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Land use change effects on breeding bird community composition

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Abstract

We identified land uses, vegetation cover types, and landscape patterns associated with avian community diversity in 2 rural landscapes in a hardwood forest-tallgrass prairie ecotone that differ with regard to human population density. We obtained long-term (24 years) changes in avian community composition through records from the North American Breeding Bird Survey. We obtained historical and present land use, vegetation cover types, and landscape structure of both landscapes from high-resolution aerial photography. Avian community composition in the low density rural population landscape was primarily related to the amount of land in deciduous forest and land treated with fire or herbicides. In contrast, avian community composition in the high density rural population landscape was primarily related to the amount of land in deciduous forest, native grassland, and roads. Changes in vegetation cover type were related to changes in the avian community composition by increasing prairie habitat associated species in the low density rural population and generalist habitat associated species in the high density rural population landscapes. Loss of neotropical migrants and increased number of generalist species in the high density rural population landscape was related to decreased native vegetation, road development, and increased landscape fragmentation. Biologists and conservationists in this region should focus attention on preserving biological diversity of rural ecosystems by maintaining native plant communities.

Key Words: Agriculture, avian species, landscape structure, urbanization, vegetation cover type

Resumen

Identificamos los usos de la tierra, tipos de cobertura vegetal y patrones del paisaje asociados con la diversidad de la comunidad de aves de dos paisajes rurales en un ecotono de bosque de madera dura - pradera de pastos altos que difieren respecto a la densidad de población humana. A través de los registros del North American Breeding Bird Survey obtuvimos los cambios a largo plazo de la composición de la comunidad de aves. Mediante el uso de fotografía aérea de alta resolución obtuvimos el uso histórico y presente de la tierra, tipos de cobertura vegetal y estructura del paisaje en ambos tipos de paisaje. En el paisaje de baja densidad de población rural, la composición de la comunidad de aves estuvo relacionada principalmente a la cantidad de tierra en el bosque deciduo y al terreno tratado con fuego o herbicidas. En contraste, la composición de la comunidad de aves del paisaje alta densidad de población rural se relaciono principalmente a la cantidad de bosque deciduo, pastizal nativo y caminos. Los cambios de tipo de cobertura vegetal se relacionaron con cambios en la composición de la comunidad de aves, en las áreas de baja densidad de población rural mediante un incremento de especies cuyo hábitat es la pradera y en las áreas de alta densidad de población rural por el aumento de especies generalistas. La perdida de especies neotropicales migrantes y el aumento de especies generalistas registrada en el paisaje de alta densidad de población rural se relaciono con la reducción de la vegetación nativa, desarrollo de caminos y el aumento en la fragmentación del paisaje. Los biólogos y conservacionistas de esta región deben enfocar su atención en preservar la diversidad biológica de los ecosistemas rurales mediante el mantenimiento de comunidades de plantas nativas.

Land use intensification often reduces ecosystem diversity on a regional scale due to the replacement of natural vegetation with managed systems of altered structure (Davis and Glick 1978, Krummel et al. 1987). These anthropogenic changes have caused concern about preserving and managing biological diversity (Grove and Hohmann 1992, Urban et al. 1992, West 1993). Management of avian diversity in urban environments has become increasingly important because of increasing urbanization, growth in non-consumptive uses, and economic returns of urban wildlife (Gill and Bonnett 1973, DeGraaf and Payne 1975, Smith 1975, George 1982). Although the effects of urbanization on many wildlife species are well documented, the dynamics of heterogeneous environments, such as the wildland to suburban ecotone, have been largely ignored by ecologists. As the human population expands, more emphasis should be placed on maintaining

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avian biodiversity to protect desirable species (Rodiek 1991). However, few studies have compared the avifauna and vegetation of urban areas with the outlying, less intensively used areas (Beissinger and Osborne 1982).

The relationship between vegetation cover types, habitat structure, and avian communities is useful for examining effects of land use on breeding birds at both stand and landscape level and should be addressed when assessing habitat quality (DeGraaf 1991, Scott et al. 1993). However, most population surveys of avian species have been at spatial scales of about 40 ha and in monocultures (Urban and Shugart 1984). Therefore, habitat management to maintain high historical diversity of avian species depends on the knowledge of changes that can or will occur in a given landscape because the landscape is a mosaic of stands and local ecosystems (DeGraaf 1991).

Implications of increasing human activity on the avifauna in the hardwood forest-tallgrass prairie ecotone must largely be extrapolated from previous studies conducted in contiguous forests (Johnson and Temple 1986). However, native birds in North America's prairies have undergone more widespread declines over the past 25 years than any other U.S. bird group, which warrants the increasing concern for the conservation of these birds (Knopf 1994). Therefore, we chose 2 rural landscapes in northern Oklahoma that differed in human population density to test the hypothesis that human activity alters avian community structure in a hardwood forest-tallgrass prairie ecotone. Specifically, we hypothesized that 1) avian community composition in a high density, rural population and a low density, rural population landscape differed in 1966 and diverged over time as the high density rural population landscape became more urbanized, and 2) different vegetation cover types between the landscapes, in part reflecting different human activities and agricultural practices, influenced avian community composition.

Study Site

Our study was centered around suburban Tulsa, Okla., and included the surrounding rural areas in northeastern Osage and southern Washington counties. We selected 2 U.S. Fish and Wildlife Service Breeding Bird Survey routes, 024 (Collinsville) and 026 (Bartlesville) (Baumgartner and Baumgartner 1992), within the ecotonal area of the Cherokee Prairie grassland formation and oak (*Quercus* spp.)-hickory (*Carya* spp.) savanna of the Cross Timbers (Bruner 1931, Soil Conservation Service 1981). The Cherokee Prairie of Oklahoma extends as a long narrow strip, 240 km southward from the Kansas state line with a width of 50–100 km throughout most of its length. The strip is better adapted to support grasses, forbs, and legumes than forests because of climate and underlying geology (Harlan 1957). The Cross Timbers lie west of the Cherokee Prairie and the Lower Arkansas Valley, extending 290 km southward from Kansas with a width of 80 km wide. The region is a transitional oak forest with interspersed prairie (Bruner 1931, Gray and Galloway 1959).

