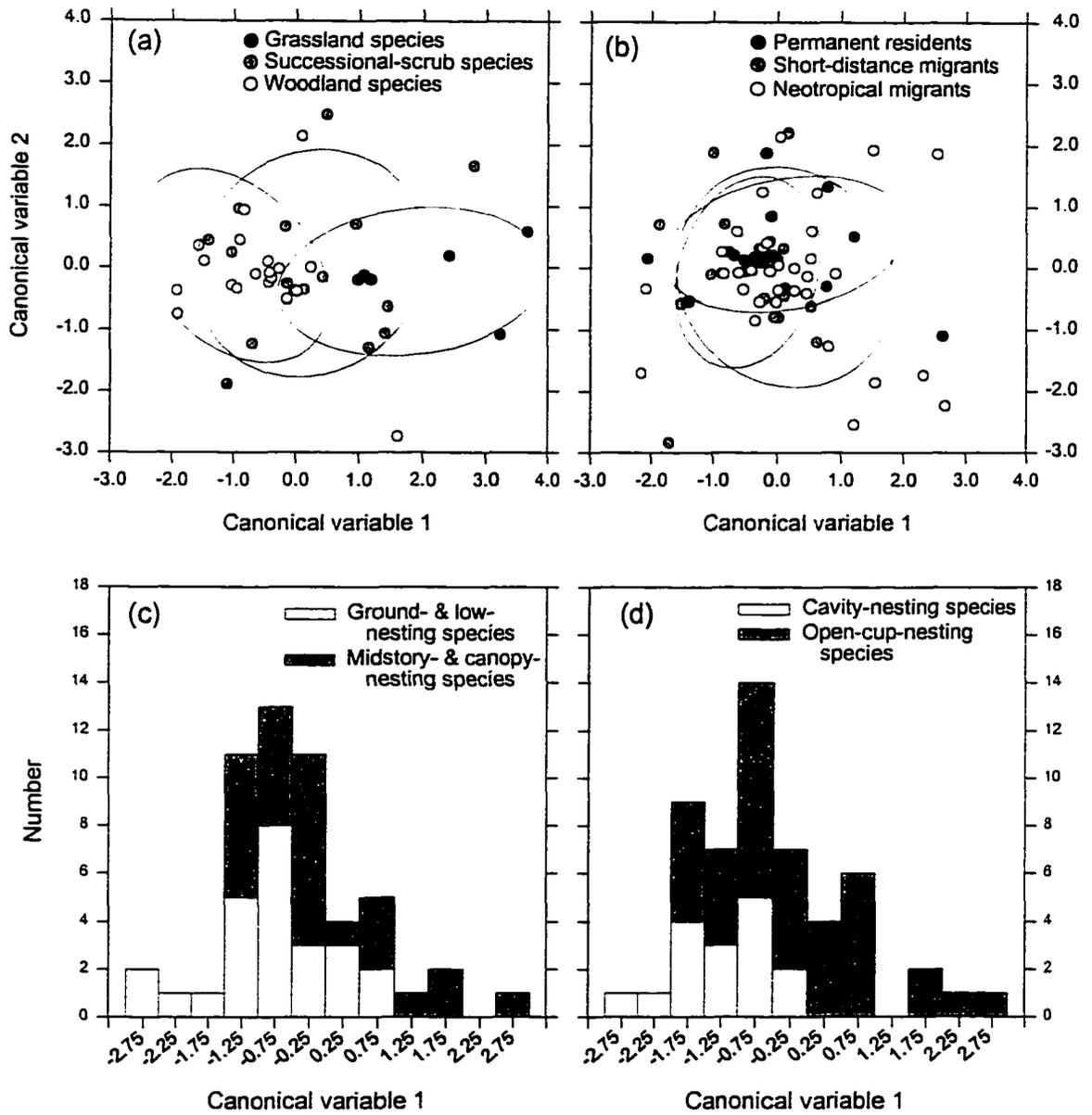


Fig. 9



Effects of Local and Landscape Habitat

Characteristics on Prairie Birds

Running head: Habitat Influences on Prairie Birds

Word Count: 7090

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Abstract: *Songbird populations in North American prairies have exhibited the most widespread and steepest declines of any group. According to the North American Breeding Bird Survey, only 10% of grassland birds have shown positive growth. Of particular concern are prairie birds that are sensitive both to local habitat and area characteristics of the landscape. We studied the influence of local- and landscape-level habitat factors on breeding-bird communities in a prairie landscape in southwestern Oklahoma, U.S.A. Local habitat characteristics were sampled at study plot transects, and landscape measures were computed from a land-cover map digitized from aerial photography. Habitat regression models using local and landscape habitat components explained 79% of the variation in bird species richness and 41% of the variation in abundance. Bird species richness was best explained by landscape habitat variables, while overall bird abundance was related to a combination of local and landscape variables. Abundance of woodland and grassland/savanna species was accounted for by local habitat variables representing vegetation and a slope gradient. Models for typical woodland species—Tufted Titmice (*Parus bicolor*), Red-eyed Vireos (*Vireo olivaceus*), Great Crested Flycatchers (*Myiarchus crinitus*), and Northern Cardinals (*Cardinalis cardinalis*)—were explained primarily by local vegetation characteristics ($r^2=0.52-0.74$). A combination of local and landscape habitat features accounted for the variation (local, 42-100%; landscape, 0-60%) in abundance of four typical grassland/savanna species—the Field Sparrow (*Spizella pusilla*), Eastern Meadowlark (*Sturnella magna*), Grasshopper Sparrow (*Ammodramus savannarum*), and Dickcissel (*Spiza americana*). In general, avian-community indices were related both to landscape and local habitat*

characteristics. Ecological groups of birds and individual species were accounted for primarily by local habitat characteristics. Conservation strategies for prairie birds should take into consideration that particular species respond differently to local- and landscape-level habitat characteristics and that broad-scale conservation recommendations are likely to be ineffective across a variety of landscapes.

Introduction

Reports of declining populations of migratory songbirds have generated much concern in recent years. Efforts to examine the causes of these declines have focused on changes that have occurred in the forested landscapes of eastern North America. Forest fragmentation, agricultural practices, and urban development have had substantial impacts on the native habitats of eastern forests (Freemark & Collins 1989).

Although eastern forests of North America have been more extensively studied, prairie grasslands also have deteriorated as a result of intensification of row-crop agriculture practices and other human-induced modifications. Losses of habitat due to agricultural practices and urban development have severely reduced and fragmented native grasslands throughout the central United States (Vance 1976; Herkert 1994). In the southern Great Plains, land used for agriculture has increased more than 20% over the last 60 years, and now more than 30% of the total area is cultivated lands. For example, in Kansas over 50% of the total land area is comprised of cropland, while only 25% is grassland (U.S. Department of Agriculture 1934-1994). The effects of habitat loss and

fragmentation on grassland communities have received comparatively little attention despite the fact that loss of grassland habitat has exceeded loss of forest habitat throughout much of the central United States (e.g., Smith 1981; Iverson 1988; Sample 1989).

Concurrent with the increase in agriculture in the United States, there have been conspicuous declines in populations of grassland birds. In fact, many grassland bird species currently are experiencing decreases that exceed those exhibited by most forest species (Robbins et al. 1986, 1989; Herkert 1991a). Population trends derived from the Breeding Bird Survey (BBS) indicate that grassland birds show the most consistent declines of any group of birds monitored by the BBS (Goriup 1988; Herkert 1991b; Askins 1993; Senner 1994; Sauer et al. 1997). Other data suggest that in the United States numbers of Grasshopper Sparrows (*Ammodramus savannarum*) and Field Sparrows (*Spizella pusilla*) have decreased more than 50% (Herkert 1994). Fewer than 30% of North American grassland species have increasing populations (Sauer et al. 1997).

Populations of prairie birds can be influenced by changes in the landscape that alter the suitability of a particular habitat patch. Habitat suitability undoubtedly is influenced by the composition and structure of the local vegetation, but also may be affected by the spatial arrangement of habitat patches within the landscape. Small habitat patches connected or adjacent to large habitat patches may be more suitable for particular species than an isolated habitat patch in a matrix of unsuitable habitat. Landscape characteristics—such as habitat area, fragmentation, and isolation—influence the

distribution of some prairie bird species. In a study of grassland birds in Illinois, Herkert (1994) found that variation in bird species richness was a result of differences in habitat area. The presence of Grasshopper Sparrows, Henslow's Sparrows (*A. henslowii*), and Bobolinks (*Dolichonyx oryzivorus*) in old fields and pastures of the northeastern United States is predictable based on variation in habitat area (Bollinger & Gavin 1992; Smith 1992). Thus, in at least some cases, landscape-level factors influence the distribution of birds within prairie landscapes. Here we evaluate the relative influence of local- and landscape-level habitat factors on prairie bird populations. Statistical models are generated that explain the relative influence of these factors on the variation in abundance and richness of prairie birds.

Methods

Study Area

The study area (160,535 ha) is located in southwestern Oklahoma, U.S.A. (Fig. 1). It is centered on the Fort Sill Military Reservation (38,292 ha) and includes approximately 80% of the Wichita Mountains National Wildlife Refuge. Several small communities are included in the study area.

The area is transitional, containing vegetation communities typical of both mesic and xeric environments. Typical habitats found in the study area include: (1) grasslands of short, mixed and tall grasses; (2) rangeland, which is a grassland that has been grazed or cut for hay; (3) agricultural fields of cultivated crops; (4) mesquite savanna composed of

mixed grasses with scattered mesquite (*Prosopis glandulosa*); (5) oak savanna that is intermediate between grassland and upland deciduous forest; (6) bottomland forest; (7) riparian vegetation; (8) woody-vegetation patches, which are small patches of planted trees; and (9) small woodland patches associated with disturbed areas.

Bird sampling

Annual censuses of birds were made at 98 sample plots (Fig. 1d) from 1993 through 1995. Sample plots were established by the Land Condition Trend Analysis (LCTA; Tazik et al. 1992) program, which was implemented by the U.S. Army at Fort Sill to inventory and monitor natural resources. The LCTA plots were selected by stratified-random sampling to provide an adequate representation of the various vegetation communities. For 98 sample LCTA plots, UTM coordinates for starting position and a randomly-chosen azimuth were determined for 100-m transects at each site.

Birds were sampled at each plot using a modified point-count transect technique (Blondel et al. 1981). Each year the inventory was conducted within a two- to four-week span (falling within the period 15 April to 30 June) corresponding to the seasonal peak in breeding-bird activity. Each plot was censused twice each year, once in the morning and once in the late afternoon. In total, each site was sampled six times (twice each year for three years). All morning censuses were conducted between 0.5 h before and 4 h after sunrise. Late-afternoon censuses were conducted during the 4 h prior to sunset. D. W. Pogue censused the plots by slowly walking the length of a 100-m transect in 6 min and recording all birds seen or heard within 100 m of the transect line. He then stopped for 8

min and recorded any new birds seen or heard within 100 m. Finally, he walked back to the starting point over a period of 6 min, recording any new birds detected within 100 m. The mean abundance of each species over the six censuses was calculated for each site. Also, means were computed for two avian-community indices: total bird abundance and species richness.

