SONGBIRD COMMUNITY STRUCTURE

IN CROSS TIMBERS FOREST: INFLUENCE OF

JUNIPER INVASION AND URBANIZATION

By

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CHAPTER I

INFLUENCE OF INVASIVE EASTERN REDCEDAR ON DENSITY OF BREEDING WARBLERS IN CROSS TIMBERS FOREST

Abridged title: Invasive eastern redcedar and warblers

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Abstract. Several species of North American wood-warblers with population centers in the eastern U.S. reach the southwestern limit of their breeding range in Oklahoma cross timbers forest. Historically, the cross timbers was dominated by post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*), but increasingly, these patches are influenced by eastern redcedar (*Juniperus virginiana*) encroachment. We investigated the influence of eastern redcedar on breeding density of three focal species of Neotropical migrant warblers: Kentucky Warbler (*Oporornis formosus*), Black-and-white Warbler (*Mniotilta varia*), and Louisiana Waterthrush (*Seiurus motacilla*). From May–June in 2007 and 2008, we surveyed seven cross timbers forest patches in Payne County, Oklahoma. The 25 study plots within these patches represented a gradient of condition from low to high prevalence of redcedar. We used repeated samples of a modified spot-mapping approach for focal species, and fixed-radius point counts to reflect the larger breeding bird assemblage. Songbird species richness, diversity, and Partners in Flight conservation value were not affected by cedar encroachment. Among focal warblers, breeding density of Kentucky Warbler was negatively correlated with the abundance of eastern redcedar.

Key words: Black-and-white Warbler, cross timbers forest, eastern redcedar, eastern songbirds, invasive species, Juniperus virginiana, *Kentucky Warbler, Louisiana Waterthrush.*

La influencia del arbol conífero *Juniperus virginiana* en las reinitas (Parulidae) nidificantes de los cruz de madera de bosques

Resumen. Varias especies de chipes (Parulidae) que nidifican en Norteamérica y que tienen poblaciones centradas en el este de Estados Unidos alcanzan el límite suroccidental de su zona de distribución veraniega en los cruz de madera de bosques del estado de Oklahoma. Antiguamente, la zona del cruz de madera de bosques era dominada por las especies de roble *Quercus stellata* y *Q. marilandica*. Sin embargo, *J. virginiana* incrementa cada vez más su rango de distribución en estos bosques. Investigamos la influencia de *J. virginiana* en la densidad de nidificación de tres especies de chipes migrantes neotropicales: *Oporornis formosus, Mniotilta varia,* y *Seiurus motacilla*. Durantes los meses de mayo y junio del 2007 y 2008, examinamos viente y cinco puntas en siete areas en la zona de cruz de madera de bosques en el ayuntamiento de Payne en Oklahoma. Las áreas representan una zona de transición de baja a alta presencia de *J. virginiana* en el subdosel en zonas cubiertas de roble. Utilizamos ejemplos repetidos del territorio de la cartografía para las especies objetivas y conteos de punto con radio fijo para hacer una representación completa de la comunidad de aves nidificantes. Riqueza de especies, la diversidad, y Compañeros en Vuelo valor de conservación no fueron afectadas por la invasión de cedro. Entre focales currucas, la densidad de cría de *O. formosa* se correlacionó negativamente con la abundancia *J. virginiana.*

INTRODUCTION

Several species of North American wood-warblers with population centers in the eastern U.S. reach the southwestern limit of their breeding range in Oklahoma cross timbers forest patches (DeGraaf and Rappole 1995, Sauer et al. 2008). Louisiana Waterthrush (*Seiurus motacilla*), Northern Parula (*Parula americana*), Prothonotary Warbler (*Protonaria citrea*), Kentucky Warbler (*Oporornis formosus*), and Black-and-white Warbler (*Mniotilta varia*) are relatively common breeding birds as far west as central Oklahoma (approx. 97° W), with isolated occurrences extending even farther west (Reinking 2004). These warblers contribute to an assemblage of eastern forest songbirds that are able to breed successfully in cross timbers forests; other eastern forest songbirds (e.g., Ovenbird [*Seiurus aurocapilla*] and Wood Thrush [*Hylocichla mustelina*]) do not typically breed in cross timbers forest and reach their western distributional limit in the state approximately 150 km east (Reinking 2004). Cross timbers forests represent a stark contrast to typical breeding habitats in the core range of eastern forest songbirds, where annual precipitation may average 100–150 cm, and a more diverse community of larger canopy trees is supported. In central Oklahoma cross timbers, landscapes receive an average 75–90 cm of annual precipitation, with high interannual variability.