Survey routes also varied in their proximity from Tulsa, a major metropolitan area in northern Oklahoma with an estimated population of 361,628 (U.S. Department of Commerce 1990). The Collinsville route is located in Washington County and the Bartlesville route is located in Osage County. A 50% increase in human use areas was observed in the Collinsville route while a 4% decrease was observed in the Bartlesville route between 1966 and 1990 (Boren et al. 1997). Human population density of Washington and Osage County in 1990 was 3,340 km^{-2} and 520 km^{-2}, respectively. In addition, rural population density differed between the 2 routes. Rural population density of Washington and Osage County in 1990 was 10.3 km^{-2} and 4.9 km^{-2}, respectively. Rural population is defined the by U.S. Department of Commerce (1990) as residing in communities of less than 2,500 people. Hence, from this point forward, the 2 landscapes will be discussed as high density rural population or low density rural population. Each landscape includes the breeding bird survey route (40.2 km in length) and 0.8-km on each side of the route boundary. The resulting coverage was approximately 6,430 ha for each landscape.

Methods

Bird Surveys and Database Construction

We used breeding bird survey routes from the U.S. Fish and Wildlife Service to obtain our avian diversity data. The U.S. Fish and Wildlife Service Breeding Bird Survey is the only data set that indexes the population status of many species of birds over a large geographical area and time (Bystrak 1981, Geissler and Noon 1981). Although a roadside count misses some species and is limited by road placement, the results are considered to be fairly reliable indexes for a prairie-woodland ecosystem (Baumgartner and Baumgartner 1992).

We classified avian species as neotropical migrants, temperate migrants, and residents and grouped species into 5 designations of habitat occurrence: forest, forest edge and shrubland, prairie, wetland, and developed areas. We further grouped species into foraging zones: aerial (open zones), ground and shrub (foliage 0–3 m), midstory (foliage 3–10 m), canopy (foliage > 10 m), bole (trunks and limbs), and water. Nesting zones included ground, shrub (0–3 m), midstory (3–10 m), canopy (> 10 m), cavity, and other (variable heights and substrates). Classification of avian species was adapted from Harrison (1975), Bull and Farrand (1988), and Hamel (1992).

Bird abundances from 1967 to 1991 were segregated around 4 years (1966, 1973, 1980, and 1990) for which vegetation cover type and landscape structure data were documented from a previous study for both landscapes (Boren et al. 1997). Thus, breeding bird data from 1967 to 1970 corresponded to the 1966 landscape data, breeding bird survey data from 1971 to 1976 corresponded to the 1973 landscape data, breeding bird survey data from 1977 to 1984 corresponded to the 1980 landscape data, and breeding bird survey data from 1985 to 1991 corresponded to the 1990 landscape data. Relative abundance was then calculated for each of the 4 time periods by averaging relative abundance for the 4 years. Landscape data included land use and vegetation cover types (Table 1), and landscape structure measures included mean patch size, fractal dimension, landscape richness, Shannon diversity, dominance, contagion, and angular second moment (Boren et al. 1997).

Table 1. Classification system used to map vegetation cover types (adapted from Stoms et al. 1983).

Land use and cover type	Description
Developed area	Land occupied by residential, industrial, or other human structures and non-agricultural activities. Also includes transportation and utility facilities.
Roads	Black top, gravel, dirt roads, and driveways
Water	Ponds, lakes, streams, and rivers
Cropland	Land cultivated for row crops and cereal grains but excluding grazing lands
Pasture land and hay meadows	Includes pasture land (seeded grasslands used for grazing by cattle, sheep, goats, and horses) and hay meadows
Native grassland	Native grasslands with less than 10% cover by shrubs or trees
Scrub forest	Vegetation dominated (>10%) by cover of broadleaf hardwoods. Mostly post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*)
Brush-treated land	Native vegetation subjected to herbicides, fire, or chaining to control woody brush encroachment
Bare ground	Land with less than 5% vegetation cover

Data Analysis

Avian Community Change

We performed detrended correspondence analysis (DCA) with the program CANOCO (ter Braak 1988) to determine if avian community composition differed between landscapes and to document shifts in avian community composition over time by using year as the passive environmental variable. Detrended correspondence analysis is an indirect gradient analysis in which samples (species abundances) are arranged according to species composition alone. The important environmental gradients are indirectly inferred from the trends in species abundances. The first 2 axes of the DCA ordination were selected as the main ordination framework because higher eigenvalues indicate more importance in explaining avian community variability (Table 2). Detrended correspondence analysis has the advantage of producing axes that correspond to actual ecological distances, as defined by the abundance of species, and are not forced to be equal in length (Malanson and Trabaud 1987). We plotted the centroids for avian community composition for individual years in DCA space as points. We used these points to indicate trajectories through time in the avian space defined by the ordination axes (Whisenant and Wagstaff 1991).

We used species scores generated by DCA to determine the avian species responsible for temporal shifts in avian community composition. Visual observation of axis 1 and 2 of the ordination diagram indicated bird species (with overall abundances > 3) most responsible for temporal change in avian community composition. Therefore, DCA provided a multivariate approach to identify species that were declining or increasing within each landscape.

Influence of Landscape Cover Type and Structure

We performed canonical correspondence analysis (CCA) with the program CANOCO (ter Braak 1988) to determine the influence of vegetation cover type and landscape structure on the breeding bird community for each landscape. Canonical correspondence analysis is an eigenvector ordination technique for multivariate direct gradient analysis (ter Braak 1986). This technique explains community variation by detecting patterns of variation in species abundance that can best be explained by a set of environmental variables (ter Braak 1986). By applying CCA, it is possible to identify important environmental variables that explained avian community composition with no *a priori* knowledge about possible predictor variables (Saetersdal and Birks 1993).

