HISTORICAL CHANGES IN A FOREST-GRASSLAND ECOTONE AND THE EFFECTS OF LANDSCAPE CHANGE ON AVIAN REPRESENTATION

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CHAPTER I

INTRODUCTION

This thesis is composed of 2 manuscripts formatted for submission to selected scientific journals. Each manuscript is complete as written and does not require any additional support material. The order of arrangement for each manuscript is text, literature cited, tables, and figures. Chapter II, "Landscape composition and structure changes in a hardwood forest-tallgrass prairie ecotone of northern Oklahoma, U.S.A.", is written in Landscape Ecology format. Chapter III, "Effects of landscape changes on bird representation in a hardwood forest-tallgrass prairie ecotone", is written in Conservation Biology format.

CHAPTER II

LANDSCAPE COMPOSITION AND STRUCTURE CHANGES IN A HARDWOOD FOREST-TALLGRASS PRAIRIE ECOTONE OF NORTHERN OKLAHOMA, U.S.A.

Abstract: Temporal analysis of landscape cover types and landscape structure was conducted on a hardwood forest-tallgrass prairie ecotone in northern Oklahoma, U.S.A. A geographic information system (GIS) was used with 1990 aerial photography and 1900 General Land Office survey maps to document temporal changes in landscape cover types and landscape structure, to determine if landscape changes occurred more in a high population density rural or low population density rural landscape, and to determine if fragmentation was more prevalent in one of the matrix cover types. All landscape cover types changed in area from 1900 to 1990. The general trend of landscape cover types and landscape structure change was the same for both landscapes, but the amount of change individual landscape cover types and landscape structure measures underwent differed between landscapes. Decreases in cropland, native grassland, and deciduous forest in both landscapes were offset by increases in human impact areas, intensively managed land, brush treated land, roads, water, and bare ground. Intensively managed land, which was not present in either landscape in 1900, covered 31% of the high population density rural landscape by 1990. The addition of 3 human-influenced cover types resulted in increased diversity and decreased dominance on both landscapes with the largest change on the low population density rural landscape. Patch perimeter complexity increased on both landscapes as a result of decreased cropland and increased brush treatment of

forested land. Mean patch size decreased by more than 80% on both high population density rural and low population density rural landscapes, indicating that both landscapes were equally fragmented from 1900 to 1990. Mean patch size decreased by approximately 90% for both grassland and deciduous forests, suggesting that fragmentation did not occur more on one vegetation type. Documentation of temporal changes in landscape cover types and structure provided by this study will aid ecologists in understanding the past to help manage the future of the landscape.

INTRODUCTION

As human population increases in the United States, wildlands continue to be altered and fragmented. This alteration of natural land cover pattern by humans has been recognized for some time (Curtis 1956). Urbanization, forestry, and agriculture practices remove part of the natural vegetation and replace it with managed systems of altered structure (Krummel et al. 1987). The size-shape relationships of the altered land cover can influence important ecological and environmental phenomena (Burgess and Sharp 1981).

According to Simberloff (1993), habitat fragmentation is the major global environmental change occurring and the most likely to destroy biodiversity and ecological processes. The primary result of fragmentation is quantitative and qualitative loss of habitat for species originally dependent on the habitat type (Temple and Wilcox 1986). Declines in abundance and diversity of original species accompany fragmentation with greatest losses in the smallest fragments (Faaborg et al. 1992).

Much research has been conducted concerning fragmentation of forests, but grasslands and grassland-forest ecotones have only been studied minimally. Past ecological studies avoided the complexities of ecotones and worked in the centers of relatively homogeneous areas (Gosz 1989). However, an increasing number of scientists now believe that study of ecotones is of both theoretical and practical importance (Risser

1985, Naiman et al. 1988). Because ecotones typically have high biological diversity (Holland and Risser 1989, Risser 1990, Johnston et al. 1992), these boundary areas may be very important ecological sinks. Moreover, many believe that ecotones are highly susceptible to alteration and thus are good early indicators of change (Solomon 1986, di Castri et al. 1988, Dyer et al. 1988, Holland 1988, Holland and Risser 1989, Hansen et al. 1992, Noble 1993).

In this study, a geographic information system (GIS) was used with aerial photography and historic land survey maps to assess landscape change from 1900 to 1990 in a hardwood forest-tallgrass prairie ecotone in central North America. The working hypotheses were: 1.) landscapes were more fragmented in 1990 than in 1900 2.), landscape changes occurred more on a high population density rural landscape than on a low population density rural landscape, and 3.) fragmentation was greater for one of the matrix vegetation cover types over the other in the ecotone. This study supplies quantitative measures of landscape structure for two transects in a hardwood forest-tallgrass prairie ecotone at two points in time, approximately one century apart. The objectives of this study were to document temporal changes in landscape cover types and landscape structure, determine if landscape changes occurred more in a high population density rural or low population density rural landscape, and determine if fragmentation occurred more for one of the matrix vegetation types.

METHODS

Study Area

The study area centers around U. S. Fish and Wildlife Service Breeding Bird Survey route numbers 024 and 026 located in northeastern Oklahoma near the cities of Collinsville and Bartlesville, respectively (Figure 1). Legal description of these survey routes are provided by Baumgartner and Baumgartner (1992). The area includes the BBS routes and a 0.25 mile (400 m) area on each side of a route as the boundary. Selection of the study area was based on proximity to a metropolitan area and availability of historical aerial photography.

The survey routes lie on an ecotonal area between the grassland formation of the Cherokee Prairies and oak-hickory savannah of the Cross Timbers. The Cherokee Prairie of Oklahoma extends as a long, narrow strip, 150 miles southward from the Kansas state line with a width ranging from 30 to 60 miles during the majority of its length (Bruner 1931, Soil Conservation Service 1981). This area lies west of the Ozarks, extending far across the Arkansas river valley (Bruner 1931). The Cherokee Prairies region is underlain by fine textured soils developed from weathering of Pennsylvanian limestones and shales (Bruner 1931, Harlan 1957, Gray and Galloway 1959). The underlying geology in conjunction with the climate of the area are better adapted to produce grasses than forests (Bruner 1931, Harlan 1957). Tallgrass prairie is the predominate vegetation of the region. The Cross Timbers of Oklahoma lie west of the Cherokee Prairie and the Lower Arkansas Valley, extending 180 miles southward from Kansas, approximately 50 miles wide (Bruner 1931, Soil Conservation Service 1981). The region is underlain by alternating beds of Pennsylvanian sandstone and shales (Bruner 1931, Harlan 1957, Gray and Galloway 1959). The Cross Timbers region is covered with scrubby, transitional, oak forest with abundant grassy areas (Bruner 1931).

Study landscapes are both in proximity to Tulsa county, which is the major metropolitan area of northeastern Oklahoma. The estimated population of Tulsa County is 503,341 (Bureau of the Census 1990). Route 024 is in Washington County and route 026 is in Osage County. The human population density of Washingtion County in 1990 was 3340 km^{-2} and the population density of Osage County was 520 km^{-2}. We considered the Collinsville landscape to be subjected to more urban influence than the Bartlesville landscape. Thus, the Collinsville landscape will be referred to as the high population density rural landscape and the Bartlesville landscape will be referred to as the low population density rural landscape.

Data Collection

Black and white aerial photographs for 1990 were obtained from the U. S. Department of Agriculture, ASCS, Aerial Photography Field Office, Salt Lake City, Utah. Photographs were 24" X 24" enlargements with a representative fraction (RF) of 1:7,920. Photography was ordered to cover each BBS route (40.2 km in length) with an area at least 400 m wide on each side of the route as the boundary. The resulting area for each route was approximately 3150 ha.

Topographic quadrangle maps, photo inspected in 1976, showing the natural and man-made features of the land at 1 to 24,000 scale were ordered from the Oklahoma Geological Survey, Norman, Oklahoma. The quadrangles indicate both geographical coordinates and elevation as well as specific features such as vegetation, water, roads, towns, political boundaries, etc.

General Land Office (GLO) field notes of the area surrounding each route were ordered from the Oklahoma Department of Libraries, Oklahoma City, Oklahoma. These historical data are composed of the field notes taken by U. S. Surveyors as well as maps derived by the surveyors from their field notes. Surveys were run in 1908 and 1896 for the Bartlesville and Collinsville landscapes, respectively. For ease of discussion, the survey year will be referred to as 1900. The field notes constitute a definite sample of the vegetation and are usable for quantitative as well as qualitative analysis (Bourdo 1956).

Database Construction

In order to transform the aerial photography into a usable form, clear acetate was placed on each photograph, supervised photo interpretation was conducted, and all interpreted polygons of interest were marked. The following features were identified: BBS route boundaries, all roads, buildings and houses, land use, and vegetation cover types. Landscape cover types were interpreted based on an adaptation from Stoms et al. (1983) (Table 1).