Historically, cross timbers habitat existed as a north–south band at the zone of transition between broad-leaf deciduous forest and tallgrass and mixed-grass prairies in the Southern Plains. A drought- and fire-maintained mosaic of cross timbers forest and tallgrass prairie was the historically dominant habitat in central Oklahoma (Rice and Penfound 1959). Cross timbers forest is characterized by a low (< 18 m), continuous canopy of post (*Quercus stellata*) and blackjack oak (*Q. marilandica*), with eastern redcedar (*Juniperus virginiana*), pecan (*Carya illinoensis*), hackberry (*Celtis occidentalis*), and cottonwood (*Populus deltoides*) occasionally dominant in the canopy, especially in riparian areas. The understory may be relatively open, including regenerating canopy tree species, or it may be densely vegetated with dominants such as buckbrush (*Symphoricarpos orbiculatas*), briars (*Smilax* spp.), and poison ivy (*Toxicodendron radicans*). Understory condition is strongly influenced by the frequency and intensity of fire. Generations of fire suppression have led to a profusion of eastern redcedar in central Oklahoma rangeland and in cross timbers forest patches (Briggs et al. 2005, Clark et al. 2005).

Eastern redcedar can exert multiple ecological influences on forest patches in which it becomes invasive. The dense foliage extending to the ground physically prevents vegetative growth beneath the trees, potentially limiting regeneration of canopy oaks. Shading from redcedar also inhibits understory growth, thus decreasing the amount of fuel (e.g., grasses, forbs) that can accumulate beneath stands. Leaf-litter from this species also significantly increases the pH of surface soil beneath the trees effectively limiting vegetative growth immediately beneath the tree (Bekele et al. 2005). These factors greatly reduce the chances of ignition in low intensity fires. As more redcedars within a stand survive periodic low intensity fires, the species becomes increasingly dominant in the canopy (DeSantis et al., *in press*), and the effectiveness of burning as a means of control is rapidly limited as tree height increases (Engle and Kulbeth 1992).

The ecology of eastern forest songbirds breeding in cross timbers forest has received little study (e.g., Schulz et al. 1992), despite the fact that at least 4 million ha of these forests remain. At least 9 of 30 species considered regional priorities for the Oaks and Prairies Bird Conservation Region of Partners in Flight (Panjabi et al. 2005) are widely distributed in cross timbers forest patches in central Oklahoma. The relative importance of these patches for these species could change due to increased fragmentation from exurban development, climatic changes (e.g., prolonged drought) that influence primary productivity, and structural and compositional changes resulting from the proliferation of invasive species, especially eastern redcedar.

To begin to understand the ecological relationships of breeding songbirds in cross timbers forest, we surveyed 25 study plots in 7 cross timbers forest patches during the spring of 2007 and 2008. We used a combination of spot mapping and point counts to obtain species assemblage data and calculate breeding density of three focal warblers: Kentucky Warbler, Black-and-white Warbler, and Louisiana Waterthrush. Our specific objectives were to 1) characterize the breeding songbird community in cross timbers forest patches, and 2) determine if the breeding density of the focal warblers is influenced by redcedar invasion.

METHODS

We surveyed cross timbers songbirds in 7 forest patches approximately 15 km west of Stillwater in Payne County, Oklahoma (36° 05' N 97° 12' W). We established three or four survey plots within each of the patches, resulting in 25 bird sampling plots. Plots were centered at least 100 m from the nearest forest edge, and arranged spatially so that plot centers within each patch were separated from each other by at least 250 m. The plots represented a gradient of eastern redcedar canopy cover from 0 to nearly 100%. We recorded UTM coordinates for plot centers in the field using a hand held GPS (Garmin Geko 201, Garmin International, Olathe, KS, USA). We used optical rangefinders to judge distances from the plot center in the field. We mapped survey plots in a GIS (ArcMap 9, ESRI, Redlands, CA, USA) using a National Agriculture Imagery Program (NAIP) 2003 photograph (USDA 2003) as the base map.

We sampled birds from the plot centers of the 25 sampling plots using a combination of 100-m, fixed-radius point counts (Toms et al. 2006) and a modified spot-mapping approach (Christman 1984) for the focal warblers. We conducted point counts during early morning hours (0530 – 0930 CDT) in May and June 2007 and 2008 under dry conditions with relatively light winds. We followed standard songbird sampling procedures for counts of singing males as recommended in Ralph et al. (1995) with some modifications. Point counts lasted seven minutes, and we counted only those singing males judged to be within 100 m of the plot center and using the habitat, excluding flyovers. We surveyed plots six times each in 2007 and 2008, using the mean abundance of each survey as our estimate of abundance for the season. We used counts from a single observer (JRH) to minimize observer biases. We omitted from analysis all species detected on two or fewer surveys, and assumed that species detected on at least three surveys were representing individuals on breeding territories.

To estimate breeding density of Louisiana Waterthrush, Black-and-white Warbler, and Kentucky Warbler, we made six visits (separated by at least seven days) to the plots from April through June (of 2007 and 2008) and applied a modified spot-mapping procedure. From the center point, a single observer (JRH) mapped the relative location of singing males on a schematic map of the plot (Christman et al. 1984). We conducted these counts for seven minutes per sample for a total of 42 minutes of sampling per plot per season. We considered males detected in the same region of the plot on at least three of the six visits to have been territorial. We assumed that the six visits would provide a detection probability of 1.0 for the three focal species so we estimated density within each plot as the number of territories identified divided by the area sampled (3.14 ha for each 100-m radius plot). We expressed density as the number of territories per 10 ha.