Local Habitat Sampling

At each of the 98 LCTA plots, data on vegetation and other site characteristics were gathered for 16 variables (listed in Table 1). Ground cover, canopy cover, and surface disturbance were sampled at 100 points along a line transect beginning at the 0.5-m point and continuing at 1-m intervals, thus ending at 100.5 m. A 1-m measuring rod was placed perpendicular to the ground at each point to determine ground cover, surface disturbance, and vertical distribution of vegetation up to 1 m. Canopy cover above 1 m was measured using a telescoping range pole.

Plant-species composition and density, along with the height distribution of woody and succulent vegetation, were evaluated along a belt transect. The belt transect extended the length of the 100-m line transect. The belt had a standard width of 6 m, but sometimes the width was reduced for high-density species.

The heights of all woody plants above a predetermined minimum height were mapped. In nonwooded areas (e.g., grasslands, savannas), where most woody plants are less than 1 m high, the minimum height of species recorded was 0.1 m. In woodlands and

forest, where woody plants commonly exceed 1 m in height, the minimum height of species recorded was 1.0 m (Tazik et al. 1992).

Landscape Habitat Sampling

Landscape measurements were computed from a land use/land cover map of the study area produced from 1990 National High Altitude Photography (NHAP) panchromatic aerial photographs. We obtained 172 61 cm × 61 cm photographs (scale 1:7920) from the U.S. Agricultural Stabilization and Conservation Service, Salt Lake City, Utah. Photographs were taken 24 November to 9 December 1990. Each photograph was georeferenced using 7.5-minute topographic maps (1:24000) obtained from the U.S. Geological Survey. Land-cover categories, including 12 vegetation and 3 land-use types (detailed descriptions included in Pogue 1998), were identified by visual interpretation. Polygons defining land-cover boundaries were manually delineated using the Geographic Resources Analysis Support System (GRASS), a geographic information system (GIS; CERL 1989). After completing a digitized vector map for each photograph, the individual vector maps were patched together to create a single vector map of the study area. Each polygon (ca. 9,000 total) representing a defined land-cover patch was labeled appropriately. The labeled vector map was rasterized at 1-m resolution to produce the final land-cover classification map of the study area. The land-cover map was checked for accuracy by ground-truthing.

Using the GIS, a 400-m-radius concentric band was delineated around each 100-m transect (Fig. 2). Within each concentric band, the following 14 landscape indices were computed using a series of landscape-ecology computer programs (Baker 1997): (1-2)

mean area and standard deviation of all habitat patches; (3-4) mean patch shape and standard deviation of all habitat patches using corrected perimeter/area (Austin 1984, MacEachren 1985); (5) fractal dimension, a measure habitat patch complexity (Krummel et al. 1987); (6) total perimeter length of habitat patches; (7-8) mean perimeter length and standard deviation of habitat patches; (9) habitat patch richness, the number of different habitats in the sampling area; (10) contagion, an index that quantifies the degree of aggregation or clumping (O'Neill et al. 1988); (11) angular second moment, a measure of habitat homogeneity; and (12) entropy, a measure of the adjacency of habitats (Musick & Grover 1990); (13) contrast, a measure of the contrast or amount of local variation present in the landscape; and (14) total edge length of habitat patches.

Statistical Analysis

We generated local and landscape habitat datasets of 16 and 14 variables, respectively. Principal-components analysis was used to reduce the number of variables in each dataset and to summarize covariation among variables along orthogonal gradients. Calculations were carried out on each dataset separately using the computer package NTSYS-pc (Rohlf et al. 1993). From a matrix of correlations among habitat variables, major trends were represented on principal-component axes (Sneath & Sokal 1973). Correlations (i.e., loadings) of original variables with principal components were generated, and component scores of each sample plot were projected onto the components. Before projection, the habitat variables were standardized to a mean of 0 and standard deviation of 1 (Sneath & Sokal 1973).

Principal-components analysis is effective for summarizing information from a large number of variables into a few components. However, a potential problem is determining the number of components to retain for evaluation of the data. An incorrect choice can lead to underextraction of components, but commonly results in overextraction (Franklin et al. 1995). Parallel analysis is a Monte Carlo test for determining the significance of components, variable loadings, and analytical statistics (Franklin et al. 1995). Following this procedure, eigenvalues from principal-components analysis are compared with those from parallel analysis of a random data matrix of the same number of p variables and n samples. Principal-component eigenvalues that are greater than their respective parallel-analysis eigenvalues from the random data matrix should be retained. All components with eigenvalues below their respective parallel-analysis eigenvalue threshold are considered to be spurious.

Longman et al. (1989) provided models that generate mean and 95th percentile eigenvalues. With these models, p and n sizes can be incorporated to calculate parallel-analysis threshold eigenvalues. Multiplying the total number of variable loadings (number of variables \times number of extracted components) by the significance level (i.e., 0.05 = 95th percentile) results in an empirical estimate of the 95th percentile. This empirical estimate is an objectively determined threshold for significant loadings and is appropriate for either correlation or covariance matrix principal-component loadings.

Parallel analyses were performed using a SAS program by Franklin et al. (1995) that employs equations derived by Longman et al. (1989). The principal components retained

by parallel analysis and their projections represented interpretable measurements of variation that could be used in subsequent analysis (Johnson & Wichern 1988).

Using the principal-component projections, multiple-regression models were produced to describe the variation in the prairie bird communities. The response variables included avian-community indices, ecological groups of birds, and individual species. Species richness and total bird abundance were the avian-community indices. We used cluster analysis with *K*-means (Gower 1967; SPSS 1997) to determine membership of the ecological groups. For each species, we computed an average value for the local habitat variables based on the plots where the bird species occurred. The average value for the habitat variables were used in the cluster analysis. Three groups of birds were identified: (1) woodland; (2) grassland/savanna, and (3) other species, which was comprised of ecologically diverse species (see Appendix). Analyses of ecological groups were limited to (1) woodland and (2) grassland/savanna species; we analyzed the total number of individuals of all species in each group. Also, we selected the four most abundant species in each of the woodland and grassland/savanna groups for analysis of individual species.

Stepwise multiple regression was used to evaluate the explanatory power of local and landscape habitat factors for these models. No regression components having a $P > 0.05$ or $r^2 < 0.10$ were included in the models. The residuals from each regression were plotted against the habitat components in the models to detect nonlinearity between the bird and habitat components. Regressions were performed using SYSTAT (SPSS 1997).

Results

Principal-components analysis can be helpful in summarizing habitat data and possibly identifying fundamental gradients, thus providing an overview of relationships among sample plots (Grzybowski et al. 1984). The first six components had eigenvalues greater than 1 (Table 2) and accounted for 78% of the total variance in the local habitat variables. The first three principal-component eigenvalues were greater than the eigenvalue generated through parallel analysis (Table 2). Therefore, only three components were retained for further analysis. The total number of loadings (3 eigenvalues \times 16 variables = 48) was multiplied by the significance level ($0.05 \times 48 = 2.4$, or 2), providing an empirical estimate of the 95th percentile loading. Thus, the second-highest random-structure loading is an estimate of the 95th percentile value. The absolute value of the second-highest loading was $|0.568|$ and, thus, all loadings below this value were considered nonsignificant in our analyses.

Component 1 is a composite of local habitat variables representing tall herbaceous and broadleaf vegetation (high negative loadings for vertical herbaceous structure [41 to 85 dm], three variables concerning vertical broadleaf structure [> 15 dm], and total broadleaf trees; Table 1) and low herbaceous vegetation (high positive loadings for vertical herbaceous structure [0 to 15 dm] and total count grasses; Table 1). Thus, component 1 represents a gradient from wooded areas (high negative projections) to open grassland areas (high positive projections). Component 2 has high positive loadings for average slope and standard deviation of slope (Table 1), reflecting a gradient from areas

with steep slope and considerable slope variation (high positive projections) to those that are relatively flat and uniform (high negative projections). Component 3 has a high negative loading for vertical herbaceous structure (16 to 40 dm; Table 1); loadings of other variables on component 3 were not significant. Component 3 represents abundance of herbaceous vegetation (primarily perennial grasses) that range in height from 16 to 40 dm; sites with considerable herbaceous vegetation have high negative projections on component 3 and those with high positive projections have sparse herbaceous vegetation.

Principal-components analysis of landscape habitat variables resulted in four components with eigenvalues greater than 1 that together explained 83% of the total variance among variables. Compared with parallel-analysis eigenvalues, the first three principal-component eigenvalues were larger (Table 2); thus, three components were retained. The absolute value of the second highest loading ($|0.597|$) was estimated as the 95th percentile loading (total number of loadings, 3 eigenvalues \times 14 variables = 42; 95th percentile loading, $0.05 \times 42 = 2.1$, or 2). Loadings below $|0.597|$ were not considered to be significant in our analysis.

Component 1 had high negative loadings for landscape variables that are local measures of diversity (entropy, contrast; Table 3), habitat patch richness, sum of patch perimeters, and sum of edge length. In addition, three had high positive loadings on component 1—mean patch size, standard deviation of patch size, and angular second moment (Table 3); these are measures of homogeneity. Thus, component 1 reflected a gradient of sites that are relatively heterogeneous (high negative projections) to those that are homogeneous (high positive projections). Component 2 had a high negative loading

for contagion, which represents the degree of clumping or aggregation of habitat types in the landscape (Table 3). Sites with a substantial aggregation or clumping of habitat types have high negative projections on component 2, while those with well-dispersed habitat types have high positive projections. Mean patch shape, which was computed using the corrected perimeter/area method, had a high negative loading on component 3 (Table 3) and indicates the degree of habitat fragmentation. Sites with considerable habitat fragmentation have high negative projections on component 3, and those with little habitat fragmentation have high positive projections.

By definition, principal components within a given analysis (e.g. landscape components) are uncorrelated. In addition, correlations between local and landscape components were very low (the highest was -0.262 between local component 1 and landscape component 3). Thus, these new composite variables can appropriately be used in multiple regression.

Habitat Regression Models

AVIAN-COMMUNITY INDICES

The variation ($r^2 = 0.79$) in bird species richness was positively correlated with the landscape component representing heterogeneity (Land-PC1; $r^2 = 0.55$, Table 4). The slope gradient (Local-PC2), a local habitat component, also was positively correlated with species richness. The landscape component (Land-PC2) representing the degree of clumping of habitat types or homogeneity was negatively correlated with species richness, which is in accordance with a positive association for landscape heterogeneity. Therefore,

species richness in this prairie system is best explained by the degree of landscape-level heterogeneity among habitat types and the slope of the local area.

The habitat model for the abundance of birds was explained by both local and landscape components. The local component representing variation in slope of the area was positively correlated with the abundance of birds (Local-PC2; Table 4). Landscape heterogeneity also was positively correlated with the abundance of birds, but to a lesser degree than the local slope component. Thus, abundance of birds is related to slope in the local area and landscape heterogeneity.

ECOLOGICAL GROUPS

The habitat model for woodland species explained 68% of the variation in the number birds. The local component (Local-PC1) representing the gradient from wooded areas to open grassy areas accounted for 49% of the total variation explained. This indicates that the number of woodland birds is best explained by local vegetation characteristics. The presence of herbaceous perennial vegetation (Local-PC3) and landscape homogeneity also contributed in explaining the numbers of woodland birds, but were less important in the overall model.