The marked acetate sheets were digitized using a digital scanner. Scanned images were edited, rectified, and vectorized using LTPlus (United States Forest Service and Soil Conservation Service 1991) and imported into the GIS GRASS (Geographic Resource Analysis Support System) (Shapiro et al. 1992). Vector images were then patched together to form complete routes, labeled, and converted to raster images with 5m resolution. Accuracy checks of photo interpretation were verified in the field from hardcopy output of the labeled images for each route.

The GLO maps were copied from microfiche to paper with a RF of 1:17,182. The present day BBS routes were located on the GLO maps by tracing portions of the route that ran along section lines. Portions of the route that did not run along section lines were located by determining numerous registration points along the route on the topographic quadrangles and then locating the same points on the GLO maps. After the route boundaries were drawn on the GLO maps, the maps were overlaid with acetate, marked, scanned, edited, rectified, vectorized, rasterized, and labeled with the same methods used on the aerial photographs. The GLO field notes that correspond to the maps were transcribed from a copy of the surveyor's original handwriting. The field notes supplemented the maps in assigning landscape cover types to the polygons.

Data Analysis

The GIS was used to examine temporal changes in land use and vegetation cover types between and within landscapes. Total area (ha) and change (%) from 1900 to 1990 for landscape cover types were determined (Table 2).

Landscape structure was analyzed using the raster landscape ecological (r.le) spatial analysis package within GRASS (Baker and Cai 1992). The r.le program was used to generate landscape measures of mean patch size, patch size standard deviation, fractal dimension, richness, Shannon diversity, and dominance. Texture measures of angular second moment, and contrast were measured using eight neighbor analysis to quantify the adjacency of similar patch types.

Mean patch size is the mean size or area of the patches in the sampling area. It is calculated for all patches in the sampling area by dividing the sampling area size by the number of patches (Baker et al. 1994).

Perimeter-area interpretation of fractal dimension (Mandelbrot 1977, Lovejoy 1982, Krummel et al. 1987) was implemented to measure the complexity of patch perimeter (Baker and Cai 1992). The formula for fractal dimension, *d*, is:

$$d=2*s$$

where *s* is the slope of the regression of the log of the patch perimeter versus the log of the patch area (Lovejoy 1982, Baker and Cai 1992). Values of *d* range from 1 to 2. Simple geometric shapes (circles and rectangles) have values of *d* close to 1. As polygon perimeters become more complex, the value of *d* approaches 2 (Krummel et al 1987).

Three diversity measures of patch attributes were calculated: 1.) richness, 2.) Shannon index, 3.) dominance. Richness is simply the number of different patch attributes present in the sampling area (Baker and Cai 1992). Shannon index is a widely used measure of diversity that includes both richness and eveness (Smith 1990). The formula for the Shannon index, *H*, is:

$$H=-\sum_{i=1}^{m} P_i * \ln(P_i)$$

where p_i is the fraction of the sampling area occupied by attribute *i*, and *m* is the number of attributes in the sampling area (Baker and Cai 1992). The larger the value of *H*, the more diverse the landscape (O'Neill et al. 1988). Dominance is an index related to the Shannon index which emphasizes the deviation from eveness. The formula for dominance, *D*, is:

$$D=\ln(n)-H$$

where n is the number of attributes in the sampling area (Baker and Cai 1992). Large values of D indicate a landscape that is dominated by one or a few attribute types. At small values of D, many land use types are found in approximately equal proportions (O'Neill 1988).

Angular second moment and contrast, which are measures of texture, were determined. Angular second moment is a measure of homogeneity of the landscape. Larger values indicate more homogeneity (Baker and Cai 1992). Contrast is a measure of the contrast or amount of local variation in the landscape (Baker and Cai 1992).

Changes in landscape cover types and landscape structure between 1900 and 1990 were compared for the high population density rural and low population density rural landscapes. Mean patch size and fractal dimension were also determined for grasslands and forests within the high population density rural and low population density rural landscapes to determine if fragmentation rate differed between these vegetation cover types.

RESULTS AND DISCUSSION

Fragmentation of Low Population Density Rural and High Population Density Rural Landscapes

Landscape cover types --Area of all landscape cover types changed between 1900 and 1990 (Table 2). Decreases in cropland, native grassland, and deciduous forest were offset by increases in human impact areas, intensively managed land, brush treated land, roads, water, and bare ground on both landscapes. The general trend in landscape cover type changes was the same for both landscapes; however, amount of change individual landscape cover types underwent differed between landscapes. In contrast, native grassland and human impact areas experienced about the same amount of temporal change on both landscapes. Although the change in human impact areas was much higher on the high population density rural landscape than on the low population density rural landscape, the actual increase in area covered by human impact areas was about equal for the landscapes. The marked difference in percent change occurred because area covered by human impact areas was historically extremely small on both landscapes (Table 2). Native grassland decreased by equal proportions for both landscapes (Table 2); however, reduction in grassland since 1900 was far less than estimated declines for North American grasslands since European settlement. Estimated declines in area covered by tallgrass prairie in North America range from 82% to 99% (Sampson and Knopf 1994).

The high population density rural landscape experienced greater changes in area covered by cropland, intensively managed land, and water than the low population density rural landscape. Cropland accounted for 19% of the high population density rural landscape and less than 1% of the low population density rural landscape in 1900. Both landscapes experienced reductions in cropland from 1900 to 1990, with the high population density rural landscape experiencing the largest reduction. Reduction in cropland may be a result of continued decrease in cultivation of marginal lands (Sampson and Knopf 1994). Much of the cropland and portions of the grassland and deciduous forest on the high population density rural landscape were converted to intensively managed land. Intensively managed land, which was not present in either landscape in 1900, increased to cover 31% of the high population density rural landscape by 1990. Intensively managed land covered a mere 2% of the low population density rural landscape in 1990. From the turn of the century to 1990, water increased markedly on both landscapes with a 19 percentage unit larger increase on the high population density rural landscape than on the low population density rural landscape. The larger increase in water on the high population density rural landscape may be because the high population density rural landscape was broken up into smaller parcels of land than the low population density rural landscape by 1990. Thus, more ponds were required on the high population density rural landscape to water livestock fenced in small paddocks than on the low population density rural landscape where livestock were contained in larger expanses of land. Increased pond construction on the high population density rural landscape may also have been driven by recreational use of surface water by landowners of smaller parcels of land.

The low population density rural landscape experienced greater changes in area covered by deciduous forest and brush treatment than the high population density rural landscape from 1900 to 1990. The decrease in deciduous forest may be the result of the increase in brush treatment. Brush treatment is required on grasslands to control encroachment of woody species (Bernardo et al. 1988, Daubenmire 1968, Sauer 1950, Sauer 1975). Brush treatment is also used in the region to convert forest to grassland (Stritzke et al. 1991). Recurrent burning of either mature or regrowth forest at short intervals reduces reproduction of trees and opens up the understory to colonization by grasses and forbs (Daubenmire 1968, Sauer 1975, Engle et al. 1991, Stritzke et al 1991). Because much of the low population density rural landscape is in large ranches, extensive treatment was used in 1990 to convert forest to grassland for cattle production. No brush treated areas were indicated on the survey maps of 1900 although it is possible that some brush treatment by broadcast burning may have existed in 1900 and was not noted in the survey notes. However, it is likely that very little burning took place on the landscapes in 1900. Pyne (1982) explained that the grasslands were maintained and forests were converted to grasslands by Indian use of fire in presettlement times. However, when Europeans began to settle the land, fires were suppressed and recolonization by woody species followed (Pyne 1982). Although the landscapes in this study were Indian lands in 1900, fire may have been suppressed by cattlemen, who leased thousands of acres of Osage County before the turn of the century (Jones 1978). An 87% increase in brush treatment from 1966 to 1990 indicated that the majority of brush treatment on these landscapes occurred in recent years (Boren 1995).

The low population density rural landscape also experienced greater changes in area covered by roads and bare ground than the high population density rural landscape. The increase in roads and bare ground may be attributed to oil and gas production activities.

The changes to these two landscapes should be viewed from a longer temporal context because our study landscapes, along with virtually the entire North American landscape, have long been affected by anthropogenic activities. Changes in native vegetation caused either by primitive utilization, pioneer, or more intensive modern agro-urban occupation range from simple modification to complete destruction and replacement (Curtis 1956). Extensive use of fire by the American Indian was one of the most important agents that modified the North American landscape (Curtis 1956, Pyne 1982, Pyne 1983, Sauer 1975). The general outcome of Indian occupation was to replace forested land with grassland or savannah, or, where forest persisted, to open it up and rid it of underbrush (Pyne 1982). However, within 10 to 20 years of European settlement, the land reverted back to forest because of fire suppression (Curtis 1955, Pyne 1982). European settlement further modified the landscape through cattle grazing and cultivation (Curtis 1956).