To quantify vegetation structure and composition at the plots, we established 10 m radius subplots 15 m from plot center at 0, 120 and 240º. In these subplots, we made visual estimates of percent ground cover in leaves, grasses, forbs, rocks, woody debris, and bare soil. We also estimated shrub cover up to 5 m and total tree canopy cover, and identified to species all trees and shrubs within the subplots. We used a clinometer to estimate canopy height and an angle gauge from plot center to estimate stand basal area (Stoddard and Stoddard 1987).

We used Spearman's rank correlation to analyze relationships between mean percent eastern redcedar cover at each site and mean songbird richness, diversity, and summed regional Partners in Flight (PIF) combined scores (Panjabi et al. 2005). We then established three categories (low = 0–5%, intermediate = 5–33%, and high = 33–100%) of eastern redcedar invasion based on the percentage of redcedar cover in the tree canopy of plots. We compared territory density of focal warblers using one-way ANOVA (alpha = 0.05) among these categories. For ANOVAs, we first tested for homogeneity of variance with Levene's test. For *post-hoc* multiple comparisons, we used Tukey's test (Neter et al. 1990). We performed all statistical analysis in SPSS.

RESULTS

Vegetation characteristics were generally homogeneous among sites. For example, total canopy cover ranged from 0.31–0.61 (Tab. 1). The degree of redcedar development, however, provided a strong gradient on which sites could be categorized, e.g., the proportion of redcedar among tree stems ranged from 0.00–0.53 (Tab. 1).

We encountered 35 breeding species using cross timbers forest in the study area. Composition of the species assemblages was consistent from patch to patch. Nine of the 10 most common species occupied 63% of the forest patches, while at least eight of the 10 most commonly occurring species were present in 88% of the patches. In addition, the cross timbers forests supported several species of high conservation priority. Of the 15 most commonly occurring species, seven have been categorized by Partners in Flight as being of either regional or continental concern (Tab. 2). Mean richness (±SD) among sites was 20±2.21 (range 18–24). Neither richness (r = -0.704, P = 0.088), diversity (r = -0.357, P = 0.444), nor summed Partners in Flight combined scores (r = -0.750, P = 0.066) were correlated with percent cover of eastern redcedar in sample plots.

Frequency of occurrence for focal warblers in patches (n = 7) was high. We detected territorial Black-and-white Warbler at 100%, Louisiana Waterthrush at 86%, and Kentucky Warbler at 57% of the study sites. Kentucky Warbler density was higher in plots with low redcedar cover ($F_{2, 27}$ = 7.510, P < 0.001) than in plots with intermediate and high cedar cover (Fig. 1). Breeding densities of Black-and-white Warbler and Louisiana Waterthrush were not associated with percent cover of eastern redcedar ($F_{2, 27}$ = 0.998, P < 0.376, and $F_{2, 27}$ = 1.516, P < 0.230, respectively).

DISCUSSION

Research over the past decade has provided ample evidence to suggest that eastern redcedar can degrade native grasslands and alter grassland songbird communities (Coppedge et al. 2001, Barth 2002, Fuhlendorf et al. 2002, Chapman et al. 2004a, Briggs et al. 2005). However, little has been done to attempt to quantify this species' influence on forest bird communities. It may be that while the spread of eastern redcedar in grasslands (and the obvious conversion from grassland to shrubland communities) has been well studied (e.g., Barth 2002), the encroachment of redcedar into the midstory of forest patches has only recently attracted significant research attention. For example, we know of just one, ongoing study that quantifies the change in basal area of redcedar in cross timbers forest during the 20th Century period of encroachment (DeSantis et al., *in press*).

In terms of influence on forest birds, invasive species studies have focused instead on exotic, invasive species such as *Lonicera maackii* and *Rosa multiflora* (e.g., Borgmann and Rodewald 2004). In some studies (Schmidt and Whelan 1999, Borgmann and Rodewald 2004), birds nesting in exotic shrubs experienced lower reproductive success than those that nested in native shrubs. Leston and Rodewald (2006), however, found that nest success of Northern Cardinal (*Cardinalis cardinalis*) was similar between urban (where exotic shrubs were the preferred nest substrate) and rural sites. Schmidt et al. (2005) found that Veeries (*Catharus fuscescens*) nesting in *Berberis thunbergii* experienced lower rates of nest predation than those that opted to nest on the ground. These studies indicate no clear pattern of a consistent positive or negative influence of exotic shrubs on nesting songbirds.

In terms of nesting density of the three focal warblers in this study, our results were variable as well. Kentucky Warbler density declined with increasing redcedar encroachment, with no plots containing high levels of encroachment supporting territorial males. Black-and-white Warbler also exhibited its lowest density in plots heavily invaded by redcedar, but at approximately 2 males/10 ha this species was still well represented in plots with abundant cedar. In contrast, density of Louisiana Waterthrush was positively correlated with redcedar encroachment.