We related abundances of all bird species in the high density rural population and low density rural population landscapes (100 and 86 bird species, respectively) to both vegetation cover type and landscape structure variables in separate CCA ordinations. We used forward selection and Monte Carlo permutation tests ($P < 0.05$) to determine environmental variables that best explained variation in breeding bird abundances. We examined canonical coefficients and intraset correlations to evaluate relative contributions of environmental variables to the axes. We also used unrestricted Monte Carlo permutation tests for statistical significance ($P < 0.05$) of the first 2 ordination axes. Tests of significance in CCA do not depend on parametric distributional assumptions; therefore, we did not transform species and environmental variables (Palmer 1993).

Canonical correspondence analysis biplots provided weighted least squares approximations of the weighted averages of species identified as causing shifts in community structure (from DCA) with respect to environmental variables (ter Braak 1986). We examined bird species relationships with a given environmental variable by continuing the environmental variable line through the origin in the biplot. A perpendicular line was then dropped from each bird species position to the variable of interest. Endpoints of the perpendicular line indicate relative positions of bird species distribution centers along the environmental variable. These endpoints indicate relative relationship of each species to a given variable (ter Braak 1986, 1987).

We used CCA with year as the only environmental axis to plot species scores of the high density rural popula-

Table 2. Eigenvalues and cumulative variance (%) of species data for the first 4 axes of detrended correspondence analysis on species data, with year as a passive environmental variable, in a low density rural population (extensively managed) and high density rural population (intensively managed) landscape.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Low density rural population					
Eigenvalue	0.30	0.22	0.12	0.09	2.73
Cumulative variance of species data (%)	11.1	18.9	23.5	26.9	
High density rural population					
Eigenvalue	0.38	0.18	0.12	0.09	2.91
Cumulative variance of species data (%)	12.9	18.9	23.2	26.4	

Table 3. Temporal changes in vegetation cover types (ha) and percent change from 1966 of high density rural population and low density rural population landscapes in a hardwood forest-tallgrass prairie ecosystem in northern Oklahoma for 1966, 1973, 1980, and 1990 (Boren et al. 1997).

Index	Year				Change
	1966	1973	1980	1990	
High density rural population (Collinsville)	(ha)				(%)
Developed areas	16	7	25	24	50
Roads	88	92	101	87	-1
Water	53	76	58	71	34
Cropland	556	453	208	120	–78
Pasture land and hay meadows	676	672	850	999	48
Native grassland	1,432	1,601	1,546	1,508	5
Deciduous forest	449	294	398	377	–16
Brush–treated land	0	41	4	5	—
Bare ground	2	6	2	2	0
Low density rural population (Bartlesville)					
Developed areas	23	18	16	22	–4
Roads	108	94	121	118	9
Water	27	39	30	38	41
Cropland	25	41	12	13	–48
Pasture land and hay meadows	90	50	25	49	–46
Native grassland	1,375	1,308	1,120	1,117	–19
Deciduous forest	1,184	980	950	887	–26
Brush–treated land	397	616	877	878	121
Bare ground	20	7	10	8	–60

tion landscape against the low density rural population landscape to document divergence of avian communities. If the avian communities of the 2 landscapes were diverging in opposite directions, a negative relationship should exist. In addition, we used CCA with vegetation cover types and landscape structure as covariables and year as environmental variables to measure residual variation. If changes occur over time, some other environmental variables that were not examined in our study were affecting avian community composition.

Results and Discussion

Vegetation Cover Types and Landscape Structure

Differences in human population density and agriculture intensification in these 2 rural landscapes resulted in altered land ownership patterns and management practices that created contrasting vegetation cover types (Table 3) and landscape structure (Table 4) between the low density rural population and high density rural population landscapes (Boren et al. 1997). Land in the high density rural population landscape was subjected to intensive management practices on cropland, pasture land, and hay meadows while land in the low density rural population landscape was predominately in native vegetation that was extensively managed with prescribed burning, herbicide application, and grazing management to increase native grass production for livestock grazing. Measures of mean patch size in our study indicated the high density rural population landscape was 4 times more fragmented than the low density rural population landscape over the entire period (Boren et al. 1997). In addition, the high density rural population landscape became less diverse and more homogeneous while the low density rural population landscape became more diverse since 1966.

Avian Community Change

The trajectories of points over time (centroids of avian community composition) indicate that the avian community in the high density rural population and low density rural population landscapes diverged along axis 1 and declined along axis 2 (Fig. 1). In addition, the 2 landscapes differ from each other in avian community composition, even ignoring temporal change, which is not surprising considering differences in land use and vegetation cover types between landscapes. The trajectory of both communities progressively diverged over time, but change was greater for the avian community in the low density rural population landscape. Centroid values for the avian community in the low density rural population landscape between 1966 and 1990 changed by 0.42 and 0.20 SD units for axis 1 and 2, respectively. This suggests avian community composition was strongly affected by a temporal decrease in deciduous woodlands by prescribed burning and herbicide application to maintain tallgrass prairie in the low density rural population landscape (Boren et al. 1997). Centroid values for the avian community in the high density rural population landscape between 1966 and 1990 were only 0.20 and 0.20 SD units apart for axis 1 and 2, respectively. Species scores from CCA, with year as the only variable, of the high density rural population landscape had a negative relationship with the species scores of the low density rural population landscape.

Table 4. Measures of landscape structure and percent change from 1966 of high density rural population and low density rural population landscapes in a hardwood forest-tallgrass prairie ecosystem in northern Oklahoma for 1966, 1973, 1980, and 1990 (Boren et al. 1997).