Moreover, our 2 study landscapes had different settlement histories that influenced landscape cover type and landscape structure. The landscape where the Bartlesville BBS route is located was deeded to the Cherokee Nation in 1828 and subsequently sold to the Osage Indians in 1872 (Gittinger 1939). Large portions of this landscape were leased to ranchers for cattle production even before statehood. The landscape where the Collinsville BBS route is located was also deeded to the Cherokee Nation in 1828 but was divided into small parcels of land and sold to settlers who entered the territory via the Atlantic and Pacific and Missouri, Kansas, and Texas Rail Roads that were located on the landscape before 1900 (Gittinger 1939).

Landscape structure.--As with the landscape cover type changes, general trend of landscape structure change was the same for both landscapes. However, the amount of change for individual landscape structure measures differed between the high population density rural and low population density rural landscapes (Table 3). The only exception was dominance, which decreased on the low population density rural landscape and remained about the same on the high population density rural landscape from 1900 to 1990. Decreased dominance on the low population density rural landscape indicated a shift toward landscape cover types represented at more equal proportions.

In 1900, the landscapes were composed of large, contiguous patches with fewer human induced disturbances than in 1990. Landscapes only minimally influenced by human activity are generally composed of large patches that are few in number (Godron and Forman 1983). Patches on the high population density rural landscape were 13% smaller than patches of the low population density rural landscape in both 1900 and 1990. However, mean patch size decreased by more than 80% on both landscapes from 1900 to 1990. This indicated that fragmentation occurred equally on both landscapes. Variance in patch size was also markedly less on both landscapes in 1990 than in 1900 (Table 3). Landscapes minimally influenced by humans have large average patch size with a large variance in patch size (Pickett and Thompson 1978). Both average patch size and its variance decrease with increase in human activity (Forman and Boerner 1981). Mean patch size and its variance indicated that these two landscapes had been subjected to considerably more human activity by 1990 than in 1900.

The low population density rural landscape exhibited more complex patch perimeters than the high population density rural landscape in 1900. Fractal dimension, a measure of patch perimeter complexity, increased in both landscapes from 1900 to 1990 with the greatest increase on the high population density rural landscape (Table 3). Landscapes only minimally influenced by human activity are generally composed of irregularly shaped patches (Godron and Forman 1983). Patch perimeter complexity typically decreases with increased human activity (Curtis 1956, Forman and Godron 1986, Krummel et al. 1987, O'Neill et al. 1988). Thus, the increase in patch perimeter complexity from 1900 to 1990 contrasts with the general pattern of decreasing perimeter complexity with increasing human activities (Curtis 1956, Forman and Godron 1986, Krummel et al. 1987, O'Neill et al. 1988).

Although human impact areas increased after 1900, the increase in perimeter complexity from 1900 to 1990 may be the result of the marked decrease in cropland and increase in burning of forested areas (Table 2). Human activities related to crop production tend to simplify patch shapes (Curtis 1956, Krummel et al. 1987, O'Neill et al. 1988). So, removing large portions of cropland from production should have the reverse affect. Brush treatment of forested areas in the form of prescribed fire can also cause an increase in patch perimeter complexity (Baker 1992, Fuller 1991). Since fires differ with regard to topography, fuel type, fuel load, soil moisture, etc., disturbance patches created by burning can increase patch complexity (Biondini et al. 1989, Urban 1994). Because a large portion of the low population density rural landscape was burned in 1990 with minimal area of cropland (Table 2), the increase in patch perimeter complexity on the low population density rural landscape may have resulted primarily from fires with reduction of cropland a lesser contributor. The opposite may be true for the high population density rural landscape, where large-scale reduction of cropland has occurred since the turn of the century and only minimal burning has taken place.

Assuming all relevant landscape cover types were mapped in 1900, the landscapes at the turn of the century were more homogeneous with lower richness than the landscapes in 1990 (Table 3). Increased heterogeneity from the turn of the century to 1990 was primarily a result of increased human activity and the subsequent addition of 3 landscape cover types, intensively managed land, brush treated land, and bare ground. An unexpected outcome was that Shannon diversity, a measure of heterogeneity increased more on the low population density rural landscape than on the high population density rural landscape. Contrast and angular second moment indices also indicated that heterogeneity increased more on the low population density rural landscape than on the high population density rural landscape. This is surprising because a predominant human impact on landscape structure is an increase in contrast (Godron and Forman 1983). The smaller than expected increase in heterogeneity on the high population density rural landscape may be because much of the area covered by intensively managed land in 1990 was located on areas that were cropland in 1900. Thus, one human-influenced landscape cover type simply replaced another with very little influence on this aspect of landscape structure.

Dominance was lower on the high population density rural landscape than on the low population density rural landscape at the turn of the century (Table 3). However, dominance was about equal for both landscapes by 1990. The low population density rural landscape was historically dominated by large areas of native grassland and deciduous forest. The high population density rural landscape also historically contained a large portion of native grassland; however, the landscape cover types occurred at more equal proportions on the high population density rural landscape than on the low population density rural landscape (Table 2). From 1900 to 1990, dominance decreased on the low population density rural landscape but changed little on the high population density rural landscape. The decrease in dominance on the low population density rural landscape can be attributed to the addition of landscape cover types and the subsequent decrease of area covered by native grassland and deciduous forest. The low population density rural landscape apparently became dissected into more landscape cover types at more equal proportions by 1990. Although the number of landscape cover types also increased over time on the high population density rural landscape, the proportions of landscape cover types remained similar. Thus, dominance changed little on the high population density rural landscape from 1900 to 1990. Because dominance decreased on the low population density rural landscape but changed little on the high population density rural landscape, dominance was approximately equal for both landscapes by 1990.

Fragmentation of Grasslands and Forests

Fragmentation occurs when a large, relatively continuous tract of a vegetation type is converted to other vegetation types with only scattered fragments of the original type remaining (Faaborg et al. 1992). Mean patch size and patch perimeter complexity were examined on the grasslands and deciduous forests of both the low population density rural and high population density rural landscapes to determine if fragmentation had been selective for vegetation type. Grasslands exhibited larger patches than forests both historically (1900) and presently (1990); however, from 1900 to 1990, mean patch size of both landscape cover types decreased by about 90% (Table 4). The fact that patch size of both grasslands and forests decreased almost equally indicates that fragmentation did not occur more on one vegetation type than the other.

Grassland patch perimeters were historically more complex than deciduous forest patch perimeters (Table 4). From 1900 to 1990, grassland patch perimeter complexity decreased slightly while forest patch perimeter complexity increased slightly on both landscapes (Table 4). By 1990, there was very little difference in the perimeter complexity of these two landscape cover types.

The slight decrease in grassland patch perimeter complexity from 1900 to 1990 may be the result of an increase in human activity and the consequent addition of intensively managed land to the landscapes. Predominant human impacts on landscape structure are abundant increases in straight lines and rectangles (Godron and Forman 1983). Thus, increased human activity tends to decrease patch perimeter complexity (1956, Forman and Godron 1986, Krummel et al. 1987, O'Neill et al. 1988). Increased human influence on the low population density rural and high population density rural landscapes tended to break up the formerly vast, irregular grassland patches into smaller, more intensively managed paddocks of regular shape.

The slight increase in forest patch perimeter complexity from 1900 to 1990 may be attributed to the increase in brush treatment since the turn of the century. Prescribed burning on forested land, which was used as a method to convert forest to grassland, may increase patch complexity and landscape heterogeneity (Baker 1992, Fuller 1991, Urban 1994). The opposite is true on grasslands where fire on ungrazed sites can promote low diversity in vegetation at low spatial scales (Collins 1987, Collins and Barber 1985).

CONCLUSIONS

Compared to the landscapes of 1990, the landscapes of 1900 were composed of larger, more contiguous patches with fewer human induced disturbances. Although the landscapes had already been influenced by human activity by 1900, the land had less than 80 years of significant occupation by humans and had relatively little area subject to intensive human control. In general, area in natural vegetation decreased from the turn of the century to 1990, while area in human induced landscape cover types increased. The major impact of an additional 90 years of post-European settlement human activity has been on landscape pattern and fragmentation rather than on the area of either native grassland or deciduous forest. Native grasslands, especially the tallgrass prairies, have been greatly reduced in North America since European settlement. However, reduction of area covered by native grassland in our study area was far less than the estimated declines for North American grasslands since European settlement. In contrast, landscape structure measures indicated that the landscapes of 1990 had become dissected into smaller patches with more landscape cover types, increased diversity, and decreased dominance, resulting in landscapes of 1990 that were more heterogeneous with more local variation than the landscapes of 1900.