Grassland/savanna species were statistically explained solely by local habitat characteristics (Table 4). The local component representing the general vegetation gradient (Local-PC1) was positively correlated with the number of grassland/savanna birds, while the slope gradient (Local-PC2) was negatively associated. Thus, the abundance of grassland/savanna species was related primarily to local vegetation. In

general, grassland/savanna birds prefer areas with annual and perennial grasses that are relatively flat with little variation in slope.

INDIVIDUAL SPECIES

Landscape habitat components explained 0-44% of the variation in abundances of individuals species. Variation in abundance for bird species associated with woodland or edge habitats were primarily associated with local habitat factors. Local factors had an r^2 of 50% or greater for Tufted Titmice, Red-eyed Vireos, Great Crested Flycatchers, and Northern Cardinals. Local-PC1, summarizing habitat variables representing the vegetation gradient from wooded areas to grassland areas, was the most important factor in the models for the individual species that are generally associated with woodland or edge habitats.

In addition, numbers of Tufted Titmice were negatively correlated with the component (Local-PC3) that represents the abundance of herbaceous vegetation. Thus, numbers of Tufted Titmice are related primarily to the variation in local and herbaceous vegetation.

The habitat model for the Red-eyed Vireo indicates that the local components representing the gradient from woody areas to open grassy areas (Local-PC1) and a slope gradient (Local-PC2) were important characteristics. In addition, the numbers of vireos were negatively correlated with the degree of fragmentation (Land-PC3; Table 4). More than 85% of the variance explained by the model was accounted for by Local-PC1.

Therefore, the numbers of Red-eyed Vireos are related primarily to the variation in local vegetation characteristics.

The habitat model for the Great Crested Flycatcher explained 56% of the total variation, due largely to the contribution of the local vegetation (Local-PC1; Table 4). Local-PC2, representing the slope gradient, also entered into the model, but accounted for a small portion of the total variation. Thus, numbers of this flycatcher species were related primarily to local vegetation characteristics.

For the Northern Cardinal model, bird numbers were positively correlated with factors representing the gradient of local vegetation (Local-PC1) and the abundance of herbaceous vegetation 16-40 dm in height (Local-PC3; Table 4). Also, the number of cardinals was negatively correlated with the landscape component representing the clumping or aggregation of habitat types (Land-PC2). The landscape component (Land-PC2) accounted for only 5% of the total variation explained by the model. Therefore, the local vegetation is the primary indicator of the number of Northern Cardinals in a given area.

The contribution of landscape habitat factors for bird species typically associated with grasslands/savannas was notably greater than for woodland species. For the Field Sparrow, the landscape factor representing habitat heterogeneity (Land-PC1) explained 44% of variation in abundance, while the local habitat component representing the general vegetation gradient (Local-PC1) from wooded areas to open grassland areas explained 32% (Table 4). Thus, the degree of habitat heterogeneity and local vegetation both were important habitat characteristics for predicting the abundance of Field Sparrows.

The two components entered in the model for the Eastern Meadowlark represented local habitat features, including a general vegetation gradient (Local-PC1) and a slope gradient (Local-PC2; Table 4). The abundance of meadowlarks was positively correlated with Local-PC1, indicating a preference for sites characterized as open grasslands, and negatively correlated with Local-PC2, which suggests a preference for relatively flat sites with little variation in slope.

A combination of local and landscape variables was needed to predict numbers of Grasshopper Sparrows. Local-PC1, representing the local vegetation gradient, and the slope gradient (Local-PC2) were included in the model. However, the contribution of the slope gradient for explaining the variation in abundance of Grasshopper Sparrows was relatively small (Table 4). The landscape component, Land-PC2, which represents the degree of clumping of habitat types, also was a significant component in the model for Grasshopper Sparrows.

The habitat model for Dickcissels explained 56% of the total variation in its abundance (Table 4). Both local and landscape habitat components were included in the Dickcissel model. A local habitat component representing the vegetation gradient (Local-PC1) was positively correlated with abundance of Dickcissels, while the slope gradient (Local-PC2) was negatively associated. In addition, the landscape component indicating the degree of fragmentation (Land-PC3) was negatively correlated with numbers of Dickcissels.

Discussion

Both local and landscape components were important in the statistical habitat models derived to explain the variation in abundance of prairie avifauna. Models for avian-community indices were strongly influenced by landscape habitat characteristics. Nearly 70% of the variation in species richness was explained by landscape features representing habitat heterogeneity. Although the prairie is dominated by grasslands, the grassland landscape is interspersed with many narrow riparian woodlands that increase the overall heterogeneity of the landscape; this situation is a general characteristic of much of the Great Plains. Locally, species diversity typically increases as habitat heterogeneity increases. In particular, species diversity generally is high in grasslands or agricultural fields that are immediately adjacent to forests (Freemark & Merriam 1986). In such an area, the avifauna associated with a grassland includes bird species that typically are found in woodlands and edge habitats.

Variation in the abundance of birds (including all species) was explained primarily by a slope gradient (Local-PC2) and to a lesser degree landscape heterogeneity (Land-PC1). Local vegetation communities vary considerably along the slope gradient. Habitats found on relatively flat areas, including forests, savannas, and tallgrass prairies, typically support larger numbers of birds than those found on steep slopes, which often are covered by short-grass prairie and/or oak/juniper scrub.

Landscape heterogeneity also was an important factor in the model for overall bird abundance. As noted above, habitat heterogeneity in the grasslands is influenced largely

by the presence of narrow riparian woodlands. Numbers of organisms in a long narrow habitat patch are likely to be higher than in a circular or square habitat patch of comparable area because organisms are more likely to encounter a patch that is elongated (Hamazaki 1996). Furthermore, habitat diversity per se in such areas may result in more birds being attracted and supported. Thus, habitat heterogeneity of the grasslands affects both species richness and abundance.

Regression models of the ecologically-based groups of bird species (woodland and grassland/savanna species) were influenced strongly by local vegetation characteristics. For woodland species, the local habitat component (Local-PC1) representing a gradient from wooded areas to open grassland areas was the most important component entered in the model. More than 40% of the woodland species are cavity nesters that are closely associated with the forest or forest edge; the habitat model, governed primarily by the local gradient from wooded to open areas, was effective in explaining a large proportion of the variation among woodland birds. The abundance of herbaceous vegetation also was important for predicting numbers of woodland birds. The bottomland and upland forests in the prairie landscape have little herbaceous understory. This characteristic of prairie woodlands may account for the significant component related to the abundance of herbaceous vegetation in the model for woodland birds.

Grassland/savanna bird species appear to respond primarily to local habitat factors. The combination of components representing the local vegetation gradient and a slope gradient was the best predictor of the abundance of grassland/savanna birds. The statistical model for grassland/savanna birds was less effective than that for woodland

birds. However, the grassland/savanna group was larger than the woodland group (grassland/savanna, 27 species; woodland, 16; Appendix) and included species that were not exclusively associated with open grasslands. The Northern Bobwhite, for example, often is found in oak savanna in addition to prairie. This explains at least in part why the habitat model for the grassland/savanna group was less effective than that for the woodland group in explaining variation of bird numbers.

Habitat models for relatively abundant individual species incorporated both local and landscape components. Our findings suggest that Tufted Titmice, Red-eyed Vireos, Great Crested Flycatchers, and Northern Cardinals, all of which prefer forest habitats, were responding primarily to characteristics of the local vegetation. The first component entered in the models for these species was Local-PC1, the local vegetation gradient. In addition, Tufted Titmice preferred woodland sites that have little herbaceous vegetation. Grubb & Pravosudov (1994) indicated that Tufted Titmice preferred mostly deciduous forests with a dense canopy. Generally, forests with dense canopies have less understory vegetation than those with open canopies.

Abundance of Great Crested Flycatchers primarily was predicted by the local habitat characteristics. Habitat use of Great Crested Flycatchers varies considerably throughout their breeding range. They have a wide use of wooded habitats including deciduous or mixed woodlands, forest edges, riparian corridors, and urban woodlands (Lanyon 1997).

Numbers of Red-eyed Vireos and Northern Cardinals exhibited a weak relationship with landscape factors, and no landscape components were entered in the statistical models for the Tufted Titmouse and Great Crested Flycatcher. Unlike the deciduous

forests of eastern North America, forest patches in midcontinental prairie communities are relatively small. Bottomland forests in the Great Plains usually are associated with major perennial streams; consequently, they tend to be long and relatively narrow. Upland forests often exist as small patches interspersed with patches of grassland and oak savanna. Landscape factors such forest area and heterogeneity are important factors influencing the numbers of forest-interior birds (Freemark & Merriam 1986), but are less important for forest-edge species. Forest patches in the prairies typically are too small to sustain forest-interior bird species; thus, bird species that occur in these patches usually are forest-edge species, which are less sensitive to landscape habitat factors.

The influence of landscape habitat factors was more important for the individual species associated with grasslands/savannas than those typically found in woodlands. More than 57% of the variation explained by the statistical model for the Field Sparrow was by the landscape component representing habitat heterogeneity. Unlike other species examined, Field Sparrows preferred heterogeneous grasslands sites that were adjacent to patches of oak savanna or oak woodland. Similarly, in a study of birds on the grassland barrens in Maine, Vickery et al. (1994) found that Field Sparrows prefer heterogeneous grasslands interspersed with shrubs. Also, Carey et al. (1994) noted that Field Sparrows occupy successional old fields with scattered woody vegetation; however abundance declines with an increase in thickets of trees.

Local habitat components were most effective for explaining the amount of variation in numbers of Eastern Meadowlarks. While the vegetation gradient from wooded areas to open grasslands was important, meadowlarks also responded negatively to the local

habitat component representing an slope gradient (Local-PC2). Lanyon (1995) also indicated that Eastern Meadowlarks avoided areas with considerable slope; they prefer native grasslands in poorly-drained lowlands. In a study of grassland bird communities in Illinois, Herkert (1994) found that the incidence of meadowlarks was influenced by habitat area. With the combination of habitat characteristics we examined, habitat area was not the most important habitat feature related to numbers of Eastern Meadowlarks.

Our results suggest that abundance of Grasshopper Sparrows is related both to local and landscape habitat components. The statistical model indicated that Grasshopper Sparrows responded negatively to the clumping of habitat types and preferred areas with well-distributed habitats. Vickery (1996) found that Grasshopper Sparrows generally occupy intermediate grassland habitat, preferring drier, sparser sites in lush tallgrass prairies, and Rising (1996) noted that Grasshopper Sparrows prefer wet or dry pastures interspersed with shrubs or weeds. In our study area, Grasshopper Sparrows were most abundant in large meadows near the tops of rolling hills that were occasionally mowed or burned.

The variation in abundance of Dickcissels was related primarily to the local vegetation and the slope gradient; habitat fragmentation contributed to a lesser degree. Herkert (1994) found that Dickcissel abundance was not related to habitat area or vegetation structure in his study of grassland birds in Illinois, indicating a lack of association both with landscape and local habitat characteristics. Habitat fragmentation in Illinois is much more extensive than in our area, which may explain in part the disparate findings.

Conservation measures to protect grassland species should recognize that both local vegetation and landscape habitat characteristics have a significant influence on the overall richness and abundance of grassland species, as well as the abundance of individual species. Habitat heterogeneity, as reflected in the statistical models, was an important landscape factor affecting both community-wide indices and some individual species. Variation in the numbers of woodland birds, individually and as a group, was primarily associated with the local vegetation characteristics. Abundance of grassland/savanna birds, as a group, was best predicted by characteristics of the local habitat, although statistical models for particular grassland species suggest that they respond primarily to landscape features of the prairie.