Index	Year				Change
	1966	1973	1980	1990	
High density rural population (Collinsville)	(ha)				(%)
Mean patch size (ha)	4.16	3.93	3.22	2.96	- 29
Fractal dimension	1.23	1.25	1.27	1.28	+ 4
Shannon diversity	1.43	1.39	1.33	1.28	- 11
Dominance	0.65	0.75	0.81	0.86	+ 3
Contagion	2.69	2.83	2.85	2.91	+ 8
Angular second moment	0.27	0.30	0.30	0.32	+ 19
Contrast	0.33	0.46	0.50	0.50	+ 52
Low density rural population (Bartlesville)					
Mean patch size (ha)	3.96	4.29	3.63	3.42	- 8
Fractal dimension	1.27	1.24	1.27	1.30	+ 2
Shannon diversity	1.21	1.29	1.29	1.31	+ 8
Dominance	0.93	0.78	0.78	0.83	- 11
Contagion	2.99	2.82	2.81	2.88	- 4
Angular second moment	0.35	0.30	0.29	0.29	- 17
Contrast	0.41	0.35	0.35	0.42	+ 2

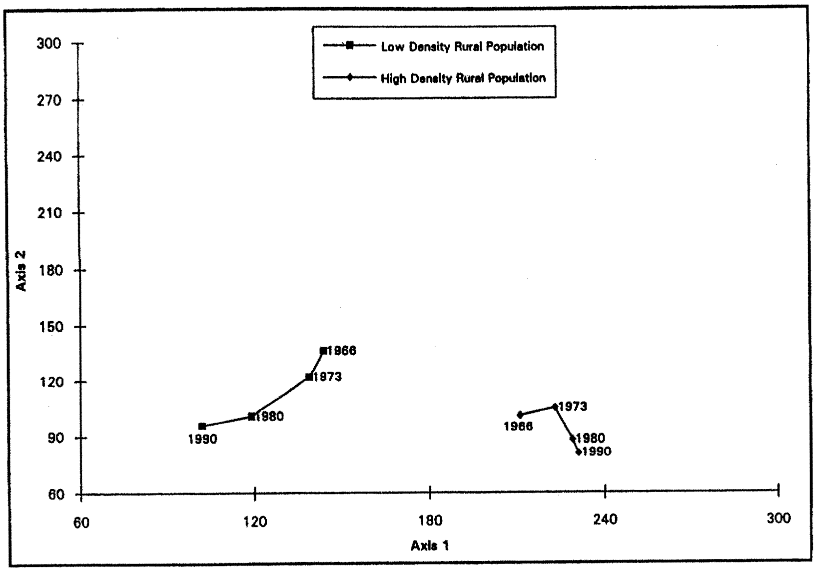

Fig. 1. Detrended correspondence analysis (DCA) ordination of centroids for avian community composition in the low density rural population (extensively managed) and high density rural population (intensively managed) landscapes. Lines indicate trajectories of avian community change between 1966 and 1990 defined by the ordination axes.

This confirms the DCA results that the avian communities were diverging in opposite directions over time (Fig. 2).

Detrended correspondence analysis provides a scaling of axes in units of compositional turnover (SD units; Hill and Gauch 1980). This scaling provides a robust estimate of beta diversity (Okland et al. 1990) that reflects rate of change in community composition along a gradient (Wilson and Mohler 1983, Samson and Knopf 1993). Based on the small SD axis units, both avian communities exhibited low beta diversity with relatively small temporal movement along axis 1 (Fig. 1). Therefore, change or turnover in avian community species composition in the low density rural population and high density rural population landscapes was relatively slow between 1966 and 1990.

Although the avian community in the high density rural population and low density rural population landscapes diverged over time, the great-tailed grackle (*Quiscalus mexicanus*) and rock dove (*Columba livia*) increased in both landscapes (Table 5). This suggests a temporal increase in some generalist species by immigration from nearby source habitats. An aggressive trap and transplant program most likely accounted for the observed increase of wild turkey (*Meleagris gallopavo*) in both landscapes. We observed none of the 10 species endemic to grasslands (Knopf 1994) in our study area. However, grasshopper sparrow (*Ammodramus savannarum*) and dickcissel (*Spiza americana*), secondary species that have exhibited significant declines in grasslands (Knopf 1994), increased in the low density rural population landscape but remained relatively unchanged in the high density rural population landscape. Grasshopper sparrow and dickcissel declines are localized to areas with inadequate breeding habitats (Knopf 1994). The grasshopper sparrow breeds in fields of several types but prefers vegetation about 30 cm tall (Hamel 1992). However, the grasshopper sparrow is sensitive to small changes in its habitat. When herbaceous material becomes too thick or trees encroach on prairies and abandoned fields, these habitats become unsuitable as breeding sites (Bull and Farrand 1988). The dickcissel also requires herbaceous cover (about 60 cm tall) for breeding (Hamel 1992). Therefore, prescribed burning and herbivory related to cattle grazing in the low density rural population landscape favored these species by maintaining breeding habitat. The eastern meadowlark (*Sturnella magna*) and lark sparrow (*Calamospiza melanocorys*), species of high concern, exhibited relatively little change in both landscapes.

The yellow-breasted chat (*Icteria virens*), an edge species of high concern that requires dense thickets and brush for nesting habitat (Bull and Farrand 1988), declined in both landscapes. The conversion of deciduous forests to brush-treated lands in the low density rural population landscape and to pasture land and hay meadows in the high density rural population landscape from 1966 to 1990 (Boren et al. 1997) may account for the decline of this species in both landscapes. The greater prairie chicken (*Tympanuchus capido*) declined only in the high density rural population landscape where brush-treated land accounted for only 1% of the total area (Boren et al. 1997). This species nests in

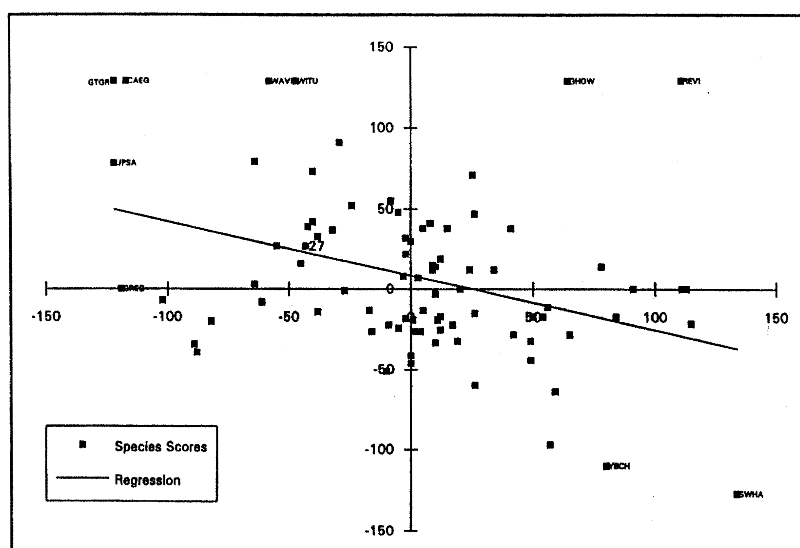

Fig. 2. Species scores from canonical correspondence analysis (CCA), with year as the only variable, of the high density rural population landscape against the plotted species scores of the low density rural population landscape (r^2 = 0.13, $P < 0.05$).