Our results indicate that both high population density rural and low population density rural landscapes in this area are susceptible to fragmentation. Temporal analysis revealed that the general trend in change in landscape cover type was the same for both high population density rural and low population density rural landscapes; however, the amount of change individual landscape cover types and landscape structure measures underwent differed between landscapes. Although the high population density rural and low population density rural landscapes exhibited different proportions of change for individual landscape cover types, overall amount of fragmentation was equal for both landscapes from 1900 to 1990.

Similarly, native grassland and deciduous forest were equally fragmented between 1900 and 1990. From the turn of the century to 1990, mean patch size decreased approximately 90% for both landscape cover types, indicating that fragmentation did not occur more for one vegetation type.

Documentation of temporal changes in landscape cover types and landscape structure provided by this study will aid ecologist in understanding the past to help manage the future of these landscapes. In this area, no one landscape type or vegetation type is more susceptible to landscape change than the other. Thus, conservation efforts should not be preferential for landscape type or cover type. Landscape structure and cover types have changed dramatically since 1900. If these changes continue, the altered landscape will bear little resemblance to the post-settlement condition of 1900.

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Table 1. Landscape cover type descriptions used for aerial photography interpretation, adapted from Stoms et al (1983).

Landscape Cover Type	**Description**
Human impact areas	Land occupied by residential, industrial, or other human structures and non-agricultural activities. Also includes transportation and utility facilities.
Cropland	Land cultivated for row crops and cereal grains, but excluding grazing lands.
Intensively managed land	Pasture lands (seeded grasslands used for grazing by cattle, sheep, goats, horses, etc.), hay meadows, and orchards.
Native grassland	Natural grasslands with less than 10% canopy cover of shrubs or trees.
Deciduous forest	Land dominated (>10% canopy cover) of broadleaf hardwoods, mostly post oak (*Quercus stellata*) and black-jack oak (*Q. marilandica*).
Brush treated land	Land that has been subjected to brush control by herbicides, chaining, and/or fire.
Roads	Driveways, black top, gravel, and dirt roads.
Water	Lakes, rivers, streams, and ponds.
Bare ground	Land with less than 5% vegetative cover.

Table 2. Landscape cover types (ha) and percent change from 1900 to 1990 on two, 40.2 km transects in a hardwood forest-tallgrass prairie ecotone.

	Low density rural		High density rural		Change (%)	
Cover type	**1900**	**1990**	**1900**	**1990**	**Low density rural**	**High density rural**
Human impact areas	2	22	1	24	+1000	+2300
Cropland	23	13	630	120	-43	-81
Intensively managed land	0	49	0	999		
Native grassland	1580	1117	2108	1508	-29	-29
Deciduous forest	1433	877	428	377	-39	-12
Brush treated land	0	878	0	5		
Roads	35	118	29	87	+237	+200
Water	24	38	40	71	+58	+77
Bare ground	0	8	0	2		

Table 3. Measures of landscape pattern and percent change from 1900 to 1990 on two, 40.2 km transects in a hardwood forest-tallgrass prairie ecotone[1].

	Low density rural		**High density rural**		**Change (%)**	
Index	**1900**	**1990**	**1900**	**1990**	**Low density rural**	**High density rural**
Mean patch size (pixels)	7744	1368	6668	1184	-82	-82
Patch size standard deviation	27149	6637	25627	4099	-76	-84
Fractal dimension	1.18	1.30	1.04	1.28	+10	+23
Richness	6.00	8.50	6.00	8.50	+42	+42
Shannon diversity	0.79	1.31	0.95	1.28	+66	+35
Contrast	0.13	0.42	0.18	0.50	+223	+178
Angular second moment	0.48	0.29	0.46	0.32	-40	-30
Dominance	1.00	0.83	0.84	0.86	-17	+2

[1]Data represent means of two halves of a transect.

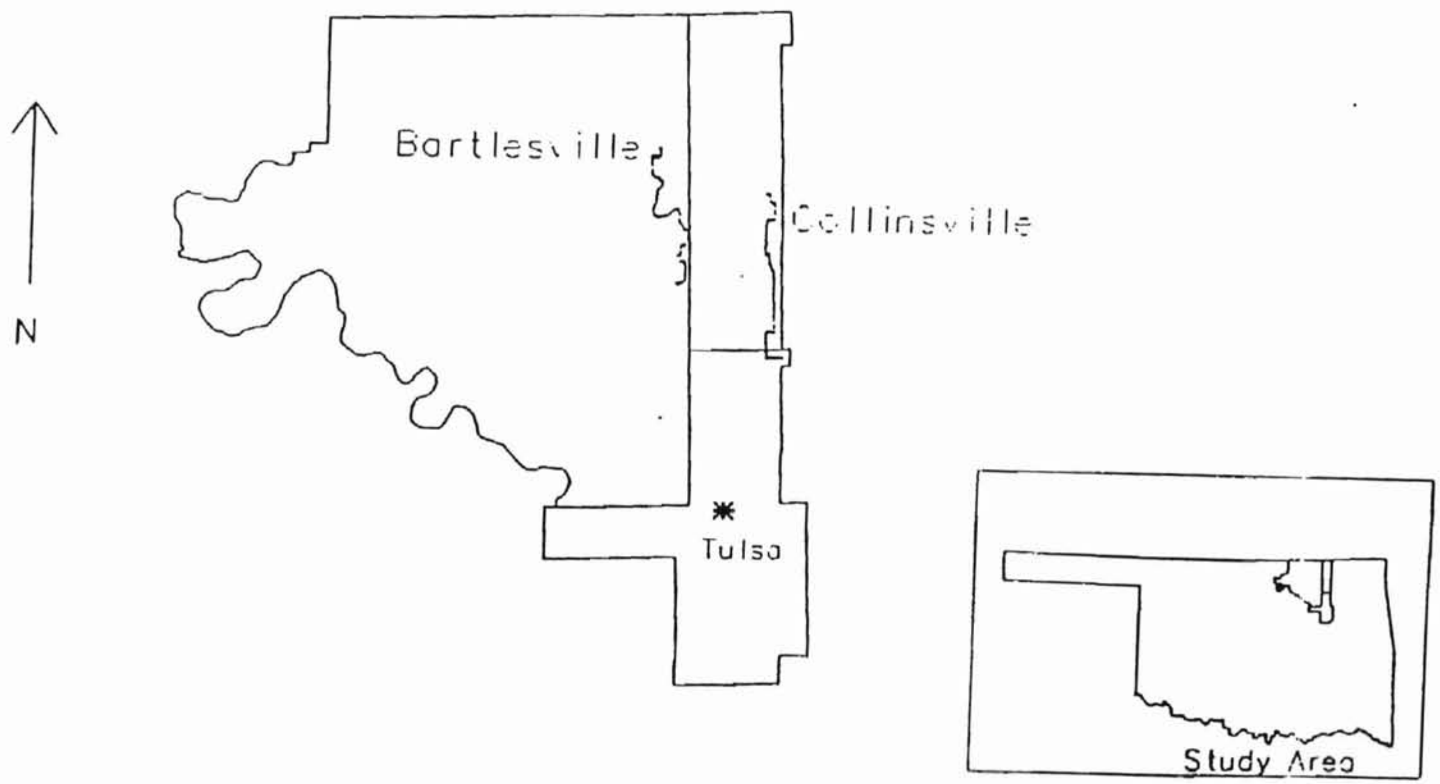
Table 4. Measure of landscape pattern and change for grasslands and deciduous forest from 1900 to 1990 on two, 40.2 km transects in a hardwood forest-tallgrass prairie ecotone.

Index	Year		Change (%)
	1900	1990	
Low density rural			
Grassland			
Mean patch size (pixels)	50684	7422	-85
Fractal dimension	1.72[1]	1.41	-18
Deciduous forest			
Mean patch size (pixels)	22610	2187	-90
Fractal dimension	1.17	1.31	+12
High density rural			
Grassland			
Mean patch size (pixels)	76534	6102	-92
Fractal dimension	1.35	1.25	-7
Deciduous forest			
Mean patch size (pixels)	9269	802	-91
Fractal dimension	1.25	1.35	+8

[1] Data represent means of two halves of a transect.

Figure 1. U. S. Fish and Wildlife Service Breeding Bird Survey route numbers 024 and 026.