Degradation and fragmentation of native prairies throughout North America have contributed to the decline of many grassland birds. Conservation efforts to protect threatened grassland birds should take into account the influence of both local and landscape habitat factors. In addition, broad-scale conservation strategies for grassland birds should address the variability among prairie landscapes. Although the prairie landscape in our study is similar to others in the midcontinental region, the vegetation composition and spatial arrangement of habitats differs markedly from what is found in northern prairies of North America. In addition, grassland/savanna birds, as a group, responded differently than individual grassland/savanna species to local and landscape features in our prairie landscape. Thus, conservation strategies for particular grassland/savanna species should take into account such variability within and among prairie landscapes.

When devising management strategies for prairie birds it is important to recognize that it is inappropriate to treat all species comprising the prairie avifauna in the same way because members of some groups (e.g. woodland species) are responding primarily to local habitat characteristics, while others (e.g. field sparrow, grasshopper sparrow) are responding to a combination of local and landscape factors. Thus, development of sound conservation strategies for prairie birds requires consideration of differences in the effects of local- and landscape-level habitat characteristics on individual species.

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Appendix. Groupings of bird species based on *K*-means cluster analysis of local habitat variables for sites where species were recorded.

Woodland species

Red-bellied Woodpecker (*Melanerpes carolinus*), Downy Woodpecker (*Picoides pubescens*), Eastern Wood-Pewee (*Contopus virens*), Great Crested Flycatcher (*Myiarchus crinitus*), American Crow (*Corvus brachyrhynchos*), Carolina Chickadee (*Parus carolinensis*), Tufted Titmouse (*P. bicolor*), White-breasted Nuthatch (*Sitta carolinensis*), Carolina Wren (*Thryothorus ludovicianus*), Blue-gray Gnatcatcher (*Poliophtila caerulea*), White-eyed Vireo (*Vireo griseus*), Red-eyed Vireo (*V. olivaceus*), Black-and-white Warbler (*Mniotilta varia*), Summer Tanager (*Piranga rubra*), Northern Cardinal (*Cardinalis cardinalis*), Indigo Bunting (*Passerina cyanea*).

Grassland/savanna species

Green Heron (*Butorides striatus*), Northern Harrier (*Circus cyaneus*), Red-tailed Hawk (*Buteo jamaicensis*), Ring-necked Pheasant (*Phasianus colchicus*), Northern Bobwhite (*Colinus virginianus*), Killdeer (*Charadrius vociferus*), Mourning Dove (*Zenaida macroura*), Common Nighthawk (*Chordeiles minor*), Chimney Swift (*Chaturra pelagica*), Ladder-backed Woodpecker (*Picoides scalaris*), Western Kingbird (*Tyrannus verticalis*), Eastern Kingbird (*T. tyrannus*), Scissor-tailed Flycatcher (*T. forficatus*), Barn Swallow (*Hirundo rustica*), Northern Mockingbird (*Mimus polyglottos*), Brown Thrasher (*Toxostoma rufum*), Loggerhead Shrike (*Lanius ludovicianus*), European Starling (*Sturnus*

vulgaris), Bell's Vireo (*Vireo bellii*), Dickcissel (*Spiza americana*), Field Sparrow (*Spizella pusilla*), Lark Sparrow (*Chondestes grammacus*), Grasshopper Sparrow (*Ammodramus savannarum*), Red-winged Blackbird (*Agelaius phoeniceus*), Eastern Meadowlark (*Sturnella magna*), Common Grackle (*Quiscalus quiscula*), Northern Oriole (*Icterus galbula*).

Other species

Turkey Vulture (*Cathartes aura*), Mississippi Kite (*Ictinia mississippiensis*), Yellow-billed Cuckoo (*Coccyzus americanus*), Canyon Wren (*Catherpes mexicanus*), Bewick's Wren (*Thryomanes bewickii*), Eastern Bluebird (*Sialia sialis*), Blue Grosbeak (*Guiraca caerulea*), Painted Bunting (*Passerina ciris*), Cassin's Sparrow (*Aimophila cassinii*), Rufous-crowned Sparrow (*A. ruficeps*), Brown-headed Cowbird (*Molothus ater*), House Sparrow (*Passer domesticus*).

Table 1. Principal-component loadings of 16 local habitat variables. Significant ($P < 0.05$) loadings on each component are in bold.

<i>Variable</i>	<i>Component</i>		
	<i>1</i>	<i>2</i>	<i>3</i>
Slope			
Mean	0.007	0.775	0.451
Standard deviation	-0.013	0.604	0.423
Vertical herbaceous structure			
0 to 15 dm	0.619	-0.237	-0.364
16 to 40 dm	0.530	0.402	-0.575
41 to 85 dm	-0.743	0.168	-0.409
>85 dm	-0.543	-0.015	-0.385
Vertical broadleaf structure			
0 to 15 dm	-0.064	-0.255	0.484
16 to 40 dm	-0.776	-0.338	0.390
41 to 85 dm	-0.762	-0.356	0.371
>85 dm	-0.772	-0.397	0.220
Total count			
Grasses	0.676	-0.406	-0.071
Forbs	0.537	-0.273	0.077
Coniferous shrubs	0.045	0.289	0.219
Broadleaf shrubs	-0.195	-0.133	-0.052
Coniferous trees	-0.327	0.023	-0.161
Broadleaf trees	-0.957	-0.013	-0.136

Table 2. Comparison of eigenvalues of principal-components analysis and parallel analysis for local and landscape data. Eigenvalues for first three principal components for both local and landscape analyses are larger than corresponding parallel analysis and, thus, are significant at $P < 0.05$. Retaining these components for interpretation and subsequent analysis is appropriate.

<i>Component</i>	<i>Eigenvalue</i>	
	<i>Principal-components analysis</i>	<i>Parallel analysis</i>
Local-level habitat variables		
1	5.103	2.007
2	2.017	1.762
3	1.839	1.596
4	1.328	1.446
5	1.177	1.333
6	1.051	1.234
Landscape-level habitat variables		
1	6.636	1.925
2	2.024	1.682
3	1.798	1.518
4	1.213	1.366
5	0.934	1.254
6	0.546	1.157

Table 3. Principal-component loadings of 14 landscape habitat variables.

Significant ($P < 0.05$) loadings on each component are in bold.

<i>Variable</i>	<i>Component</i>		
	<i>1</i>	<i>2</i>	<i>3</i>
Mean patch size	0.822	0.378	0.025
Standard deviation of patch size	0.778	-0.439	0.031
Mean patch shape (corrected perimeter/area)	-0.268	-0.312	-0.672
Standard deviation of patch shape	-0.461	-0.480	-0.390
Fractal dimension	-0.279	0.008	-0.519
Sum of patch perimeters	-0.908	0.110	-0.291
Mean perimeter length	0.604	0.534	-0.443
Standard deviation of perimeter length	0.102	-0.059	-0.552
Habitat patch richness	-0.877	-0.139	0.300
Contagion	-0.587	-0.625	0.335
Angular second moment	0.719	-0.586	-0.087
Entropy	-0.793	0.537	0.156
Contrast	-0.834	0.013	0.132
Sum of edge length	-0.915	0.131	-0.291

Table 4. Habitat models generated by stepwise regression analysis. Variable names with “local” and “land” prefixes denote local and landscape habitat factors, respectively, while suffix indicates given principal component. Partial r^2 for each component given in parentheses. Model r^2 is coefficient of determination for entire regression equation. Local r^2 and landscape r^2 indicate amount of variation explained by local and landscape components.

<i>Bird variable</i>	<i>Habitat components^a</i>	<i>Model r^2</i>	<i>Local r^2</i>	<i>Landscape r^2</i>
Avian-community indices				
Species richness	+Land-PC1*** (0.31) +Local-PC2** (0.24) -Land-PC2** (0.24)	0.79	0.24	0.55
Abundance	+Local-PC2*** (0.26) +Land-PC1* (0.15)	0.41	0.26	0.15
Ecological groups				
Woodland species	+Local-PC1*** (0.62) +Local-PC3*** (0.04) -Land-PC2* (0.02)	0.68	0.66	0.02
Grassland/savanna species	+Local-PC1*** (0.36) -Local-PC2*** (0.13)	0.49	0.49	0.00

Table 4. Continued.

<i>Bird variable</i>	<i>Habitat components</i> ^a	<i>Model</i> <i>r</i> ²	<i>Local</i> <i>r</i> ²	<i>Landscape</i> <i>r</i> ²
Individual species				
Tufted Titmouse	+Local-PC1*** (0.71) -Local-PC3* (0.03)	0.74	0.74	0.00
Red-eyed Vireo	+Local-PC1*** (0.45) +Local-PC2** (0.05) -Land-PC3* (0.02)	0.52	0.50	0.02
Great Crested Flycatcher	+Local-PC1*** (0.55) +Local-PC2* (0.01)	0.56	0.56	0.00
Northern Cardinal	+Local-PC1*** (0.53) +Local-PC3* (0.03) -Land-PC2* (0.03)	0.59	0.56	0.03
Field Sparrow	+Land-PC1*** (0.44) -Local-PC1** (0.32)	0.76	0.32	0.44
Eastern Meadowlark	+Local-PC1*** (0.36) -Local-PC2*** (0.12)	0.48	0.48	0.00

Table 4. Continued.

<i>Bird variable</i>	<i>Habitat components</i> ^a	<i>Model</i> <i>r</i> ²	<i>Local</i> <i>r</i> ²	<i>Landscape</i> <i>r</i> ²
Grasshopper Sparrow	+Local-PC1*** (0.27)	0.52	0.29	0.23
	-Land-PC2*** (0.23)			
	-Local-PC2* (0.02)			
Dickcissel	+Local-PC1*** (0.33)	0.56	0.46	0.10
	-Local-PC2*** (0.13)			
	-Land-PC3** (0.10)			

^a Significant response variables: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Figure captions

Figure 1. Location in USA of study area in (A) Oklahoma and (B) southwestern portion of state. (C) Detailed map of study area (indicated by dashed rectangle) including Fort Sill Military Reservation, a portion of the Wichita Mountains National Wildlife Refuge, and surrounding communities. Dotted lines indicate county boundaries and heavy solid lines indicate major highways. (D) Location of 98 sample plots on Fort Sill Military Reservation.

Figure 2. Concentric band (400-m radius) centered on 100-m line transect used to compute landscape indices.