Table 5. Avian species responsible for shifts in avian community composition in a low density rural population (extensively managed) and high density rural population (intensively managed) landscape over a 24-year period, 1966 to 1990. Minor species (those that occurred 3 or fewer times) were omitted.

Species	Code	Scientific name	Type[a]	Habitat[b]	Concern[c]	Foraging[d]	Nesting[e]
Low density rural population							
Loss							
Yellow-breasted chat	YBCH	*Icteria virens*	Neotrop	Edge	High	Ground	Shrub
Blue-gray gnatchatcher	BGGN	*Polioptila caerulea*	Neotrop	Edge	Moderate	Canopy	Midstory
Greater roadrunner	GRRO	*Geococcyx californianu*	Resident	Prairie	High	Ground	Shrub
Bewickís wren	BEWR	*Thryomanes bewickii*	Temp	Edge	High	Ground	Cavity
Black and white warbler	BAWW	*Mniotilta varia*	Neotrop	Forest	Moderate	Midstory	Ground
Field sparrow	FISP	*Spizella pusilla*	Temp	Edge	High	Ground	Ground
Painted bunting	PABU	*Passerina ciris*	Neotrop	Edge	High	Ground	Shrub
Pileated woodpecker	PIWO	*Dryocopus pileatus*	Resident	Forest	Moderate	Bole	Cavity
Summer tanager	SUTA	*Piranga rubra*	Neotrop	Forest	High	Midstory	Midstory
Eastern tufted titmouse	ETTI	*Parus bicolor*	Resident	Forest	High	Midstory	Cavity
White-breasted nuthatch	WBNU	*Sitta carolinensis*	Resident	Edge	Moderate	Bole	Cavity
Gain							
Dickcissel	DICK	*Spiza americana*	Neotrop	Prairie	High	Ground	Ground
Wild turkey	WITU	*Meleagris gallopavo*	Resident	Edge	High	Ground	Ground
Barn swallow	BARS	*Hirundo rustica*	Neotrop	Develop	Moderate	Aerial	Other
Grasshopper sparrow	GRSP	*Ammodramus savannarum*	Neotrop	Prairie	High	Ground	Ground
Great-tailed grackle	GTGR	*Quiscalus mexicanus*	Resident	Edge	Moderate	Ground	Shrub
Little blue heron	LBHE	*Egretta caerulea*	Temp	Water	Moderate	Water	Shrub
Rock dove	RODO	*Columba livia*	Resident	Develop	Low	Ground	Other
Black-billed cucko	BBCU	*Coccyzus erythropthaim*	Neotrop	Edge	High	Midstory	Shrub
Cattle egret	CAEG	*Bubulcus ibis*	Resident	Prairie	Low	Ground	Shrub
Yellow-breasted chat	YBCH	*Icteria virens*	Neotrop	Edge	High	Ground	Shrub
Chipping sparrow	CHSP	*Spizella passerina*	Neotrop	Forest	Moderate	Ground	Shrub
Common yellowthroat	COYE	*Geothlypis trichas*	Neotrop	Edge	Moderate	Ground	Shrub
Great-horned Owl	GHOW	*Bubo virginianus*	Resident	Edge	Moderate	Ground	Cavity
Greater prairie chicken	GPCH	*Tympanuchus capido*	Resident	Prairie	High	Ground	Ground
Kentucky warbler	KEWA	*Oporornis formosus*	Neotrop	Forest	High	Ground	Ground
Northern-parula warbler	NOPA	*Parula americana*	Neotrop	Forest	High	Midstory	Canopy
Red-shouldered hawk	RSHA	*Buteo lineatus*	Temp	Edge	Moderate	Ground	Canopy
Yellow-bellied sapsucker	YBSA	*Sphyrapicus sp.*	Temp	Edge	High	Bole	Cavity
Gain							
American robin	AMRO	*Turdus migratorius*	Temp	Develop	Low	Ground	Shrub
Gray catbird	GRCA	*Dumetella carolinensis*	Neotrop	Edge	High	Ground	Shrub
Common grackle	COGR	*Quiscalus quiscula*	Resident	Edge	Low	Ground	Midstory
Great-tailed grackle	GTGR	*Quiscalus mexicanus*	Resident	Edge	Moderate	Ground	Shrub
House sparrow	HOSP	*Passer domesticus*	Resident	Develop	Low	Ground	Cavity
Purple martin	PUMA	*Progne subis*	Neotrop	Develop	Moderate	Aerial	Cavity
Rock dove	RODO	*Columba livia*	Resident	Develop	Low	Ground	Other
European starling	EUST	*Sturnus vulgaris*	Resident	Develop	Low	Ground	Cavity
Wild turkey	WITU	*Meleagris gallopavo*	Resident	Edge	High	Ground	Ground

[a]Species classified as neotropical migrants (Neotrop), temperate migrants (Temp), and residents (Resident) (Bull and Farrand 1988; Hamel 1992).
[b]Species grouped into designations of habitat occurrence: forest (Forest), forest edge and shrubland (Edge), prairie (Prairie), and developed areas (Developed) (Bull and Farrand 1988; Hamel 1992).
[c]Species grouped into population trends: low concern (Low), moderate concern (Moderate), and high concern (High).
[d]Species grouped into foraging zones: open zones (Aerial), foliage 0–3 m (Ground), foliage 3–10 m (Midstory), and trunks and limbs (Bole) (Bull and Farrand 1988; Hamel 1992).
[e]Species grouped into nesting zones: ground (Ground), 0–3 m (Shrub), 3–10 m (Midstory), > 10 m (Canopy), cavity (Cavity), and variable heights and substrates (Other) (Harrison 1975).

habitats of standing residual vegetation from a preceding growing season and is dependent upon stand rejuvenation by fire (Kirsch 1974).