Breeding Bird Survey data for Black-and-white Warbler show no significant trend either rangewide (+0.1 % per year) or in Oklahoma (+0.3 % per year) between 1966 and 2000. The breeding distribution of this species in central Oklahoma and throughout the cross timbers is ill-defined. The Black-and-white Warbler was indicated only as a "probable" breeding resident in Payne County in Oklahoma's Breeding Bird Atlas (Reinking 2004). Area searches of our 7 sites in 2007 produced 35 territorial males, and point count data suggest that Black-and-white Warbler is the fifth most commonly occurring songbird in these forest patches (Tab. 2). We also observed several (20+) cases of successful breeding over the two field seasons (all sightings were of either one or two successfully fledged young) both in forest patches with minimal cedar component as well as forest patches dominated by eastern redcedar, suggesting that despite lower breeding densities in patches with moderate to high cedar component, cedar encroachment did not significantly impact the breeding success of this species.

The density of breeding Kentucky Warblers in the study area was negatively associated with eastern redcedar invasion. We found an average breeding density of 2.1 males/10 ha at sites with low percent cover of eastern redcedar, and an overall density of 0.6 males/10 ha in cross timbers forest throughout the study site. Across its range Kentucky Warbler densities within large forest patches averaged 2.2 males/10 ha as compared to 1.4 males/10 ha in smaller forest fragments (Gibbs and Faaborg 1990).

Louisiana Waterthrush breeding density estimates from southern IIlinois, New York, and Connecticut were 2.5 pairs/km, 2.8 pairs/km, and 1.0 pair/km of stream respectively (Eaton 1958, Craig 1981, Robinson 1990). We surveyed an estimated 5.4 km of stream with a mean of 0.2 km surveyed per plot. Across all plots we had a breeding density of 1.3 singing males/km of stream. Our density estimate is comparable to other density data from sites nearer the center (IL) and the northeastern limits (NY, CT) of the species' range, suggesting that the cross timbers forests may provide quality habitat for this species. Our data suggest that waterthrush distribution and abundance may be positively correlated with eastern redcedar, but this is likely an artifact of the abundance of redcedar along riparian zones in the cross timbers.

Preliminary research has provided evidence that both Kentucky Warbler and Black-and-white Warbler densities may have been reduced by redcedar encroachment. We also conclude based on this limited research that cedar is not detrimentally affecting breeding densities of Louisiana Waterthrush. We recommend that future investigations of breeding warblers in cross timbers forests examine additional aspects of breeding biology related to eastern redcedar encroachment. While this study has illustrated some patterns in the density of breeding males, we lack basic information on survivorship, nest success, and recruitment for multiple forest songbirds near the western edge of their respective ranges. This information will become increasingly important in providing a more complete picture of the use and condition of all forest habitat used by forest songbirds.

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Table 1. Summary vegetation characteristics (mean±SE) of seven cross timbers forest patches. Canopy cover is expressed as a proportion of total leaf canopy > 5m in height. *Juniper* stems are expressed as a proportion of total stem counts of trees > 10 cm dbh. All other cover classes are indicated as proportions of total ground cover.

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
canopy height (m)	12.78 (±2.48)	12.17 (±10.08)	11.22 (±5.15)	14.83 (±2.14)	13.08 (±2.75)	12.42 (±3.86)	8.00 (±4.25)
canopy cover	0.58 (±0.03)	0.47 (±0.03)	0.51 (±0.02)	0.31 (±0.01)	0.61 (±0.01)	0.46 (±0.02)	0.33 (±0.02)
Juniper stems	0.49 (±0.05)	0.28 (±0.05)	0.08 (±0.01)	0.24 (±0.04)	0.00 (±0.00)	0.02 (±0.00)	0.53 (±0.04)
litter depth (cm)	2.28 (±2.06)	2.39 (±0.31)	2.44 (±1.16)	1.13 (±0.03)	2.17 (±0.83)	1.25 (±0.32)	0.75 (±0.16)
low shrub cover	0.05 (±0.00)	0.21 (±0.01)	0.30 (±0.02)	0.44 (±0.02)	0.35 (±0.02)	0.40 (±0.01)	0.25 (±0.02)
high shrub cover	0.03 (±0.00)	0.07 (±0.00)	0.12 (±0.00)	0.25 (±0.02)	0.11 (±0.01)	0.18 (±0.01)	0.10 (±0.01)
bare ground cover	0.12 (±0.01)	0.10 (±0.01)	0.01 (±0.00)	0.08 (±0.00)	0.05 (±0.01)	0.06 (±0.00)	0.15 (±0.01)
rock cover	0.00 (±0.00)	0.02 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.02 (±0.00)	0.03 (±0.00)	0.07 (±0.01)
grass cover	0.04 (±0.00)	0.08 (±0.00)	0.19 (±0.02)	0.09 (±0.01)	0.35 (±0.02)	0.20 (±0.02)	0.16 (±0.01)
moss cover	0.01 (±0.00)	0.08 (±0.02)	0.01 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.03 (±0.00)	0.08 (±0.00)
total herb cover	0.15 (±0.03)	0.08 (±0.00)	0.10 (±0.00)	0.21 (±0.00)	0.12 (±0.00)	0.29 (±0.01)	0.10 (±0.00)
downed wood cover	0.18 (±0.01)	0.14 (±0.00)	0.18 (±0.01)	0.12 (±0.00)	0.17 (±0.01)	0.16 (±0.00)	0.09 (±0.00)
leaf cover	0.49 (±0.03)	0.57 (±0.02)	0.52 (±0.02)	0.51 (±0.01)	0.29 (±0.02)	0.25 (±0.01)	0.35 (±0.04)

Table 2. Partners in Flight species assessment scores by species for the Oaks and Prairies (Region 21). Species are listed in descending order of mean relative abundance as encountered on study plots.