Fig. 1

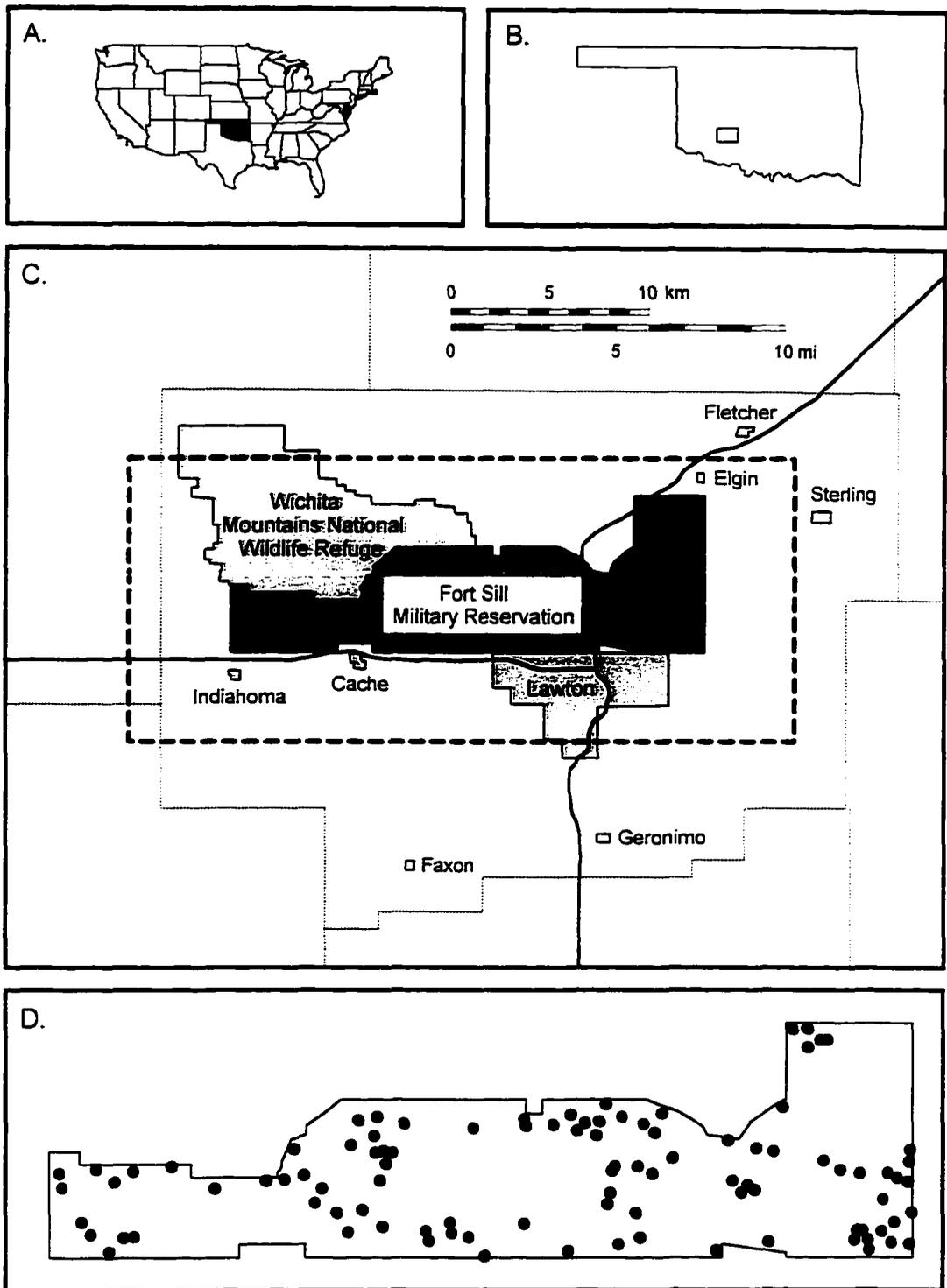
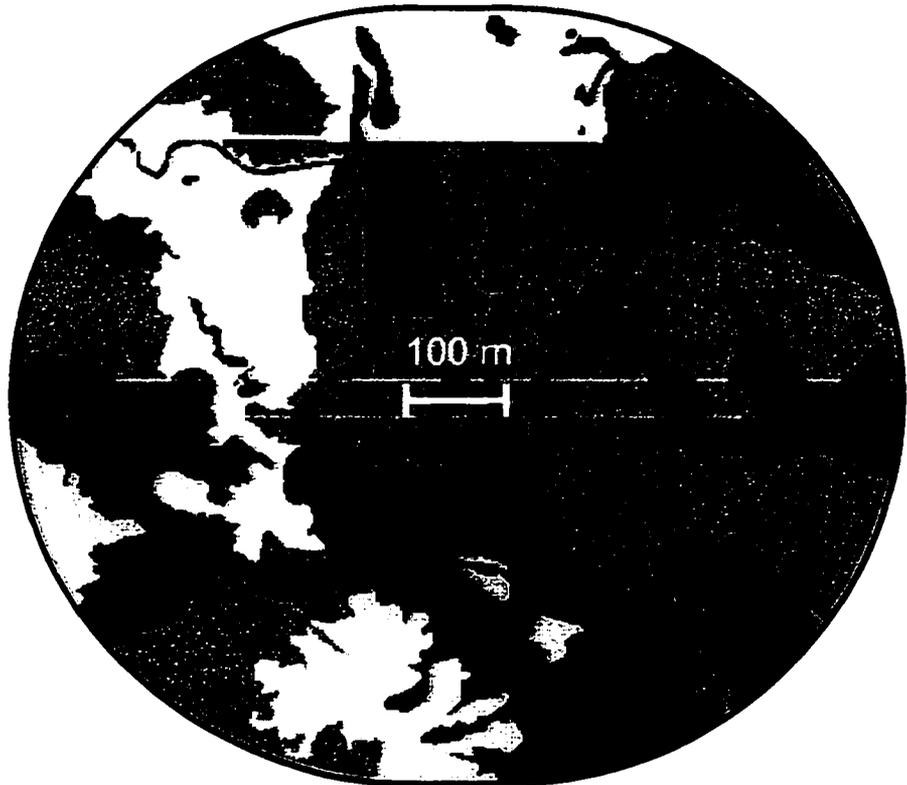


Fig. 2



Running Head: *Pogue and Schnell* • FRAGMENTATION EFFECTS ON GRASSLAND
BIRDS

EFFECTS OF HABITAT FRAGMENTATION ON
GRASSLAND BIRDS

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ABSTRACT.—We evaluated the degree of fragmentation of habitats used by grassland and savanna bird species in a prairie landscape. Habitat fragmentation was estimated using perimeter-area fractal dimension computed at 13 spatial scales ranging from 10 to 1,000 ha. Fractal dimension measures of habitats used by grassland/savanna birds were compared with those of randomly-selected sites. Habitat fragmentation, measured by fractal dimension, is not a scale-independent feature of the landscape. Habitats occupied by grassland/savanna birds were significantly different from randomly-chosen sites at spatial scales of 50 and 75 ha. Mourning Doves (*Zenaida macroura*), Dickcissels (*Spiza americana*), Field Sparrows (*Spizella pusilla*), and Eastern Meadowlarks (*Sturnella magna*) occurred in habitats that exhibited a higher level of fragmentation than random sites. The spatial configuration of habitat patches is an important factor for determining the appropriate spatial scale to evaluate habitat fragmentation. Natural fragmentation of the grasslands by woodlands associated with intermittent streams has a strong influence on the distribution of grassland/savanna birds.

In North America, much of the landscape has been altered by urban and agricultural development. Consequently, native habitats are becoming increasingly fragmented. Fragmentation has been defined as “the breaking up of a large habitat into smaller parcels” (Forman 1995). The effects of habitat fragmentation on bird population dynamics has been a central issue in avian conservation. Most reports of declining populations of songbirds have focused on changes that have occurred in the forested landscapes of eastern North America. An emerging consensus is that habitat fragmentation in North America has contributed to the population declines of many Neotropical migrant species (e.g., Robbins et al. 1989, Freemark and Collins 1989, Askins et al. 1990).

Although eastern forests of North America have been studied most extensively, prairie grasslands also have deteriorated resulting from agricultural and urban development. Loss of habitat due to agricultural practices and urban development have severely reduced and fragmented native grasslands throughout central United States (Vance 1976, Herkert 1994). In the southern Great Plains, land used for agriculture has increased more than 20% over the last 60 years, and now more than 30% of the total area is under cultivation (U.S. Department of Agriculture 1934-1994). The effects of habitat fragmentation on grassland communities have received comparatively little attention despite the fact that loss of grassland habitat has exceeded loss of forest habitat throughout much of the central United States (e.g., Smith 1981, Iverson 1988, Sample 1989).

A variety of consequences can result from habitat fragmentation, including an overall loss of habitat, a reduction in the size of habitat patches, and the isolation of habitat patches (Merriam 1988, Bennett 1990, Wiens 1994). Populations of area-sensitive species

can decline as a result of the reduction in habitat area. Dispersal of organisms tends to be limited within isolated habitat patches. Also, predation and parasitism generally are more prevalent in fragmented habitats, primarily as a result of edge effects.

Fragmentation in native prairies undoubtedly has influenced populations of grassland birds. Population trends derived from the Breeding Bird Survey (BBS) indicate that grassland birds have shown consistent populations declines throughout the 30-year period that bird populations have been monitored (Goriup 1988, Herkert 1991b, Askins 1993, Senner 1994, Sauer et al. 1997). In fact, many grassland bird species currently are experiencing decreases that exceed those exhibited by most forest species (Robbins et al. 1986, 1989; Herkert 1991a). In the United States, for example, numbers of Grasshopper Sparrows (*Ammodramus savannarum*) and Field Sparrows (*Spizella pusilla*) have decreased more than 50% (Herkert 1994), and fewer than 30% of North American grassland species have increasing populations (Sauer et al. 1997).

Some difficulties in understanding fragmentation effects may result from the uncertainty in defining fragmentation. Fragmentation can refer to the spatial pattern of patchiness of a habitat or to the process that produces such a pattern (Wiens 1994). Here we consider fragmentation in the context of the spatial arrangement of habitat patches and measure the degree of fragmentation using the perimeter-area fractal dimension. We evaluate the degree of fragmentation of habitats used by grassland and savanna bird species in a prairie landscape.

METHODS

Study area. —The study area (160,535 ha) is located in southwestern Oklahoma (Fig. 1a). It is centered on the Fort Sill Military Reservation (38,292 ha) and includes approximately 80% of the Wichita Mountains National Wildlife Refuge. The communities of Lawton, Cache, Indianola, and Elgin are included in the study area.

The area is transitional, containing vegetation communities typical of both mesic and xeric environments. Typical grassland habitats found in the study area include: short, mixed, and tall grasslands; rangeland; and cultivated agricultural fields. Important plants in the grassland habitats are little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), and gramma grasses (*Bouteloua* spp.) Savanna habitats are grasslands with scattered oak (*Quercus* spp.) and mesquite (*Prosopis glandulosa*). Woodland habitats include: upland cross-timbers dominated by post oak (*Q. stellata*) and blackjack oak (*Q. marilandica*); bottomland woodlands dominated by sugarberry (*Celtis laevigata*) and American elm (*Ulmus americana*); and woodlands associated with perennial and intermittent streams.

Bird sampling. —Annual censuses of birds were made at 98 sample plots (Fig. 1b) on Fort Sill from 1993 through 1995. Sample plots were established by the Land Condition Trend Analysis (LCTA; Tazik et al. 1992) program, which was implemented by the U.S. Army at Fort Sill to inventory and monitor natural resources. The LCTA plots were selected by stratified-random sampling to provide an adequate representation of the various vegetation communities.