We observed a greater loss of neotropical migrants from the high density rural population landscape compared to the low density rural population landscape (33% and 3%, respectively), which can be attributed to differences in land use and associated management practices. The ratio of neotropical migrants to resident/temperate migrants shifted from 1.2:1 to 0.75:1 in the low density rural population landscape and from 1.2:1 to 0.29:1 in the high density rural population landscape. Changes in neotropical migrant diversity and density by urban sprawl result from human-induced changes in vegetation composition. However, recent scientific studies suggest that the primary factors limiting neotropical migrants are related to fragmentation and edge effect as opposed to habitat loss (Hagan and Johnston 1992, Faaborg et al. 1993, Maurer and Heywood 1993, Thompson et al. 1993).

Landscape quality, especially with regard to landscape fragmentation and diversity, continued to erode between 1966 and 1990 in the high density rural population landscape (Boren et al. 1997), which may account for the observed loss of neotropical migrants from the high density rural population landscape. Problems associated with habitat fragmentation include increased edge habitat, parasitism rates, predation rates, and isolation effects which generally have adverse effects on neotropical migrant species (Johnson and Temple 1986, Faaborg et al. 1993). Our data also suggest that biological diversity and ecological integrity of the high density rural population landscape are lower

Table 6. Eigenvalues, correlation coefficients, and cumulative variances (%) between species and environmental axes for stepwise canonical correspondence analyses carried out on landscape cover type and landscape structure variables in a low density rural population (extensively managed) and high density rural population (intensively managed) landscape.

	Vegetation cover type		Landscape structure	
	Axis 1	Axis 2	Axis 1	Axis 2
Low density rural population				
Eigenvalue[a]	0.18	0.12	0.08	0.05
Species-environment correlation[b]	0.80	0.74	0.55	0.55
Cumulative variance explained (%)[c]	43.1	70.6	43.4	68.8
Sum of all canonical eigenvalues[d]	0.43		0.18	
Total inertia	2.74		2.74	
High density rural population				
Eigenvaluea	0.28	0.05	0.09	0.06
Species-environment correlationb	0.88	0.60	0.59	0.52
Cumulative variance explained (%)c	65.1	77.6	41.5	68.2
Sum of all canonical eigenvaluesd	0.44		0.21	
Total inertia	2.91		2.91	

[a]Eigenvalues (λ) measure the importance of the ordination axis.
[b]Species-environment correlation (r) is a measure of how well the extracted variation in community composition can be explained by the environmental variables.
[c]Cumulative percentage variance of species-environment relation.
[d]Sum of all canonical eigenvalues represents the total amount of extracted variation accounted for by the CCA ordination.

compared to the rural landscape. Neotropical migratory birds provide ideal indices of ecological integrity because they are highly sensitive to changes in landscapes that compromise the spatial continuity and integrity of natural ecosystems (Maurer 1993). However, indices of biological diversity must take into account the dynamic nature of ecosystems and include ecological processes occurring outside the area of interest (Landres 1992).

Differences in avian nesting and foraging zones between landscapes can be attributed to differences in land use and associated management practices. Prescribed burning, herbicide application, and grazing management resulted in a 26% reduction of deciduous woodland in the low density rural population landscape (Boren et al. 1997). Avian community in the low density rural population landscape shifted from tree nesting species (55% reduction) to ground and shrub nesters, which supports our observed reduction of tree foraging to ground foraging species in the low density rural population landscape. However, shifts in nesting and foraging zones are not as apparent in the high density rural population landscape. In addition, changes in vegetation cover type was related to changes in the avian community composition by decreasing some forest and edge species in both landscapes relative to prairie and generalist species in the low density rural population and high density rural population landscapes, respectively. Management practices associated with the low density rural population landscape in this study were more conducive to maintaining biodiversity of grassland species. However, community shift towards generalist species in the high density rural population landscape suggest a continued increase in exotics and species beyond their historical range which pose a significant threat to the loss of native avian assemblages (Knopf 1986, Drake et al. 1989).

Influence of Vegetation Cover Type and Landscape Structure

Landscape Cover Type

We expected a strong relationship between vegetation cover types and the distribution of breeding birds (Avery 1989). Indeed, the CCA ordination explained about 43% of the variation associated with the relationship between the vegetation cover types and both the low density rural population and high density rural population avian data sets (Table 6). The eigenvalues for axes 1 and 2 explained 71 and 78% of the cumulative variance of the bird species-landscape cover type relationship, respectively, of the low density rural population and high density rural population data sets. All land-use and vegetation cover types (Table 1) were included in forward selection analysis. Forward selection identified 5 land-use and vegetation cover type variables ($P < 0.05$) that explained 39% of variation in breeding bird abundances in the low density rural population landscape including forest (17%), cropland (9%), water (5%), developed area (4%), brush-treated land (2%), and roads (2%). Forward selection also identified 5 land use and vegetation cover type variables ($P < 0.05$) that explained 38% of variation in breeding bird abundances in the high density rural population landscape including forest (25%), cropland (4%), roads (4%), water (3%), and native grasslands (2%). Both axes were significant ($P < 0.01$) for both landscapes according to Monte Carlo permutation tests.

The relative importance of each environmental variable for predicting the community composition can be found through analysis of canonical coefficients and intraset correlations (ter Braak 1986). Canonical coefficients define the ordination axes as linear combinations of the environmental variables. Intraset correlations are the correlation coefficients between the variables and the axes (ter Braak 1986). Canonical coefficients describe the partial or residual variation and are essentially equivalent to regression coefficients. However, with intraset correlations other variables are assumed to covary with that one environmental variable in the particular way they do in the data set and thus should be used in a multivariate environment. The ordination diagram shows the relationships between the avian community in terms of main axes of variation (Kalkhoven and Opdam 1984).