Breeding Bird Survey Routes



CHAPTER III

EFFECTS OF LANDSCAPE CHANGES ON BIRD REPRESENTATION IN A HARDWOOD FOREST-TALLGRASS PRAIRIE ECOTONE

Abstract: Overwhelming evidence indicates that grassland and shrubland birds of North America are in jeopardy. The reasons for population declines among grassland and shrubland birds are not fully understood and presettlement information on native bird assemblages of the Great Plains is limited, providing little basis for constructing landscape-bird community relationships. In this study, logistic regression was used with breeding bird survey (BBS) data and landscape measures to determine the probability of occurrence of bird species in years 1900 and 1990 on both a low population density rural and a high population density rural landscape on a hardwood forest-tallgrass prairie ecotone in central North America. The avian community changed on both landscapes since 1900 because of changes in landscape cover types. Our models indicate that forest and edge species decreased on both landscapes from 1900 to 1990 because deciduous forest decreased on both landscapes. Prairie birds increased on the low population density rural landscape during the same time period. The increase in prairie species can be attributed to the use of fire and herbicides on the landscape to both covert forest to grassland and to maintain grassland for forage production for cattle grazing. Bird species associated with human development increased on the high population density rural landscape from 1900 to 1990 as natural vegetation was converted to roads, human impact areas, bare ground, and other human-influenced cover types. This study suggests that avian assemblages diverged markedly on the low population density rural and high population density rural landscapes as a result of contrasting management practices and land uses.

INTRODUCTION

With the increase in the human population in the United States, wildlands have been and continue to be altered and fragmented (Curtis 1956). Through urbanization, agriculture, and forestry, part of the natural vegetation is removed and replaced with managed systems of altered structure (Krummel et al. 1987). The size-shape relationships of the altered land cover can influence important ecological and environmental phenomena (Burgess and Sharp 1981), including bird community structure and habitat selection. Rotenberry and Wiens (1980) demonstrated strong patterns of association between bird community structure and the physical configuration of the environment. These results coincide with the widely held belief that bird habitat selection is influenced more by vegetation structure and habitat configuration than by floral composition (Cody 1985, Wiens 1989). As wildlands continue to be fragmented, this association between physical configuration of the environment and bird habitat selection may play an increasingly important role in the abundance and diversity of birds.

Overwhelming evidence indicates that grassland and shrubland birds characteristic of our study area are in jeopardy. According to North American Breeding Bird Survey (BBS) data, many species of grassland birds declined significantly in eastern and midwestern North America between 1966 and 1979 (Robbins et al. 1986). This trend has continued after 1979 in both northeastern and midwestern states (Bollinger and Gavin 1992). BBS data from eastern North America between 1966 and 1991 show that 16 bird species characteristic of open grassland or savanna and 12 bird species characteristic of shrubland had declining population trends while only 3 grassland/savanna bird species and 4 shrubland species had increasing trends (Askins 1993).

The reasons for population declines among grassland and shrubland birds are not fully understood (Knopf 1994). Moreover, presettlement information on native bird assemblages of the Great Plains is limited (Knopf 1994), providing little basis for constructing landscape-bird community relationships. Historical information about bird communities could help put the present status of birds in better perspective by providing a point of reference on which to compare present conditions.

In this study, logistic regression was used with BBS data and landscape measures to determine the probability of occurrence of bird species in years 1900 and 1990 in a hardwood forest-tallgrass prairie ecotone in central North America. The objective of this study was to model the presence of bird species on landscapes in 1900 and 1990 to determine if differences in landscape changes are reflected in bird representation. This study provides insight into the present status of bird species in a hardwood forest-tallgrass prairie ecotone by providing an historical point of reference on which to compare the presence of birds.

METHODS

Study Area

The study area centers around U. S. Fish and Wildlife Service Breeding Bird Survey route numbers 024 and 026 located in northeastern Oklahoma near the cities of Collinsville and Bartlesville, respectively (Figure 1). Legal description of these survey routes are provided by Baumgartner and Baumgartner (1992). The area includes the BBS routes and a 400 m area on each side of a route as the boundary. Selection of the study area was based on proximity to a metropolitan area and availability of historical aerial photography.

The survey routes lie on an ecotonal area between the grassland formation of the Cherokee Prairies and oak-hickory savannah of the Cross Timbers. The Cherokee Prairie of Oklahoma extends as a long, narrow strip, 240 km southward from the Kansas state line with a width ranging from 48 km to 97 km during the majority of its length (Bruner 1931, Soil Conservation Service 1981). This area lies west of the Ozarks, extending far across the Arkansas river valley (Bruner 1931). The Cherokee Prairies region is underlain by fine textured soils developed from weathering of Pennsylvanian limestones and shales (Bruner 1931, Harlan 1957, Gray and Galloway 1959). The underlying geology in conjunction with the climate of the area are better adapted to producing grasses than forests (Bruner 1931, Harlan 1957). Tallgrass prairie is the predominate vegetation of the region. The Cross Timbers of Oklahoma lie west of the Cherokee Prairie and the Lower Arkansas Valley, extending 290 km southward from Kansas, approximately 80 km wide (Bruner 1931, Soil Conservation Service 1981). The region is underlain by alternating beds of Pennsylvanian sandstone and shales (Bruner 1931, Harlan 1957, Gray and Galloway 1959). The Cross Timbers region is covered with scrubby, transitional, oak forest with abundant grassy areas (Bruner 1931).

Study landscapes are both in proximity to Tulsa county, which is the major metropolitan area of northeastern Oklahoma. The estimated population of Tulsa County is 503,341 (Bureau of the Census 1990). Route 024 is in Washington County and route 026 is in Osage County. The human population density of Washington County in 1990 was 3340 km^{-2} and the population density of Osage County was 520 km^{-2}. We considered the Collinsville landscape to be subjected to more urban influence than the Bartlesville landscape. Thus, the Collinsville landscape will be referred to as the high population density rural landscape and the Bartlesville landscape will be referred to as the low population density rural landscape.

Data Collection

North American Breeding Bird Survey (BBS) field sheets for years 1966 through 1991 of routes 024 and 026 were ordered from the U. S. Fish and Wildlife Service Office of Migratory Bird Management, Laurel, Maryland. Each route is conducted on secondary roads and consists of 50 counting stops 800 m apart (Bystrak 1981). The survey is conducted each year in late May or June by an observer who records all birds seen or heard in a 3 minute time period within 400 m of a stop. Attempts are made to have the same observer run a route for a series of years to maintain the continuity of the data

(Sauer and Droege 1989). A detailed description of the methods and the scheme used to determine where to locate the routes can be found in Robbins and Van Velzen (1967).

Black and white aerial photographs for 1990 were obtained from the U. S. Department of Agriculture, ASCS, Aerial Photography Field Office, Salt Lake City, Utah. Photographs were 24" X 24" enlargements with a representative fraction of 1:7,920, and covered each BBS route (40.2 km in length) with an area at least 400 m wide on each side of the route as the boundary. The resulting area for each route was approximately 3150 ha.

Topographic quadrangle maps, photo inspected in 1976, showing the natural and man-made features of the land at 1 to 24,000 scale were obtained from the Oklahoma Geological Survey, Norman, Oklahoma. The quadrangles indicate both geographical coordinates and elevation as well as specific features such as vegetation, water, roads, towns, political boundaries, etc.

General Land Office (GLO) field notes of the area surrounding each route were obtained from the Oklahoma Department of Libraries, Oklahoma City, Oklahoma. These historical data are composed of the field notes taken by U. S. Surveyors as well as maps derived by the surveyors from their field notes. Surveys were run in 1908 and 1896 for the Bartlesville and Collinsville landscapes, respectively. For ease of discussion, the survey year will be referred to as 1900. The field notes constitute a definite sample of the vegetation and are usable for quantitative as well as qualitative analysis (Bourdo 1956).

Database Construction

In order to transform the aerial photography into a usable form, clear acetate was placed on each photograph, supervised photo interpretation was conducted, and all interpreted polygons of interest were marked. The following features were identified: BBS route boundaries, all roads, buildings and houses, land use, and vegetation cover types. Landscape cover types were interpreted based on an adaptation from Stoms et al. (1983) (Table 1).

The marked acetate sheets were digitized using a digital scanner. Scanned images were edited, rectified, and vectorized using LTPlus (United States Forest Service and Soil Conservation Service 1991) and imported into the GIS GRASS (Geographic Resource Analysis Support System) (Shapiro et al. 1992). Vector images were then patched together to form complete routes, labeled, and converted to raster images with 5m resolution. Accuracy checks of photo interpretation were verified in the field from hardcopy output of the labeled images for each route.

The GLO maps were copied from microfiche to paper with a representative fraction of 1:17,182. The present day BBS routes were located on the GLO maps by tracing portions of the route that ran along section lines. Portions of the route that did not run along section lines were located by determining numerous registration points along the route on the topographic quadrangles and then locating the same points on the GLO maps. After the route boundaries were drawn on the GLO maps, the maps were overlaid with acetate, marked, scanned, edited, rectified, vectorized, rasterized, and labeled with the same methods used on the aerial photographs. The GLO field notes that correspond to the maps were transcribed from a copy of the surveyor's original handwriting. The field notes supplemented the maps in assigning landscape cover types to the polygons.