Birds were sampled at each plot using a modified point-count transect technique (Blondel et al. 1981) along 100-m transects, each which had a randomly-chosen azimuth. Each year the inventory was conducted within a two- to four-week span (falling within the period 15 April to 30 June) corresponding to the seasonal peak in breeding-bird activity. Each plot was censused twice each year, once in the morning and once in the evening. In total, each site was sampled six times (twice each year for three years). All morning censuses were conducted between 0.5 h before and 4 h after sunrise. Evening censuses were conducted during the 4 h prior to sunset. D. W. Pogue censused the plots by slowly walking the length of a 100-m transect in 6 min and recording all birds seen or heard within 100 m of the transect line. He then stopped for 8 min and recorded any new birds seen or heard within 100 m. Finally, he walked back to the starting point over a period of 6 min, recording any new birds detected within 100 m.

Land-cover classification.—A land-cover map of the study area was produced from 1990 National High Altitude Photography (NHAP) panchromatic aerial photographs. We obtained 172 of the 61 cm × 61 cm photographs (scale 1:7920) from the U.S. Agricultural Stabilization and Conservation Service, Salt Lake City, Utah. Photographs were taken 24 November to 9 December 1990. Each photograph was georeferenced using 7.5-minute topographic maps (1:24000) obtained from the U.S. Geological Survey. Land-cover patches were identified by visual interpretation. Polygons defining patch boundaries were manually delineated using the Geographic Resources Analysis Support System (GRASS), a geographic information system (GIS; CERL 1989). After completing a digitized vector map for each photograph, the individual vector maps were patched together to create a

single vector map of the study area. Each polygon representing a land-cover patch was labeled appropriately. The labeled vector map was rasterized at 1-m resolution to produce the final land-cover classification map with each pixel being classified in one of five categories: (1) grassland, (2) savanna, (3) woodland, (4) water, or (5) residential/disturbed area (Fig. 2). The land-cover map was checked for accuracy by ground-truthing.

Habitat sampling.—We used the GIS to compute mean patch size (ha), mean perimeter length (m), and fractal dimension for each land-cover type and all land-cover types combined for the entire study area. Fractal dimension (d) was calculated as,

$$d = 2 s,$$

(1)

where s is the slope of the regression of the log of the patch perimeter versus the log of the patch area (Krummel et al. 1987, Baker 1997). When considering a landscape as a two-dimensional system, fractal dimension ranges from near 1 for simple unfragmented patches to 2 for complex highly-fragmented patches.

In addition, a sampling square encompassing 10 ha was delineated around each of the 98 100-m transects. Fractal dimension was computed for each sampling square. This procedure was repeated for an additional 12 spatial scales, with squares ranging from 15 to 1,000 ha (see Table 1). Also, fractal dimension for 98 randomly-selected sites was calculated at the same 13 spatial scales.

Statistical analysis.—Bird species were grouped on the basis of local habitat characteristics using K -means cluster analysis (Gower 1967, SPSS 1997). For each

species, we computed an average value for local habitat variables based on the plots where the bird species was recorded at least once. These average values were used in the cluster analysis, which produced three groups of birds: (1) primarily woodland species, (2) primarily grassland/savanna species, and (3) other species, a group comprised of ecologically diverse species. More details of methods used for local habitat sampling and cluster analysis are provided in Pogue and Schnell (1998). Only species in the grassland/savanna group were included in the current study.

Our interest was in evaluating for differences in fractal dimension among sample means for sites occupied by grassland/savanna birds compared to randomly-selected sites. However, a question arose as to whether differences uncovered were due to birds preferentially selecting sites relative to fractal dimension, or whether such differences were simply an artifact introduced by our stratified-random sampling design. Therefore we compared average fractal dimension for the 98 sample sites with the 98 randomly-selected sites. No statistically significant differences were found at any of the spatial scales evaluated. Thus, it was appropriate to compare fractal dimension for bird-selected sites with those sites we chose randomly.

For each spatial scale, fractal dimensions of plots occupied by any grassland/savanna species were compared with those of the random sites using a two-way analysis of variance (Sokal and Rohlf 1995). Furthermore, a sum-of-squares simultaneous test procedure (SS-STP; Gabriel 1964), an a posteriori multiple-comparison method, was employed to test for statistical significance between means of fractal dimension for sites occupied by grassland/savanna species and random sites at each spatial scale. The SS-

STP is an extension of the Scheffé test and is more conservative than other unplanned tests, meaning that a larger difference between means is required for significance. The two-way analysis of variance and SS-STP tests were performed using BIOMstat (Rohlf and Slice 1996).

For each spatial scale at which a significant difference among means was indicated, two-sample *t*-tests were used to evaluate the differences between mean fractal dimension for individual grassland/savanna species and random plots. Two-sample *t*-tests were performed using SYSTAT (SPSS 1997).

RESULTS

General landscape characteristics.—The average patch size of all land-cover patches in the study area is 26.9 ha (Table 1). Grasslands, which comprise more than 50% of the total study area, are 10 times larger in area than the average patch size of other land-cover types. The average size of woodland and savanna patches are similar and relatively small in comparison to grassland patches. The water component in the landscape, which is comprised of a few relatively large lakes and many small ponds, has the smallest average patch size (Table 1).

Excluding woodlands, fractal dimensions for all land-cover types are similar, ranging from 1.201 to 1.260. Fractal dimension for woodland patches is considerably higher (1.414), which is a reflection of the large perimeter-to-area ratio of woodland habitats. Many of the woodland patches are associated with perennial and intermittent streams; the

shape of such patches tends to be relatively long and narrow, and they usually have convoluted edges.

Grassland/savanna bird-community characteristics.—Grassland/savanna bird species were recorded on 81 of the 98 sites sampled. Thus, we can consider these 81 sites to be at least minimally suitable for grassland/savanna birds. The mean fractal dimension of sites occupied by grassland/savanna birds and of randomly-selected sites both increased as the spatial scale increased from 50 to 1,000 ha. (Fig. 3).

The results of a two-way ANOVA indicate that mean values of fractal dimension for sites inhabited by grassland/savanna birds were significantly higher than sites that were randomly selected ($P < 0.001$). The adjusted least square mean for grassland/savanna birds was 1.197 ($n = 753$), and it was 1.183 ($n = 840$) for random sites. Multiple comparisons of mean fractal dimension at each spatial scale are provided in Table 2. Results of SS-STP tests indicate that mean values of fractal dimension for sites occupied by grassland/savanna bird species were significantly different from random sites at spatial scales of 50 and 75 ha. Perimeter-area fractal dimension is determined the slope of the regression for all patches within the sampling area. If fewer than four patches are present in the sampling area, an accurate measure of fractal dimension cannot be computed for that particular site. Thus, the sample size and degrees of freedom vary accordingly.

Individual species.—Fractal dimension of sites inhabited by each grassland/savanna species (27 total) were evaluated at spatial scales of 50 and 75 ha. Results of two-sample t -tests revealed that mean fractal dimensions for seven species were significantly different from those of random sites at a spatial scale of 50 ha (Table 3). Four of the seven species

(i.e., Mourning Dove, Field Sparrow, Dickcissel, and Eastern Meadowlark) typically are associated with grassland habitats; the Ladder-backed Woodpecker is more common in the mesquite savanna. The combination of mesquite savanna and grassland habitats tends to increase the overall fragmentation of the area, which is reflected by the significant difference between values of fractal dimension for sites inhabited by this woodpecker and randomly-selected sites.

Northern Orioles, which are relatively uncommon in the study area, were generally found along narrow woodlands interspersed among the grasslands. Usually, woodlands associated with perennial and intermittent streams are long narrow patches with considerable perimeter length, which tends to increase the overall fragmentation; consequently, the average fractal dimension for sites used by Northern Orioles is higher than for randomly-chosen sites.

Although Western Kingbirds were found in grassland habitats, they also were near human habitation. Grasslands habitats adjacent to residential/disturbed areas tend to have a relatively high fractal dimension.

At a spatial scale of 75 ha, fractal dimensions for sites used by 9 of the 27 bird species were statistically different than for randomly-selected sites (Table 3). Four of the nine species were the same as those found to have significant differences among values of fractal dimension at the 50-ha scale; these were the ones typically found in grassland habitats. In addition, Northern Bobwhites, which are common in grassland and savanna habitats, were found in areas with a higher degree of habitat fragmentation. Common Nighthawks and Chimney Swifts, which tend to forage extensively in the open grasslands,

were more frequently found flying over grassland habitats that were more fragmented than random sites. Bell's Vireos were locally common in grassland habitats interspersed with small dense thickets, which contributed to the degree of habitat fragmentation.

Loggerhead Shrikes preferred open habitats with perching and nesting sites. Sites with these habitats had a significantly higher degree of fragmentation than random sites.

DISCUSSION

Fractal dimension often is interpreted as a scale-independent measure of habitat fragmentation. However, it is clear that habitat fragmentation in this landscape is not scale independent. Similarly, fractal-dimension measures of woodland landscapes reflect a lack of scale independence (Leduc et al. 1994). Mean values for fractal dimension increased for both grassland/savanna bird sites and random sites at spatial scales greater than 50 ha. The calculation of fractal dimension at smaller spatial scales may be biased as a result of reduced sample size. At these smaller scales, sites with only a single or few patches were not included in the computation of the average fractal dimension. These, of course, are sites that would have a low fractal dimension, but because of the method we used to calculate fractal dimension, they were deleted from the analysis. Theoretically, had they been included, the average fractal dimension would have been lower for sites at small spatial scales. Thus, the lack of linearity and lack of a positive slope in the lower portion of the curve (see Fig. 3) most likely is a simple reflection of a computational bias rather than a basic difference in the trend.

The fragmentation of patches for grassland, savanna, water, and residential/disturbed areas is considerably less than that of woodland patches. Thus, the presence of woodland patches in a given area contributes to the higher overall fractal dimension. Moreover, as the spatial extent increases, woodland patches increase in number relative to other habitat types, which results in an increase in the relative degree of fragmentation.

At spatial scales of 50 ha or larger, fractal-dimension values for sites inhabited by grassland/savanna birds generally were higher than those of randomly-selected sites (see Fig. 3). Among woodland habitats in this prairie landscape, those associated with intermittent drainages have the highest perimeter-to-area ratio. Woodlands along intermittent drainages can be less 50 m wide and more than a kilometer in length. Bottomland woodlands cross-timbers have a much lower perimeter-to-area ratio relative to those along intermittent streams. Thus, the fractal dimension is markedly higher for narrow woodlands than for other woodland habitats. Much of the grassland habitat is interspersed with many narrow woodlands; consequently, the sites occupied by grassland/savanna birds have a higher fractal dimension than randomly-selected sites.

Fractal dimension for habitats of grassland/savanna birds and random sites differed only at spatial scales of 50 and 75 ha. Clearly, the spatial arrangement of habitats in the landscape will influence the scale at which patterns of fragmentation are detected. In this landscape, perennial and intermittent streams generally follow a north-south path. Secondary drainages branch perpendicularly from the main stem of the stream, typically following an east-west course. The pattern of branching, although variable, is repeated throughout the landscape. Secondary streams and drainages are located approximately

800 m apart along the main stem of the stream. The length of the sides of the sampling square is 707 m for a 50-ha sampling area, and 866 m at 75 ha. For sampling areas of 50 and 75 ha, woodlands associated with perennial and intermittent drainages are consistent characteristics in the grassland areas. Thus, the critical scales for evaluating habitat fragmentation in this prairie landscape are at 50 and 75 ha.