Species	Rel. Ab. per Plot	RCS-b*	CC**	RC***
Northern Cardinal	1.04	10	-	-
Blue-gray Gnatcatcher	0.96	10	-	-
Tufted Titmouse	0.86	13	-	-
Carolina Chickadee	0.72	16	-	-
Black-and-white Warbler	0.53	11	-	-
Indigo Bunting	0.43	9	-	-
Field Sparrow	0.42	16	-	Y
Red-bellied Woodpecker	0.32	13	-	-
Carolina Wren	0.28	13	-	-
Yellow-billed Cuckoo	0.25	15	-	Y
Summer Tanager	0.25	15	-	Y
Blue Jay	0.25	10	-	-
Great-crested Flycatcher	0.23	15	-	Y
Painted Bunting	0.22	20	Y	Y
Kentucky Warbler	0.20	14	Y	-
Louisiana Waterthrush	0.20	15	-	Y
Red-eyed Vireo	0.19	9	-	-
Brown-headed Cowbird	0.15	12	-	-
White-eyed Vireo	0.14	11	-	-
Downy Woodpecker	0.12	11	-	-
Prothonotary Warbler	0.09	14	Y	-
Northern Parula	0.07	11	-	-
Mourning Dove	0.04	12	-	-
Hairy Woodpecker	0.04	10	-	-
Brown Thrasher	0.03	10	-	-

*RCS-b: Regional Combined Score for the breeding season (sum of scores for Breeding Distribution, Population Size, regional Population Trend, breeding Relative Density, and regional Threats to Breeding).

**CC: Continental Concern species (Y=yes, blank=no)

***RC: Regional Concern species (Y=yes, blank=no)

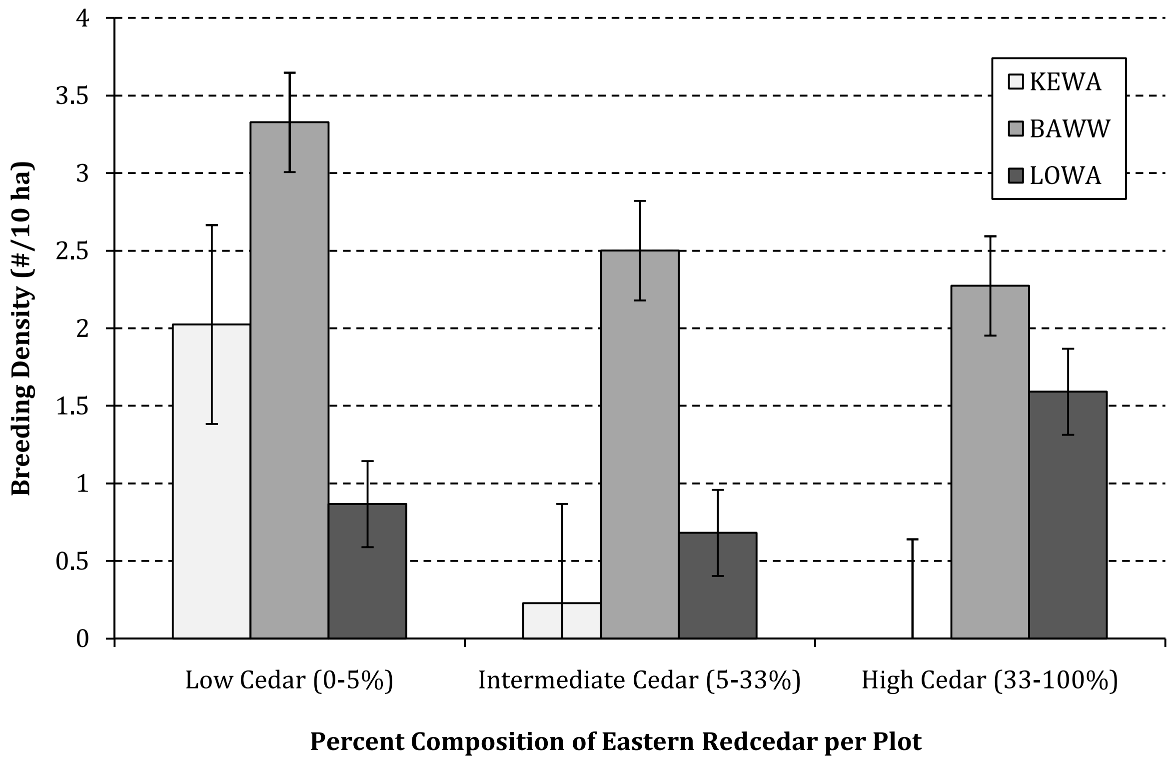

Figure 1. Mean breeding densities (±SE) of Kentucky Warbler, Black-and-white Warbler, and Louisiana Waterthrush in cross timbers forest study plots with low, intermediate, and high densities of eastern redcedar cover.