Landscape structure and area of each landscape cover type were determined for an area 400 m radius around each BBS stop by using the GIS GRASS. Landscape structure and area of each landscape cover type were determined from the 1900 GLO data and from the 1990 aerial photography. Landscape structure and area of each landscape cover type of 1966, 1973, 1980, and 1990 aerial photography were also documented for both landscapes by Boren (1995). Further discussion of the landscape structure measures generated is provided in Criner (1996). Landscape cover type data and landscape structure data determined by the GIS were saved in separate files for each route in full format setup.

The yearly BBS data were entered into a database and species abundances were lumped around 4 time periods that correspond to the years of the aerial photography. Hence, relative species abundances of years 1966 through 1970 were referred to as year 1966, relative abundances of years 1971 through 1976 were referred to as 1973, relative abundances of years 1977 through 1984 were referred to as year 1980, and relative abundances of years 1985 through 1991 were referred to as year 1990 (Boren 1995). Several years of BBS data were lumped together to represent 1 year to improve the accuracy of the data by reducing the influence of adverse weather conditions or the influence of an observer experiencing other problems discussed by Bystrak (1981).

Data Analysis

Detrended correspondence analysis (DCA) was performed on the BBS data with CANOCO (ter Braak 1988) to determine if avian community structure differed between landscapes, to document shifts in avian community structure over time (1966 to 1990), and to determine which bird species were responsible for shifts in avian community structure over time (Table 2) (Boren 1995). DCA is an indirect gradient analysis in which samples (species abundances) are arranged according to species composition and important environmental gradients are indirectly inferred from the trends in species composition (ter Braak and Prentice 1988).

Canonical correspondence analysis (CCA) was performed with CANOCO (ter Braak 1988) to determine the influence of landscape cover types and landscape structure on breeding bird abundances of each landscape. CCA is a direct gradient analysis in which species are directly related to measured environmental variables (ter Braak and Prentice 1988). Abundances of bird species were related to landscape cover types and landscape structure in separate CCA ordinations for the high population density rural and low population density rural landscapes. Separate CCA ordinations were determined for the high population density rural and low population density rural landscapes because DCA indicated that the avian community structure differed between landscapes and the avian communities diverged over time for the 2 landscapes (Boren 1995). Relative contributions of environmental variables to the axes were evaluated by examining canonical coefficients and intraset correlations produced by CCA. Forward selection and Monte Carlo permutation tests ($P<0.05$) were used to determine the environmental variables that best explained the largest amount of variation in breeding bird abundances. Moreover, unrestricted Monte Carlo permutation tests were used to test the significance ($P<0.05$) of the first two ordination axes. CCA concluded that area of landscape cover types influenced bird abundances, but landscape structure had little influence on the avian community (Boren 1995).

The bird species determined by DCA to be responsible for shifts in the avian community over time were related to the area of landscape cover types by logistic regression by using the LOGISTIC procedure in SAS (Harrell 1980). Logistic regression models of the form

$$\log_e[(p/1-p)]=b_0+b_1x_1+...b_nx_n$$

where x_n is a predictor variable and b_0 and b_n are parameters or regression coefficients Y(ter Braak and Looman 1987), provide a means to predict species distributions in relation to environmental variables (Heliovaara et al. 1991). Presence and absence of the bird species were used as the response variables and area of each landscape cover type as the predictive variables. Landscape structure measures were not used as predictive variables because CCA indicated that landscape structure had little influence on avian community structure. Equations relating predictor variables, area of each landscape cover type, to bird presence were tested ($p<0.05$) as linear, quadratic, cubic, and quartic.

Based upon the area of each landscape cover type, we used the logistic regressions to calculate the probability of occurrence of each bird species for an area 0.25 mile (400 m) radius around each BBS stop (Eyre et al. 1992, Osborne and Tiger 1992). Area of landscape cover types of 1900 and 1990 were input into the models to determine the probability of occurrence for each species on the area 0.25 mile (400 m) radius around each BBS stop location. The probability of occurrence of each bird species in 1900 and 1990 was determined by averaging the probability of occurrence of the 50 BBS stop locations for each landscape.

RESULTS

Deciduous forest was the predominant independant variable in logistic regression models of the occurrence of both decreasing and increasing species on the low population density rural landscape (Table 3) and of decreasing species on the high population density rural landscape (Table 4). Roads, cropland, and deciduous forest were the landscape cover types that most frequently occurred as independent variables for the species that increased on the high population density rural landscape and human impact areas, bare ground, intensively managed land, and grassland were less frequent variables for the high population density rural landscape (Table 4). Cropland, roads, and bare ground were less frequent variables responsible for the occurrence of species that decreased on the high population density rural landscape (Table 4). Human impact areas was a less frequent variable responsible for the occurrence of species that increased while human impact areas, water, and cropland were less frequent variables responsible for the occurrence of species that decreased on the low population density rural landscape (Table 3).

Changes that occurred on the landscapes from 1900 to 1990 were reflected in changes in bird representation on the landscapes. Our logistic regression models indicate that forest and edge species decreased on both low population density rural and high population density rural landscapes from 1900 to 1990 (Table 3, Table 4). Prairie species on the low population density rural landscape and species associated with development on the high population density rural landscape increased during the same time period (Table 3, Table 4). The forest and edge species that declined on the low population density rural landscape were species of high concern and no single migration type was prevalent among the species (Table 3). The forest and edge species that declined on the high population density rural landscape were species of moderate or high concern and were generally neotropical migrants (Table 4). The prairie species that increased on the low population density rural landscape were neotropical migrants of high concern that both foraged and nested on the ground (Table 3). However, the increasing species associated with developed habitats on the high population density rural landscape were generally resident species of low concern and no single foraging or nesting guild was prevalent among these species (Table 4).

DISCUSSION

The model indicated a decrease in forest and edge avian species on both landscapes from 1900 to 1990 (Table 3, Table 4). Because deciduous forest was the predominant independent variable in logistic regression models of the occurrence of avian species that decreased on both landscapes (Table 3, Table 4), the decrease in forest and edge species is likely in response to the decrease in deciduous forest that occurred on both landscapes from 1900 to 1990. From 1900 to 1990, deciduous forest decreased by 39 and 12% on the low population density rural and high population density rural landscapes, respectively (Criner 1996).

Of the species that decreased on both landscapes, all had population trends of moderate to high concern. The bird species that decreased on the low population density rural landscape were of no particular migration type. However, on the high population density rural landscape, the majority of the species that decreased were neotropical migrants. The fact that no migration type was prevalent for species that declined on the low population density rural landscape suggests that declines were caused by conditions on the study landscape rather than on wintering habitats. In years past, forest species that declined were predominately neotropical migrants and declines were attributed to destruction of wintering habitat (Briggs and Criswell 1978, Morton 1980). However, recent concerns in declines of forest species, including neotropical migrants, have focused on breeding habitat in North America as well as wintering habitat (Askins 1993, Butcher et al. 1981, Knopf 1994, Maurer and Heywood 1993, Terborgh 1989a, Terborgh 1989b). The model results suggest that neotropical migrants have decreased on the high population density rural landscape as a result of habitat loss on the landscape. This supports the recent notion that neotropical migrants are not only being affected by losses of wintering habitat but also by changes in temperate breeding habitat (Askins 1993, Butcher et al. 1981, Maurer and Heywood 1993, Terborgh 1989a, Terborgh 1989b).

While forest and edge species decreased on the low population density rural landscape, prairie species increased (Table 3). As with forest and edge species, deciduous forest was the predominant independent variable in logistic regression models of the occurrence of the species that increased on the low population density rural landscape (Table 3). Deciduous forest decreased 39% from 1900 to 1990 on the low population density rural landscape (Criner 1996), perhaps as a result of an increase in brush treatment. Brush treatment, the use of fire and herbicides, is required on grasslands in this region to control encroachment of woody species (Bernardo et al. 1988, Daubenmire 1968, Sauer 1950, Sauer 1975). Brush treatment is also used to convert forest to grassland (Engle et al. 1991, Stritzke et al. 1991). Recurrent light burning of forest at short intervals reduces reproduction of trees and opens up the understory to colonization by grasses and forbs (Daubenmire 1968, Sauer 1975). Because much of the low population density rural landscape is in large ranches, extensive treatment had been applied by 1990 to convert forest to grassland or to maintain grassland for cattle production. An 87% increase in brush treatment from 1966 to 1990 indicated that the majority of brush treatment on the landscape occurred in recent years (Boren 1995)

The decrease in deciduous forest and subsequent increase in brush treated land made the low population density rural landscape more suitable for prairie birds. For example, the barn swallow and dickcissel, both prairie species and neotropical migrants of high concern that forage and nest on the ground, increased on the low population density rural landscape from 1900 to 1990. The increase of these species on the low population density rural landscape suggests that while the species have declined in other areas of North America, habitat alterations on the low population density rural landscape in this study have favored prairie species since 1900.