The variables most correlated with axis 1, based on intraset correlations (Table 7), of the low density rural population landscape were forest and brush-treated land. Thus, axis 1 separated species that decreased and were dependent on deciduous woodland cover [e.g., black and white warbler (*Mniotilta varia*), pileated woodpecker (*Dryocopus pileatus*), summer tanager (*Piranga rubra*), and eastern tufted titmouse (*Parus bicolor*)] from species that increased and required more open canopy and fewer trees (e.g., barn swallow (*Hirundo rustica*), dickcissel, and grasshopper sparrow) (Fig. 3).

The variables most correlated with axis 1 of the high density rural population landscape were forest and native grassland (Table 7). Axis 1 separated forest and shrubland species [e.g., chipping sparrow (*Spizella passerina*), Kentucky warbler (*Oporornis formosus*), and northern parula warbler

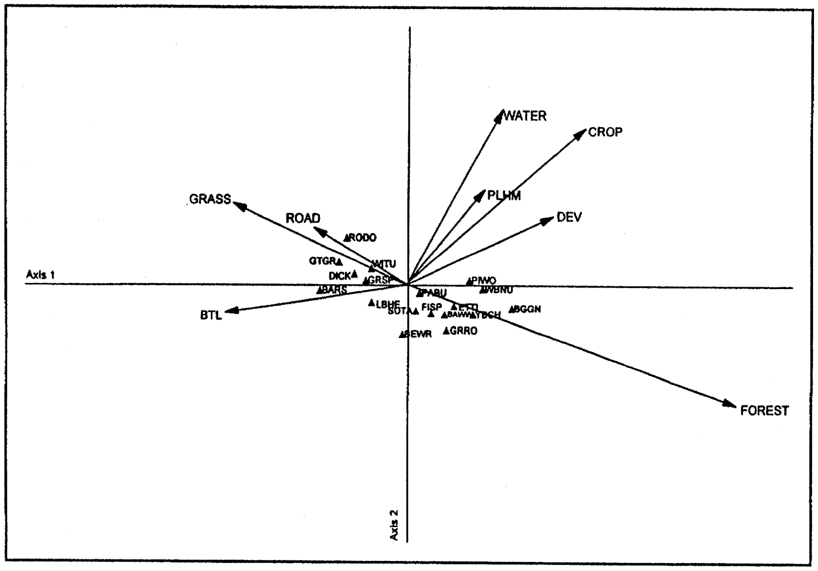

Fig. 3. Distribution of 18 species of birds in the low density rural population (extensively managed) landscape. Canonical correspondence analysis (CCA) ordination diagram with birds (▲) and environmental variables (vegetation cover types; arrows). The bird species are: YBCH = yellow-breasted chat, BGGN = blue-gray gnatchatcher, GRRO = greater roadrunner, BEWR = bewickś wren, BAWW = black and white warbler, FISP = field sparrow, PABU = painted bunting, PIWO = pileated woodpecker, SUTA = summer tanager, ETTI = eastern tufted tit-mouse, WBNU = white-breasted nuthatch, DICK = dickcissel, WITU = wild turkey, BARS = barn swallow, GRSP = grasshopper sparrow, GTGR = great-tailed grackle, LBHE = little blue heron, and RODO = rock dove. Environmental variables are: DEV = developed area, ROAD = road, WATER = water, CROP = cropland, PLHM = pasture land and hay meadows, GRASS = native grassland, FOREST = scrub forest, and BTL = brush-treated land.

(*Parula americana*)] from species preferring open grasslands (e.g., greater prairie chicken) (Fig. 4). Roads and grassland were most correlated with axis 2 of the high density rural population landscape. Axis 2 separated generalist species that increased and are commonly associated with human development [e.g., American robin (*Turdus migratorius*), house sparrow (*Passer domesticus*), purple martin (*Progne subis*), rock dove, and European starling (*Sturnus vulgaris*)] from prairie species which declined and are associated with less human disturbance [e.g., greater prairie chicken and cattle egret (*Bubulcus ibis*)] (Fig. 4).

Different vegetation cover types between the landscapes influenced avian community composition in this study. Avian community composition was primarily related to deciduous forest and brush-treated land in the low density rural population landscape compared to deciduous forest, native grassland, and roads in the high density rural population landscape. Continued urban sprawl into rural landscapes may result in increased generalist species as the result of increased roads and decreased native grassland. However, inferences on the influence of urban sprawl on rural avifauna must be made with caution. High mobility of birds makes them less dependent on local conditions than sedentary species and avian community composition may be influenced by surrounding bird communities (Jarvinen and Vaisanen 1980).

Landscape Structure

The CCA ordination explained approximately 18 and 21% of the variation associated with the relationship between the landscape structure and the low density rural population and high density rural population avian data sets, respectively (Table 6). Because vegetation cover types explained more than twice the variation of the avian data set compared to the landscape structure variables, vegetation cover type ordinations better explain temporal changes in avian community composition in this study. At the landscape scale, avian community composition is a function of vegetation structure (physiognomy) while at the within-stand level, particular plant taxonomic composition (floristics) is more important than structure in