CHAPTER II

INFLUENCE OF INVASIVE EASTERN REDCEDAR (*Juniperus virginiana*) ON BREEDING AND WINTERING BIRD ASSEMBLAGES IN CROSS TIMBERS FOREST

INTRODUCTION

In the south-central United States, cross timbers forest occupies a north–south band at the zone of transition between broad-leaf deciduous forest to the east and tallgrass and mixed-grass prairies to the west. A drought- and fire-maintained mosaic of cross timbers forest and tallgrass prairie was historically dominant in central Oklahoma (Rice and Penfound 1959). Average annual precipitation is 114–122 cm near the eastern edge of this roughly 250 km transitional zone and 76–84 cm near the western edge (Duck and Fletcher 1943, Oklahoma Climatological Survey 2002). Cross timbers forest is characterized by a low (< 18 m), continuous canopy of post (*Quercus stellata*) and blackjack oak (*Q. marilandica*), with eastern redcedar (*Juniperus virginiana*), pecan (*Carya illinoensis*), hackberry (*Celtis occidentalis*), and cottonwood (*Populus deltoides*) occasionally dominant in the canopy, especially in riparian areas. The understory may be relatively open, including regenerating canopy tree species, or it may be densely vegetated with dominants such as buckbrush (*Symphoricarpos orbiculatas*), briars (*Smilax* spp.), and poison ivy (*Toxicodendron radicans*). Understory condition is strongly influenced by the frequency and intensity of fire. Generations of fire suppression have led to a profusion of eastern redcedar in central Oklahoma rangeland and in cross timbers forest patches (Clark et al. 2005).

Eastern redcedar can exert multiple ecological influences on forest patches in which it becomes invasive. On acidic soils, cation-rich leaf litter from redcedar can have a buffering effect on soil acidity, thus increasing surface soil pH (Bekele et al. 2005, Van Els 2009).

However, this effect is not as pronounced when growing amid hardwoods. The dense foliage extending to the ground physically prevents vegetative growth beneath the trees (Van Els 2009), potentially limiting regeneration of canopy oaks. Shading from redcedar also inhibits understory growth. As little as 10 percent of available light reaches the forest floor (Van Els 2009) thus decreasing the amount of fuel (e.g., grasses, forbs) that can accumulate beneath stands. These factors render the cedars highly resistant to burning from low intensity fires. As more redcedars within a stand survive periodic low intensity fires, the species becomes increasingly dominant in the canopy (DeSantis et al., *in press*).

Several species of forest songbirds from the eastern U. S. reach the southwestern limit of their breeding range in Oklahoma cross timbers forests (DeGraaf and Rappole 1995). Louisiana Waterthrush (*Seiurus motacilla*), Northern Parula (*Parula americana*), Prothonotary Warbler (*Protonaria citrea*), Kentucky Warbler (*Oporornis formosus*), and Black-and-white Warbler (*Mniotilta varia*) are relatively common breeding birds in central Oklahoma (approx. 97° W), with isolated occurrences extending even farther west (Reinking 2004). In contrast, other eastern forest songbirds (e.g., Ovenbird [*Seiurus aurocapilla*] and Wood Thrush [*Hylocichla mustelina*]) reach their southwestern distributional limit approximately 150 km east (Reinking 2004). In central Oklahoma cross timbers, landscapes receive an average 75–90 cm of annual precipitation, with high interannual variability (Oklahoma Climatological Survey 2002). These conditions are a stark contrast to typical breeding habitats in the core range of eastern forest songbirds, where annual precipitation may average 150 cm, and a more diverse community of larger canopy trees is supported. The influence of eastern redcedar proliferation on breeding songbirds in cross timbers forest has not been investigated.

Cross timbers also provides habitat for forest birds during the winter months, and populations of these species may also be affected by invasive redcedar. Approximately 40 landbird species (includes doves, hummingbirds, woodpeckers, etc. in addition to passerines) that commonly winter in central Oklahoma occur regularly in cross timbers forest (eBird 2008). Redcedar may provide important vegetative cover for species like Hermit Thrush (*Catharus guttatus*) and Orange-crowned Warbler (*Vermivora celata*). In addition, cedar cones likely provide an important source of food for populations of wintering American Robins (*Turdus migratorius*), Cedar Waxwings (*Bombycilla cedrorum*), Yellow-rumped Warblers (*Dendroica coronata*), and Eastern Bluebirds (*Sialia sialis*) (Holthuijzen and Sharik 1985).