The model indicated that bird species associated with human activities, including American robin, European starling, and purple martin, increased on the high population density rural landscape from 1900 to 1990 (Table 4). The increase in development-associated species was associated primarily with changes in area of roads, cropland, and deciduous forest although changes in area of human impact areas, bare ground, intensively managed land, and grassland contributed to a lesser extent to increases in development-associated species (Table 4). Roads, cropland, and intensively managed land were the 3 landscape cover types that exhibited the largest change in area from 1900 to 1990 on the high population density rural landscape (Criner 1996). Roads increased by 200% and cropland decreased by 81% on the landscape (Criner 1996). Much of the cropland was converted to intensively managed land, which was not present on the landscape in 1900, but increased to 31% of the high population density rural landscape by 1990 (Criner 1996). The increase in human activities on the high population density rural landscape was reflected in increases in roads, human impact areas, and bare ground; decreases in deciduous forest and native grassland; and conversion of cropland to intensively managed land. The increase in human activities provided preferred habitat for species associated with development.

The changes to these two landscapes should be viewed from a longer temporal context because our study landscapes, along with virtually the entire North American landscape, have long been affected by anthropogenic activities. Changes in native vegetation caused either by primitive utilization, pioneer, or more intensive modern agro-urban occupation range from simple modification to complete destruction and replacement (Curtis 1956). Extensive use of fire by the American Indian was one of the most important agents that modified the North American landscape (Curtis 1956, Pyne 1982, Pyne 1983, Sauer 1975). The general outcome of Indian occupation was to replace forested land with grassland or savannah, or, where forest persisted, to open it up and rid it of underbrush (Pyne 1982). However, within 10 to 20 years of European settlement, the land reverted back to forest because of fire suppression (Curtis 1955, Pyne 1982). European settlement further modified the landscape through cattle grazing and cultivation (Curtis 1956).

Moreover, our 2 study landscapes had different settlement histories that influenced landscape cover type and landscape structure. The landscape where the Bartlesville BBS route is located was deeded to the Cherokee Nation in 1828 and subsequently sold to the Osage Indians in 1872 (Gittinger 1939). Large portions of this landscape were leased to ranchers for cattle production even before statehood. The landscape where the Collinsville BBS route is located was also deeded to the Cherokee Nation in 1828 but was divided into small parcels of land and sold to settlers who entered the territory via the Atlantic and Pacific and Missouri, Kansas, and Texas Rail Roads that were located on the landscape before 1900 (Gittinger 1939).

CONCLUSIONS

The changes in the avian community on both the low population density rural and high population density rural landscapes since 1900 are associated with changes in landscape cover types. Logistic regression models indicate that forest and edge species decreased from 1900 to 1990 because deciduous forest decreased on both landscapes (Criner 1996). Prairie birds increased on the low population density rural landscape during the same time period. The increase in prairie species on the low population density rural landscape can be attributed to the use of fire and herbicides on the landscape to convert forest to grassland and to maintain grassland for forage production for cattle grazing. Bird species associated with human development increased on the high population density rural landscape from 1900 to 1990 as natural vegetation was converted to roads, human impact areas, bare ground, and other human-influenced cover types.

This study suggests that avian assemblages diverged markedly on these two landscapes as a result of contrasting management practices and land uses. Alterations resulting from brush treatment on the low population density rural landscape favored prairie species, which is important in view of the decline in grassland birds in North America in the last quarter century (Askins 1993, Bollinger and Garvin 1992, Knopf 1994, Robbins et al. 1986). However, the increase in prairie species came at the price of a decrease in forest and edge species, which have also undergone severe population declines (Askins 1993, Briggs and Criswell 1978, Terborgh 1989, Whitcomb et al. 1981). Furthermore, forest and edge species on the high population density rural landscape have experienced the most alarming change by their replacement by species associated with loss of habitat by human development. Indeed, the most striking changes in landscapes of developed countries are occurring at the rural-urban fringe (Sullivan 1994), which makes management use of private lands the dominant force shaping North American ecosystems.

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Table 1. Landscape cover type descriptions used for aerial photography interpretation, adapted from Stoms et al (1983).

Landscape Cover Type	**Description**
Human impact areas	Land occupied by residential, industrial, or other human structures and non-agricultural activities. Also includes transportation and utility facilities.
Cropland	Land cultivated for row crops and cereal grains, but excluding grazing lands.
Intensively managed land	Pasture lands (seeded grasslands used for grazing by cattle, sheep, goats, horses, etc.), hay meadows, and orchards.
Native grassland	Natural grasslands with less than 10% canopy cover of shrubs or trees.
Deciduous forest	Land dominated (>10% canopy cover) of broadleaf hardwoods, mostly post oak (*Quercus stellata*) and black-jack oak (*Q. marilandica*).
Brush treated land	Land that has been subjected to brush control by herbicides, chaining, and/or fire.
Roads	Driveways, black top, gravel, and dirt roads.
Water	Lakes, rivers, streams, and ponds.
Bare ground	Land with less than 5% vegetative cover.

Table 2. Avian species responsible for shifts in avian community structure in a low population density rural and high population density rural landscape over a 24 year period (1966 to 1990) as determined by detrended correspondence analysis (Boren 1995). Species that occurred 3 or less times were omitted.

Species	Scientific name	Migration type*	Habitat**	Concern***	Foraging^	Nesting^^
Low density rural						
Loss						
Bewick's wren	Thryomanes bewickii	Temp	Edge	High	Ground	Cavity
Black and white warbler	Mniotilta varia	Neotrop	Forest	Moderate	Midstory	Ground
Blue-gray gnatcatcher	Polioptila caerulea	Neotrop	Edge	Moderate	Canopy	Midstory
Eastern tufted titmouse	Parus bicolor	Resident	Forest	High	Midstory	Cavity
Field sparrow	Spizella pusilla	Temp	Edge	High	Ground	Ground
Greater roadrunner	Geococcyx californianu	Resident	Prairie	High	Ground	Shrub
Painted bunting	Passerina ciris	Neotrop	Edge	High	Ground	Shrub
Pileated woodpecker	Dryocopus pileatus	Resident	Forest	Moderate	Bole	Cavity
Summer tanager	Piranga rubra	Neotrop	Forest	High	Midstory	Midstory
White-breasted nuthatch	Sitta carolinensis	Resident	Edge	Moderate	Bole	Cavity
Yellow-breasted chat	Icteria virens	Neotrop	Edge	High	Ground	Shrub
Gain						
Barn swallow	Hirundo rustica	Neotrop	Develop	Moderate	Aerial	Other
Dickcissel	Spiza americana	Neotrop	Prairie	High	Ground	Ground
Grasshopper sparrow	Ammodramus savannarum	Neotrop	Prairie	High	Ground	Ground
Great-tailed grackle	Quiscalus mexicanus	Resident	Edge	Moderate	Ground	Shrub
Little blue heron	Egretta caerulea	Temp	Water	Moderate	Water	Shrub
Rock dove	Columba livia	Resident	Develop	Low	Ground	Other
Wild turkey	Meleagris gallopavo	Resident	Edge	High	Ground	Ground
High density rural						
Loss						
Black-billed cucko	Coccyzus erythropthaim	Neotrop	Edge	High	Midstory	Shrub
Cattle egret	Bubulcus ibis	Resident	Prairie	Low	Ground	Shrub
Chipping sparrow	Spizella passerina	Neotrop	Forest	Moderate	Ground	Shrub
Common yellowthroat	Geothlypis trichas	Neotrop	Edge	Moderate	Ground	Shrub
Great-horned Owl	Bubo virginianus	Resident	Edge	Moderate	Ground	Cavity
Greater prairie chicken	Tympanuchus capido	Resident	Prairie	High	Ground	Ground
Kentucky warbler	Oporornis formosus	Neotrop	Forest	High	Ground	Ground
Northern-parula warbler	Parula americana	Neotrop	Forest	High	Midstory	Canopy
Red-shouldered hawk	Buteo lineatus	Temp	Edge	Moderate	Ground	Canopy
Yellow-bellied sapsucker	Sphyrapicus sp.	Temp	Edge	High	Bole	Cavity
Yellow-breasted chat	Icteria virens	Neotrop	Edge	High	Ground	Shrub
Gain						
American robin	Turdus migratorius	Temp	Develop	Low	Ground	Shrub
Common grackle	Quiscalus quiscula	Resident	Edge	Low	Ground	Midstory
European starling	Sturnus vulgaris	Resident	Develop	Low	Ground	Cavity
Gray catbird	Dumetella carolinensis	Neotrop	Edge	High	Ground	Shrub
Great-tailed grackle	Quiscalus mexicanus	Resident	Edge	Moderate	Ground	Shrub
House sparrow	Passer domesticus	Resident	Develop	Low	Ground	Cavity
Purple martin	Progne subis	Neotrop	Develop	Moderate	Aerial	Cavity
Rock dove	Columba livia	Resident	Develop	Low	Ground	Other
Wild turkey	Meleagris gallopavo	Resident	Edge	High	Ground	Ground

*Species classified as neotropical migrants (Neotrop), temperate migrants (Temp), and residents (Resident).