The grassland/savanna bird species, whose habitats differed significantly from random sites with regard to the degree of fragmentation, can be considered on the basis of their habitat use. Dickcissels, Eastern Meadowlarks, Common Nighthawks, and Chimney Swifts are closely associated with open grasslands. Dickcissels and Eastern Meadowlarks both typically forage and nest in dense grasses. The most obvious benefit of scattered trees in the territories of these grassland birds is for song perches. Male Eastern Meadowlarks sing from perches located throughout their territories, and particularly from perches along the perimeter, adjacent to neighboring territories (Lanyon 1995). They prefer the highest perches capable of supporting the bird's mass that also provide an unobstructed view (Harrison 1977). Common Nighthawks and Chimney Swifts do not nest in the dense grass, but both tend to forage on the wing for flying insects over open grasslands (Poulin et al. 1996). Also, nighthawks and swifts forage near bodies of water, which are likely to have higher numbers of flying insects (Brigham 1990). The landscape in our study is dotted with many small ponds, typically less than 1 ha in area. Although the ponds are small relative to the woodland patches, they do increase the level of fragmentation of the landscape.

Northern Bobwhites, Mourning Doves, and Field Sparrows use open grasslands and nearby woodland edges. Northern Bobwhites generally nest in the open grasslands, but frequently use open woodlands and woodlands for protection against predators (Ehrlich et al. 1988). Their use of woodlands and edge habitats is likely to influence their selection of breeding habitats. Consequently, the habitats are likely to be more fragmented than those in open grasslands. Mourning Doves forage primarily in the grasslands. Their main food sources are cereal grains and seeds of native grasses and other herbaceous plants (Lewis 1993, Mirarchi and Baskett 1994); however, they generally nest in trees. The woodlands scattered throughout the grasslands provide potential nest sites for this abundant species. Field Sparrows also are closely associated with woodland edges, preferring grasslands and old fields with scattered woody vegetation (Carey et al. 1994). The abundance of Field Sparrows in our study area was directly related to the degrees of landscape heterogeneity (Pogue and Schnell 1998). In a study of birds on the grassland barrens in Maine, Vickery et al. (1994) found that Field Sparrows prefer heterogeneous grasslands interspersed with shrubs. Fragmentation of the grasslands by woodland patches is an important factor for this sparrow.

Ladder-backed Woodpeckers and Bell's Vireos were associated with grasslands habitats containing particular vegetation characteristics. Ladder-backed Woodpeckers were exclusively in grasslands interspersed with mesquite savanna. The distribution of grassland and savanna patches on sites occupied by this woodpecker is reflected by the higher degree of fragmentation. Bell's Vireos generally are found in habitats with dense, low, shrubby vegetation including mesquite savanna, second-growth forest or woodland,

and scrub oak (Brown 1993). In our study, Bell's Vireos occurred only in thickets of Chickasaw plum (*Prunus angustifolia*) or sumac (*Rhus* spp.) that were scattered throughout the grassland. The dense thickets, usually small round patches (< 25 m in diameter), most likely have little effect on the overall fragmentation; however, the cumulative influence of thickets, ponds, and narrow woodlands results in a higher fractal dimension for these habitats.

For Western Kingbirds, Loggerhead Shrikes, and Northern Orioles, prairie habitats are chosen that accommodate the particular foraging and nesting requirements for these species. Important breeding habitat features for Western Kingbirds include open grassland areas and tall trees or man-made structures for perch and nest sites (Gamble and Bergin 1996). In our study, Western Kingbirds rarely were recorded at sites far from residential/disturbed areas. Perch sites are important habitat features for Loggerhead Shrikes. Shrikes use high perches with unobstructed views to scan open grasslands for insects and small vertebrates (Sutton 1967). Grassland habitats with scattered trees are more fragmented than otherwise homogeneous grasslands; thus, the habitats occupied by Loggerhead Shrikes have a higher degree of fragmentation than randomly-chosen sites. Scattered trees in the grasslands provide a place to forage and nest sites for Northern Orioles. In the Central Plains, Northern Orioles prefer constructing their nests in cottonwoods (*Populus deltoides*), which are common in woodlands associated with prairie streams (Shirley 1959). Thus, sites preferred by orioles are likely to have relatively high level of fragmentation compared with those of random-selected sites.

In summary, habitat fragmentation in this prairie, as measured by fractal dimension, is not a scale-independent feature of the landscape. The spatial configuration of habitat patches is an important factor for determining the appropriate spatial scale to evaluate habitat fragmentation. In this prairie, the natural fragmentation of the grasslands by woodlands associated with intermittent streams has a strong influence on the distribution of grassland/savanna birds.

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TABLE 1. Mean patch area, mean perimeter length, and fractal dimension derived from land-cover classification map of study area.

Land cover type	Patch area (ha)	Perimeter length (m)	Fractal dimension
Grassland	269.4	17,594.0	1.260
Forest	15.4	3,885.2	1.414
Savanna	15.2	2,222.7	1.255
Water	0.8	320.4	1.215
Disturbed area/residential	50.5	6,985.7	1.201
All categories combined	26.9	2,835.8	1.297

TABLE 2. Results of SS-STP tests of fractal dimension comparing sites used by grassland/savanna bird species with randomly-selected sites.

Spatial scale (ha)	df	Critical SS	SS
10	16	0.0373	0.0001
15	33	0.0302	0.0002
20	49	0.0429	0.0013
25	55	0.0523	0.0054
50	103	0.0568	0.0581*
75	139	0.0322	0.0468**
100	146	0.0296	0.0220
150	161	0.0299	0.0175
200	168	0.0290	0.0017
250	175	0.0367	0.0073
500	177	0.0216	0.0012
750	177	0.0205	0.0039
1,000	177	0.0192	0.0001

*, $P < 0.05$; **, $P < 0.01$.

TABLE 3. Results of two-sample *t*-tests of fractal dimension for sites used by individual bird species and randomly-selected sites at spatial scales of 50 and 75 ha.

Bird species	No. sites species occurred	<i>t</i> -value	
		50 ha	75 ha
Green Heron (<i>Butorides striatus</i>)	5	2.238	1.299
Killdeer (<i>Charadrius vociferus</i>)	12	1.678	2.062
Northern Harrier (<i>Circus cyaneus</i>)	10	0.192	0.046
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	5	-0.728	0.359
Northern Bobwhite (<i>Colinus virginianus</i>)	52	1.452	2.329*
Ring-necked Pheasant (<i>Phasianus colchicus</i>)	6	0.012	-0.306
Mourning Dove (<i>Zenaida macroura</i>)	55	-2.364*	-2.788**
Common Nighthawk (<i>Chordeiles minor</i>)	32	1.600	2.081*
Chimney Swift (<i>Cheatura pelagica</i>)	11	1.602	3.384**
Ladder-backed Woodpecker (<i>Picoides scalaris</i>)	6	3.587**	1.783
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	6	-1.099	-1.641
Western Kingbird (<i>T. verticalis</i>)	9	-3.617 **	0.171
Scissor-tailed Flycatcher (<i>T. forficata</i>)	35	-1.222	-1.217
Barn Swallow (<i>Hirundo rustica</i>)	30	1.986	1.587
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	4	2.635	3.729*

TABLE 3. Continued.

Bird species	No. sites species occurred	<i>t</i> -value	
		50 ha	75 ha
Northern Mockingbird (<i>Mimus polyglottos</i>)	8	1.879	1.758
Brown Thrasher (<i>Toxostoma rufum</i>)	8	-2.654	-2.219
European Starling (<i>Sturnus vulgaris</i>)	5	-2.945	0.999
Bell's Vireo (<i>Vireo bellii</i>)	9	-1.707	-3.012*
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)	26	0.959	1.293
Lark Sparrow (<i>Chondestes grammacus</i>)	14	0.510	1.353
Field Sparrow (<i>Spizella pusilla</i>)	23	-2.424*	-3.657***
Dickcissel (<i>Spiza americana</i>)	63	-2.310*	-2.647**
Eastern Meadowlark (<i>Sturnella magna</i>)	66	-2.453*	-2.589*
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	36	1.795	1.822
Common Grackle (<i>Quiscalus quiscula</i>)	15	0.752	1.183
Northern Oriole (<i>Icterus galbula</i>)	3	3.679*	1.123