Ecological relationships between eastern songbirds and cross timbers habitat have not been extensively researched (e.g., Schulz et al. 1992), despite the fact that at least 4 million ha of these forests remain. At least 9 of 30 breeding species considered regional priorities for the Oaks and Prairies Bird Conservation Region of Partners in Flight (Panjabi et al. 2005) are widely distributed in Oklahoma cross timbers forest. The relative importance of these forest patches could vary with structural and compositional changes resulting from the proliferation of invasive species, especially eastern redcedar. In addition, cross timbers forests are negatively influenced by fragmentation from exurban development. Climatic changes (especially prolonged drought) could reduce primary productivity in cross timbers forests, tipping the balance toward more open canopies that may be unsuitable for forest birds. The ranges of at least 19 Oklahoma breeding birds that use cross timbers forest are predicted to contract in response to forecast global warming scenarios (American Bird Conservancy, 2006).

To begin to understand the ecological relationships between songbirds and cross timbers forest, I surveyed breeding and wintering assemblages at multiple locations in Payne County, Oklahoma (Fig. 1). I selected survey locations of cross timbers forest from a gradient of eastern redcedar invasion. My specific objectives were to (1) quantify use of cross timbers forest by breeding songbirds, (2) characterize the community of wintering songbirds in cross timbers forests, (3) assess the degree to which redcedar invasion influences use of cross timbers by breeding and wintering species, and (4) identify other vegetation and site parameters that play an important role in the distribution of these species.

METHODS

Study Area

This study took place at multiple sampling locations in western Payne County, OK (36° 05' N 97° 12' W; Fig. 1). Payne County receives an average of 94.8 cm of precipitation annually with May and June receiving the most rainfall (a combined average of ~25 cm [OK Climatological Survey 2002]). County land cover is comprised of approximately 54% herbaceous, 21% deciduous forest, 8% cultivated cropland, 6% developed open space, 5% hay/pastureland, and 2% each urban, evergreen forest, and open water (NLCD 2001). The study area is included in the Oaks and Prairies Bird Conservation Region (Rich et al. 2004).

I surveyed breeding and wintering songbirds (surveys included doves, hummingbirds, cuckoos, and woodpeckers) in 7 forest patches covering an estimated geographic area of 550 ha. Approximate forest patch sizes ranged from 15 to 200 ha. Sampling plots within the patches comprised a gradient of mature cross timbers forest with minimal cedar invasion to plots heavily invaded by cedar. I selected plots with a total forest canopy cover of at least 33% and a minimum

5 m canopy height. For winter surveys, I used the same 7 cross timbers forest patches, but did not restrict sampling to the plots.

Study Design

I established 3–4 survey plots within forest patches, resulting in 25 bird sampling plots. I established plot centers at least 100 m from the nearest forest edge and located the plots spatially so that plot centers within each patch were separated from each other by at least 250 m. These plots represented a gradient of eastern redcedar canopy cover from 0 to nearly 100%. I conducted four total surveys (two breeding and two winter season) of the study area. I recorded Universal Transverse Mercator [UTM] coordinates for plot centers in the field using a hand held global positioning system (Garmin Geko 201, Garmin International, Olathe, KS, USA). From plot centers, I used a laser rangefinder to judge distances to singing and calling birds in the field.

Breeding Bird Surveys

I surveyed for breeding birds using a modified point count technique based on recommendations in Ralph et al. (1995). Counts were focused on detection of singing males, and were conducted from 0530–0930 hrs CDT on days with light winds and no rain. To eliminate inter-observer bias, a single observer conducted all counts. I mapped locations of all singing male songbirds (as well as calling woodpeckers, cuckoos, hummingbirds, and doves) encountered within a 100 m, fixed radius sampling area (excluding flyovers) during a 6-minute sampling period. I began each count facing azimuth 0° (using a magnetic compass) so that individuals could be consistently mapped to a location within the schematic map for the plot, if indeed that individual occupied the same area on subsequent counts. I estimated distance to each individual using a laser rangefinder. I conducted six weekly counts per season (n = 12 total), using the average abundance of each count as the estimate of abundance for the survey. I omitted from analysis all species detected on two or fewer surveys and assumed that individuals detected at the same plot on at least three surveys within a season were occupying breeding territories.

Winter Bird Surveys

To sample assemblages of wintering birds in cross timbers forest, I used the standardized search method described by Watson (2003). This involved a single observer conducting in-depth area searches of each forest patch (n = 7). Every individual of each species seen or heard was recorded until 30 minutes had elapsed without the addition of a new species for the site list. I used care in the field to avoid counting the same individuals more than once. This method allowed me to create species/effort curves of accumulation that indicated a consistent detection of a high proportion of species to the richness estimates of the hypothetical species pool. The hypothetical species pool estimate was determined through examination of published data for wintering birds in Payne County, OK (eBird 2008), as well as comparison to historical data from the Stillwater, OK Christmas Bird Count (National Audubon Society 2002). Surveys consisted of three searches (one search per month Dec.–Feb.) at each site in 2007/2008 and 2008/2009 (n = 6 total searches). I considered species to be winter residents in cross timbers forest if they occurred on at least 10% of surveys or if they occurred at only a single site but were present at that site in consecutive seasons.