**Species grouped into designation of habitat occurrence: forest (Forest), forest edge and shrubland (Edge), prairie (Prairie), and developed (Develop).

***Species grouped into population trends: low concern (Low), moderate concern (Moderate), and high concern (High).

^Species grouped into foraging zones: open zones (Aerial), foliage 0-3m (Ground), foliage 3-10m (Midstory), and trunks and limbs (Bole).

^^Species grouped into nesting zones: ground (Ground), 0-3m (Shrub), 3-10m (Midstory), >10m (Canopy), cavity (Cavity), and variable heights and substrates (Other).

Table 3. Logistic regression models and probability of occurrence of selected birds in the avian community of the low population density rural landscape modeled by logistic regression for years 1900 and 1990.

	Logistic regression models							
		Parameter coefficients[a]					Probability of occurrence	
Species	Intercept	X_1	X_2	X_3	X_4	c[b]	1900	1990
Barn swallow[c]	-0.5964	0.0597(*df*)	-0.0544(*hia*)^4			0.695	0.39	0.48
Bewick's wren	1.5540	-0.0710(*df*)	-0.0322(*btl*)	0.5087(*water*)^2		0.750	0.42	0.39
Blue-gray gnatcher	3.6225	-0.00495(*df*)^2	1.629E-6(*df*)^4			0.840	0.18	0.14
Dickcissel	-1.9541	0.1146(*df*)				0.845	0.48	0.60
Eastern tufted titmouse	1.1322	-0.1132(*df*)				0.834	0.63	0.54
Field sparrow	-2.4018	1.0428(*hia*)	0.2866(*crop*)	-0.0770(*df*)	2.1470(*water*)	0.840	0.89	0.75
Grasshopper sparrow	0.8318	1.8728(*hia*)	0.0828(*df*)			0.795	0.37	0.35
Painted bunting	1.1226	-0.0471(*df*)				0.680	0.46	0.39
Pileated woodpecker	3.2282	-0.1492(*water*)^4				0.588	0.10	0.05
Summer tanger	2.5757	-0.00159(*df*)^2				0.758	0.27	0.14
White-breasted nuthatch	3.9605	2.0870(*hia*)	-0.0620(*df*)	0.2639(*hia*)^3		0.804	0.11	0.12
Yellow-breasted chat	3.9086	-0.0657(*df*)				0.746	0.12	0.06

[a]*btl* is area of brush treated land.
crop is area of cropland.
df is area of deciduous forest.
hia is human impact area.
water is area of water.
[b]*c* is rank correlation between observed responses and predicted responses.
[c]Refer to Table 2 for scientific name.

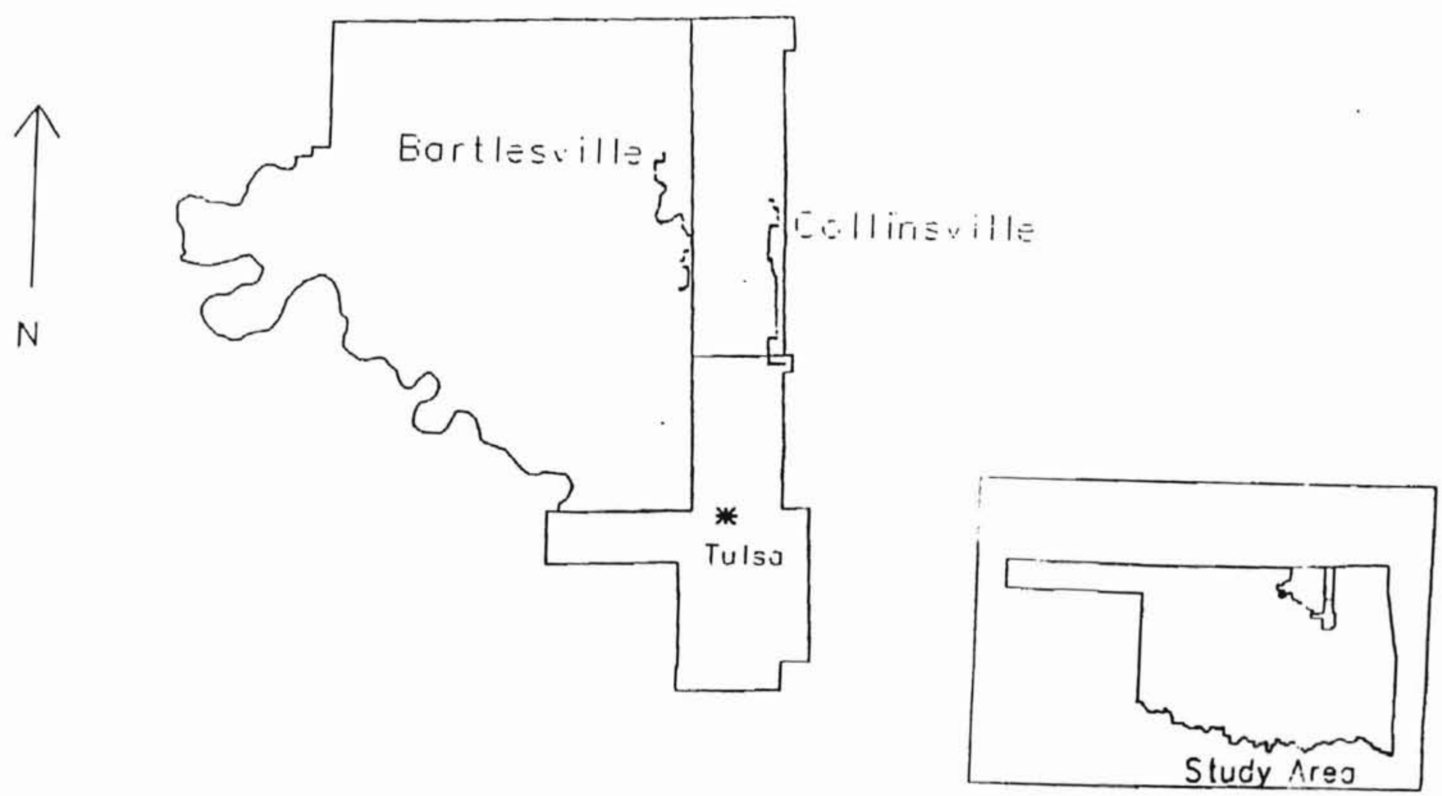
Table 4. Logistic regression models and probability of occurrence of selected birds in the avian community of the high population density rural landscape modeled by logistic regression for years 1900 and 1990.

	Logistic regression models								
		Parameter coefficients[a]						Probability of Occurrence	
Species	Intercept	X_1	X_2	X_3	X_4	X_5	c[b]	1900	1990
American robin[c]	1.7063	-0.0550(*iml*)	-0.3970(*road*)^{2}	0.000075(*crop*)^{3}			0.755	0.14	0.54
Chipping sparrow	6.1290	-0.1337(*df*)	-7.1416(*bg*)^{2}				0.941	0.03	0.01
Common grackle	-0.1777	0.0669(*df*)	-0.3011(*road*)^{2}				0.695	0.47	0.64
Common yellowthroat	2.4834	-0.0686(*df*)	-0.00161(*crop*)^{2}	-0.0272(*road*)^{4}			0.701	0.21	0.17
European starling	1.9879	-0.0835(*crop*)	-1.5680(*road*)	3.3145(*bg*)	0.00219(*df*)^{2}	4.452E-6(*crop*)^{4}	0.788	0.22	0.57
Great-horned owl	4.1533	-0.0771(*df*)					0.686	0.04	0.03
Greater prairie chicken	6.6794	-1.5277(*water*)					0.932	0.01	0.01
House sparrow	-0.2098	-2.2877(*hia*)	0.0704(*df*)	3.427E-7(*grass*)^{4}			0.732	0.28	0.51
Kentucky warbler	4.7888	-0.00272(*df*)^{2}					0.773	0.03	0.01
Northern parula warbler	4.6781	-0.1094(*df*)	-0.00006(*crop*)^{3}				0.868	0.08	0.03
Purple martin	3.5664	-0.9440(*road*)					0.653	0.04	0.12
Red-shouldered hawk	5.8621	-0.1132(*df*)					0.896	0.02	0.01
Yellow-breasted chat	3.0055	-1.58E-6(*crop*)^{4}					0.587	0.05	0.05

[a] *bg* is area of bare ground.
crop is area of cropland.
df is area of deciduous forest.
grass is area of native grassland.
hia is human impact area.
iml is area of intensively managed land.
road is area of roads.
water is area of water.

Figure 1. U.S. Fish and Wildlife Service Breeding Bird Survey route numbers 024 and 026.

Breeding Bird Survey Routes



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