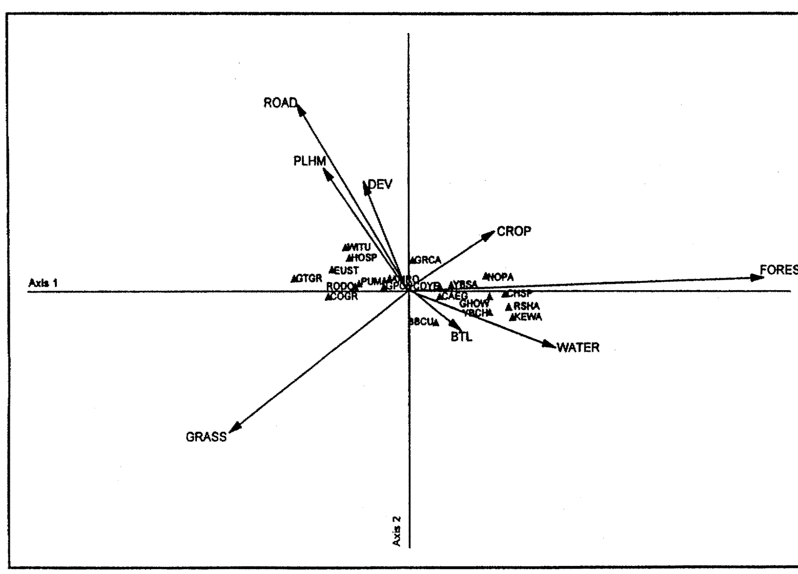

Fig. 4. Distribution of 20 species of birds in the high density rural population (intensively managed) landscape. Canonical correspondence analysis (CCA) ordination diagram with birds (▲) and environmental variables (vegetation cover types; arrows). The bird species are: BBCU = black-billed cucko, CAEG = cattle egret, YBCH = yellow-breasted chat, CHSP = chipping sparrow, COYE = common yellowthroat, GHOW = great-horned owl, GPCH = greater prairie chicken, KEWA = Kentucky warbler, NOPA = northern-parula warbler, RSHA = red-shouldered hawk, YBSA = yellow-bellied sapsucker, AMRO = American robin, GRCA = gray catbird, COGR = common grackle, GTGR = great-tailed grackle, HOSP = house sparrow, PUMA = purple martin, RODO = rock dove, EUST = European starling, and WITU = wild turkey. Environmental variables are: DEV = developed area, ROAD = road, WATER = water, CROP = cropland, PLHM = pasture land and hay meadows, GRASS = native grassland, FOREST = scrub forest, and BTL = brush-treated land.

Table 7. Canonical coefficients and intraset correlations for variables of the stepwise canonical correspondence analysis carried out on landscape cover type and structure in a low density rural population (extensively managed) and high density rural population (intensively managed) landscape.

	Canonical coefficients		Intraset correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
Low density rural population				
Vegetation covery types				
Developed area	0.1886	0.3512	0.3773	0.2696
Cropland	0.2381	0.5417	0.4600	0.5967
Pasture land/hay meadows	0.0137	0.0671	0.2043	0.3519
Native grassland	-0.3543	0.1984	-0.4498	0.3153
Scrub forest	0.4993	-0.4171	0.8592	-0.4816
Brush-treated land	-0.3345	0.0373	-0.4836	-0.1067
Roads	-0.0772	0.1264	-0.2431	0.2208
Water	0.1993	0.4134	0.2424	0.6642
Bare ground	-0.0204	0.0211	0.0368	-0.1659
Landscape structure				
Mean patch size	0.2962	-0.1888	0.6066	-0.3657
Fractal dimension	0.3953	0.3719	0.1616	0.5995
Richness	-0.6962	3.8510	-0.6140	0.5035
Shannon diversity	-0.9746	-4.4340	-0.5840	0.2190
Dominance	-1.2727	-4.0655	0.2108	0.0841
Contagion	1.3820	-0.4068	0.2636	0.4771
Angular second moment	-0.4582	1.0816	0.7338	0.2551
High density rural population				
Vegetation cover types				
Developed area	-0.0909	0.2804	-0.1122	0.4117
Cropland	-0.1380	0.2842	0.2237	0.2307
Pasture land/hay meadows	-0.4134	0.4857	-0.2183	0.4710
Native grassland	-0.6146	-0.0212	-0.4644	-0.5497
Scrub forest	0.5798	0.2718	0.9362	0.0521
Brush-treated land	0.0144	-0.0606	0.1327	-0.1508
Roads	-0.0822	0.6983	-0.2805	0.7025
Water	0.2035	0.0395	0.3795	-0.2206
Bare ground	-0.0030	-0.3156	0.0046	-0.2329
Landscape structure				
Mean patch size	0.5554	0.4059	0.8089	0.3836
Fractal dimension	-0.0703	-0.3182	-0.3795	-0.2690
Richness	-0.4051	2.1382	-0.4256	-0.4442
Shannon diversity	-0.1789	-0.6500	-0.7334	-0.1809
Dominance	0.0057	0.1669	0.6437	-0.1278
Contagion	0.8441	-2.8708	0.6586	-0.4575
Angular second moment	-0.4587	2.3910	0.7392	0.1250

determining avian community composition (Rotenberry 1985). However, Flather and Sauer (1996) concluded resident species showed few correlations with landscape structure in the eastern United States. In addition, most biodiversity studies focused on forests or woodland areas, but little research was conducted in the tallgrass prairie ecosystem. Our results support Roth (1976) and Wiens (1974) comments that generalizations relating vegetation structure and complexity to avian community composition were unrealistic for grasslands. While brush and forests vary broadly in vegetation structure and composition, which correlate with avian diversity, the degree of variability of heterogeneity among grasslands at the landscape scale is so subtle that its affect on avian diversity can be obscured (Knick and Rotenberry 1995). This may explain the inability of our landscape structure variables to explain temporal changes in avian community composition.

Conclusions and Management Implications

Changes in land use and vegetation cover types were related to changes in the avian community composition in this study. Avian communities in the high density rural population (intensively managed) and low density rural population (extensively managed) landscapes diverged over time because of different land use and management practices associated with each landscape. Temporal shifts in avian community composition were reflected in increases of some prairie species in the low density rural population and generalist associated species in the high density rural population landscapes. To preserve prairie birds and maintain biological diversity of prairie bird assemblages, management practices should increase the abundance and quality of native plant communities, especially grasslands. Maintenance of the tallgrass prairie by prescribed burning, judicious herbicide use for control of exotic and invasive plants, and grazing management are generally conducive to this objective. However, intensive land uses and management practices associated with areas surrounding urban centers pose a threat to the integrity of native plant communities. Although different variables explained avian community composition in the 2 landscapes, management practices that alter landscape structure may have less impact on avian community composition than changes in vegetation cover types.

Hence, biologists and conservationists in this region should focus attention on preserving biological diversity of rural ecosystems by maintaining native plant communities. In 1989, 74% of the United States population resided in urban areas, and that number is expected to increase to >80% by the year 2025 (Haub and Kent 1989). Considering the growth of metropolitan areas in the United States, knowledge of ecosystems under the influence of urbanization can only become increasingly important (McDonnell and Pickett 1990). In the absence of societal pressure to halt urban sprawl and agricultural intensification in rural landscapes, ecosystem integrity and bird communities may continue to degrade.

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