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

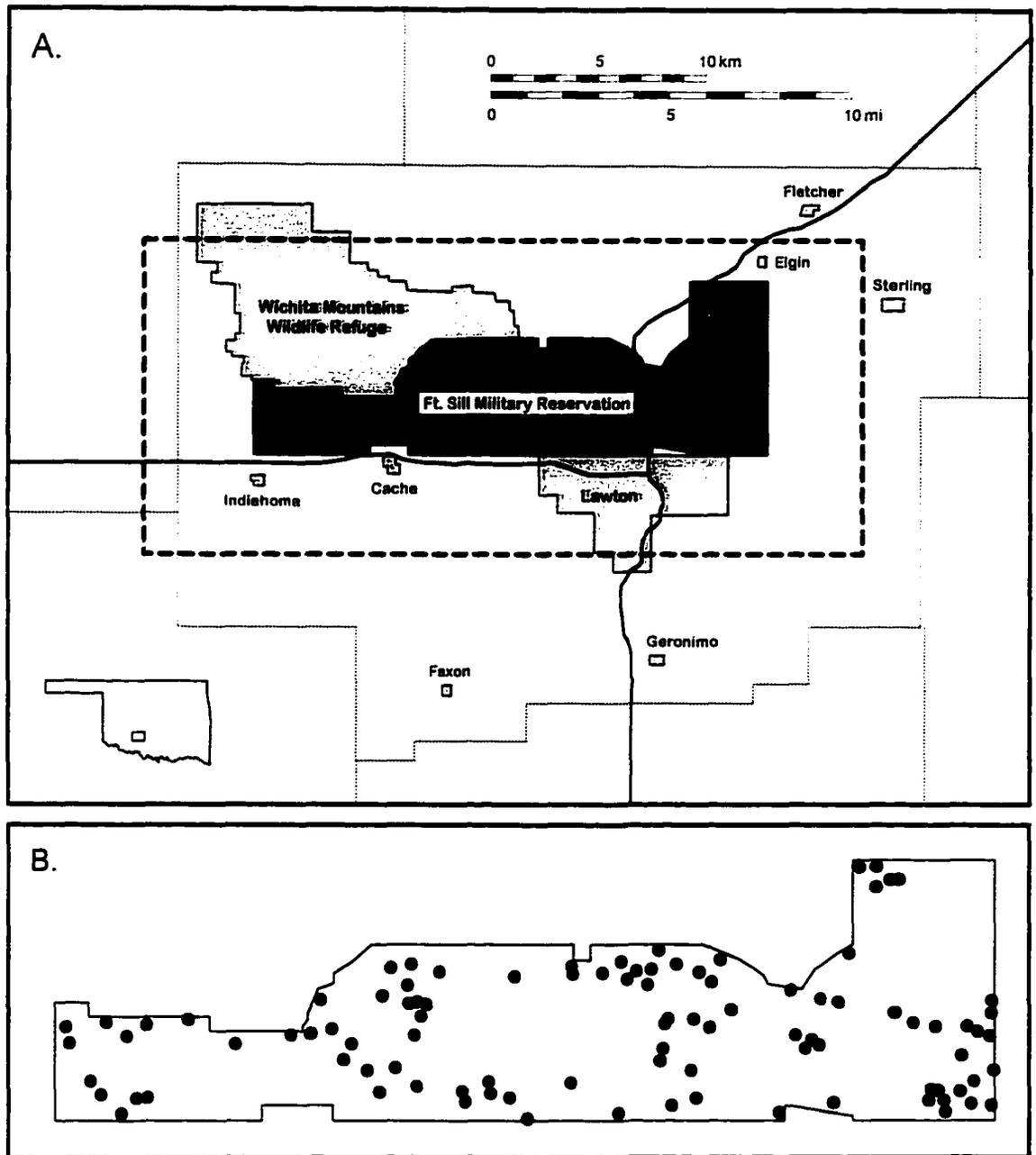
FIGURE CAPTIONS

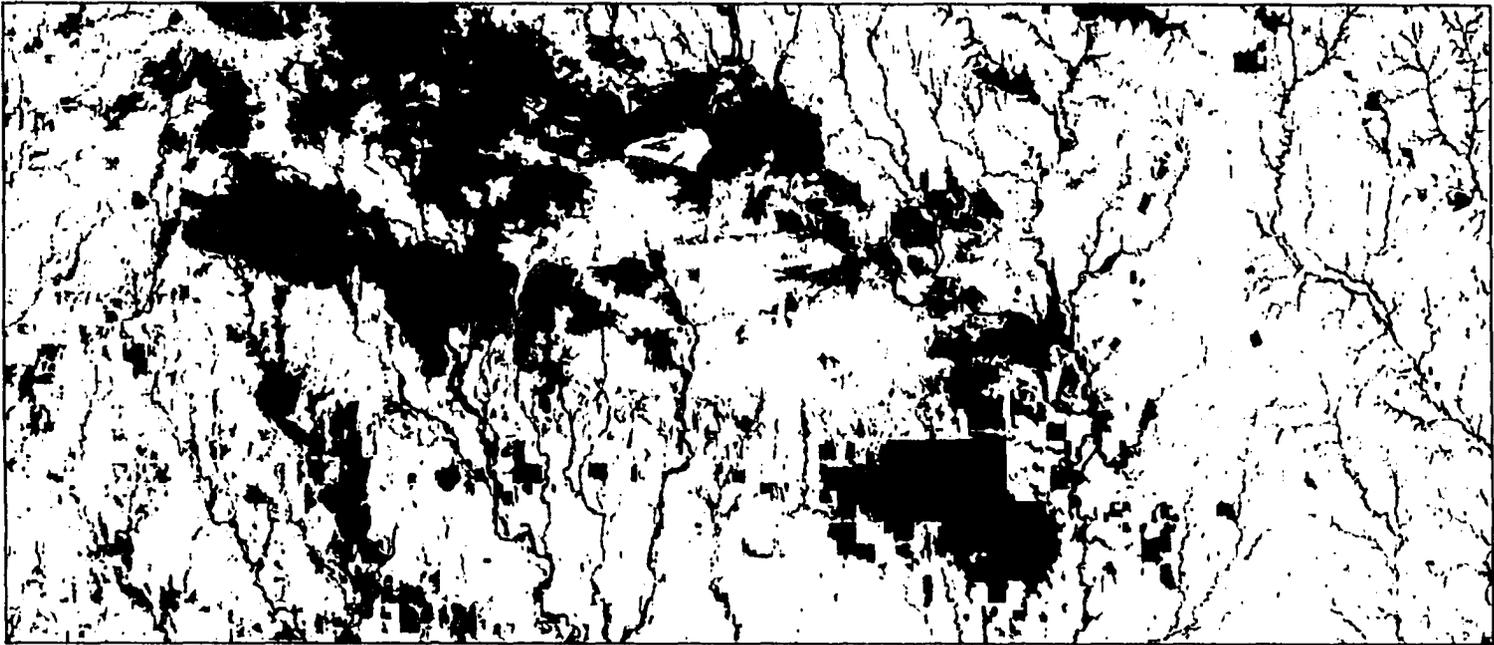
FIG. 1. (A) Detailed map of study area (indicated by dashed rectangle) including Fort Sill Military Reservation, a portion of Wichita Mountains National Wildlife Refuge, and surrounding communities. Dotted lines indicate county boundaries and heavy solid lines indicate major highways. (B) Location of 98 sampling plots on Fort Sill Military Reservation.

FIG. 2. Habitat classification of study area.

FIG. 3. Mean values of fractal dimension for sites occupied by grassland/savanna species and randomly-selected sites for spatial scales ranging from 10 to 1,000 ha.

Fig. 1





□ Grassland ■ Savanna ■ Woodland ■ Water ■ Residential/disturbed area

Fig. 2

Fig. 3

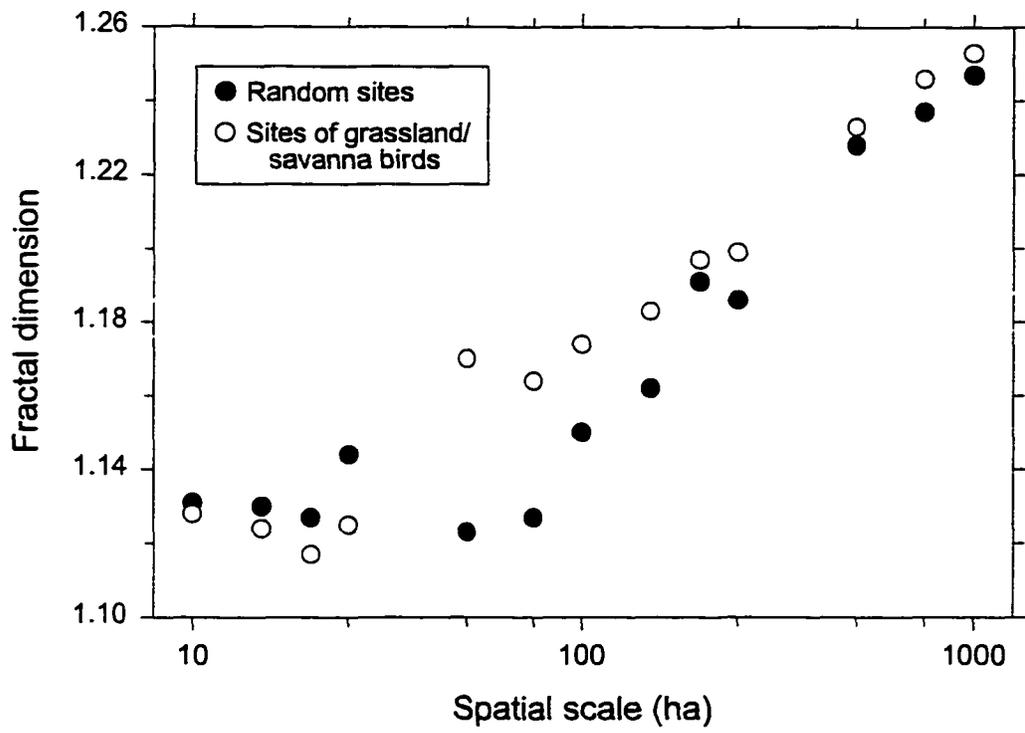
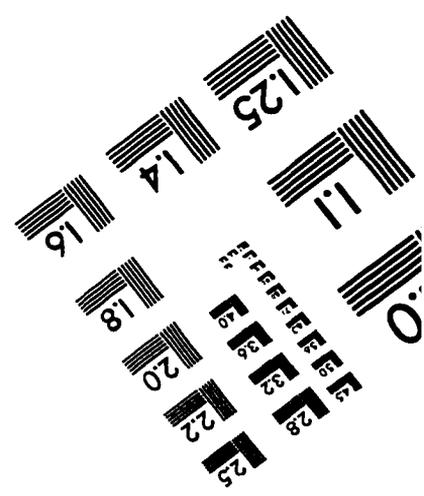
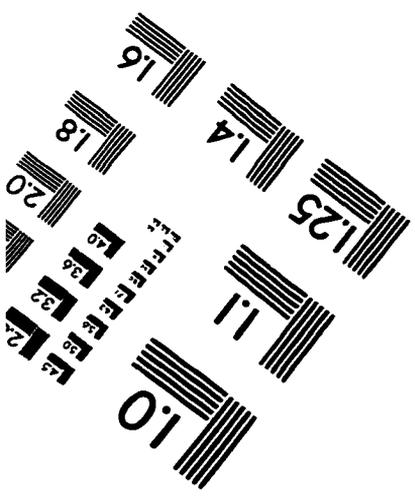
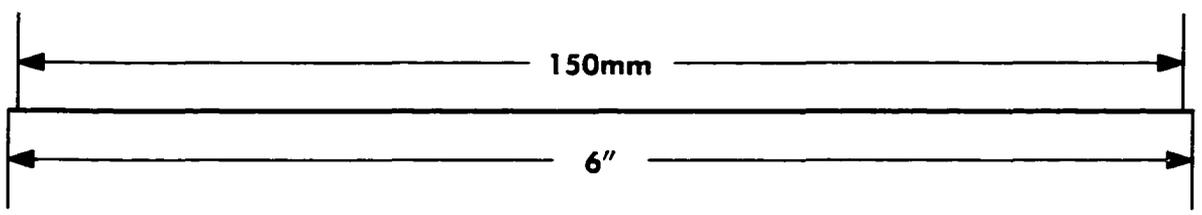
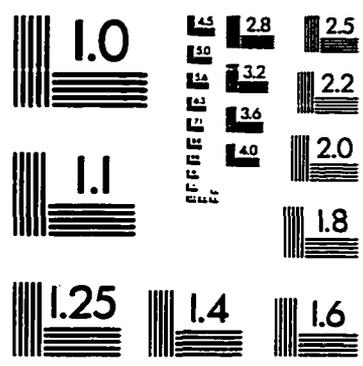
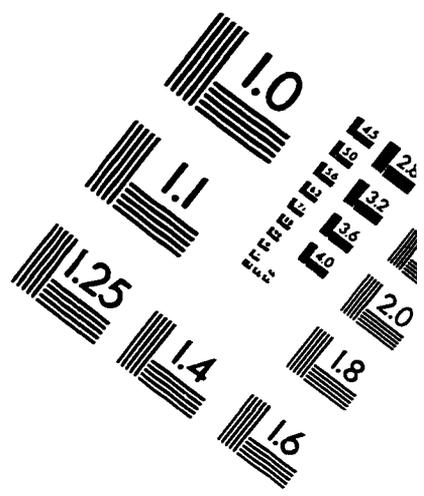
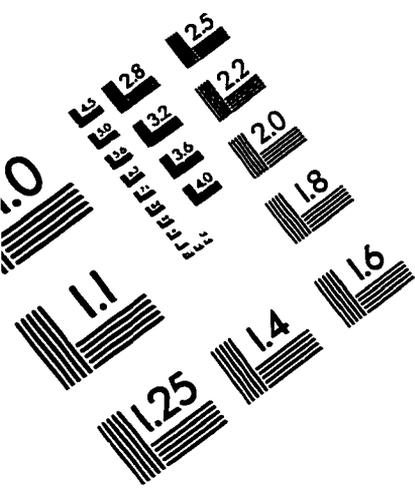


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