Vegetation Sampling and Analysis

To quantify vegetation structure and composition at the 25 plots, I established 10 m radius subplots 15 m from plot center at 0, 120, and 240º. In these subplots, I made visual estimates of percent ground cover in leaves, grasses, forbs, mosses, rocks, woody debris, and bare soil. I also estimated shrub cover up to 5 m (low ≤2m, high >2m) and total tree canopy cover and identified to species all trees and shrubs within the subplots. I used both a clinometer and a laser rangefinder to estimate canopy height and an angle gauge from plot center to estimate stand basal area (Stoddard and Stoddard 1987). I gathered these data during June of 2007 and assumed similar canopy and ground cover composition for the following breeding season.

To quantify the abundance of redcedar within the canopy, I took hemispherical photos at 16 locations associated with each plot within each forest patch (Whitmore et al. 1993, Macfarlane et al. 2007). Because eastern redcedar is the only evergreen present at these study sites, I took all hemispherical photos during the winter months (January, February 2009) to minimize influence of deciduous trees. I used a Nikon Coolpix 8400 equipped with a calibrated fisheye lens and attached it to a leveled tripod placed 0.5m from the forest floor. One photo was taken at each plot center, 5 were taken at 25 m from the center, and 10 were taken at 50 m from the center. To estimate redcedar canopy density, I used WinSCANOPY software to calculate mean openness (percent open sky) estimates for each plot and forest patch (Fig. 2). After gathering these openness estimates, I converted the data to percent canopy cover by subtracting percentages from 100. I next subtracted the overall mean percent canopy cover where no redcedar was present to determine the percent cover in redcedar. Because the photos were taken during the winter and because variance of tree height and density across patches was very small**,** canopy cover contributed by leafless deciduous trees was relatively uniform. In the instances where canopy was comprised either entirely of cedar or zero cedar, I did not apply the post-hoc adjustments to percent canopy cover.

GIS Characterization and Analysis

I imported color aerial photography from the National Agriculture Imagery Program (NAIP; USDA 2003) into a geographic information system (ArcMap 9, ESRI, Redlands, CA, USA) to serve as a base map for survey plot locations and aid in the delineation of forest patch boundaries. To calculate forest patch area, I used the zonal statistics function in the ArcMap Toolbox applied to digitized polygons of forest boundaries visible on the NAIP base map. I used forest patch area calculations in conjunction with the associated plot-level species abundance data to estimate avian density within forest patches.

Statistical Analysis

For exploratory data analysis, I used Spearman's rank correlation to illustrate relationships among environmental variables and avian richness, diversity, and summed regional, combined Partners in Flight (PIF) conservation value ranks (Panjabi et al. 2005). I also calculated the proportion of Neotropical migrant species presence for each survey plot by dividing the number of Neotropical migrant species determined to be breeding on a given plot by the total number (13) of Neotropical migrants found breeding across all plots. For breeding season data, I analyzed estimated density of singing males and vegetation and cover characteristics at the plot scale (n = 25). To examine the relative influence of environmental gradients on breeding abundance and distribution, I applied multivariate analyses [Principle Components Analysis (PCA), Canonical Correspondence Analysis (CCA), and Detrended Correspondence Analysis (DCA)] using the XLSTAT 2009 statistics software add-in for Microsoft Excel. I considered all recorded environmental variables during each ordination analysis (Tab. 1). For wintering data, I summed avian survey data at the site scale (n = 7) and compared abundance and community measures (e.g. landbird species richness and combined Partners in Flight Conservation scores) to vegetation characteristics also summarized to that scale. Due to the small number of patches, I present only descriptive statistics for this analysis.

RESULTS

Environmental variables were relatively consistent among the 25 survey plots. Mean tree canopy height ranged 14.83–8.00 m, and litter depth ranged from 2.39–0.75 cm. All other variables represented proportions of either ground cover or vegetation cover, and variance of these variables could therefore be directly compared. Degree of eastern redcedar encroachment was the main difference between sites in terms of proportion of cedar stems as well as proportion of canopy cover attributed to cedar (Tab. 2).

During May–June of 2007 and 2008, I found at least 35 species of passerines, doves, hummingbirds, woodpeckers, and cuckoos breeding in cross timbers forest in the study area (Tab. 3). The five most abundant breeding birds were Northern Cardinal, Blue-Gray Gnatcatcher, Tufted Titmouse, Carolina Chickadee, and Black-and-white Warbler, respectively. The breeding bird assemblage included approximately 12 species (34% of total) that reach a western limit of their global breeding range in the cross timbers, of which 9 were Neotropical migrants.

Among breeding birds, there were 13 species of Neotropical migrants and 9 annual residents encountered frequently enough (i.e., they occurred at survey plots for at least 3 weeks during the breeding season) to compare density among plots with various degrees of redcedar encroachment. Figures 3 and 4 illustrate breeding density for six species with a strong response to the proportion of eastern redcedar stems. Species richness (R^2=0.140, P<0.008) and proportion of Neotropical migrants (R^2=0.241, P<0.001) were both higher among plots with low cedar encroachment than those with heavy encroachment (Fig. 5, Fig. 6). Among the 13 migrant species compared, breeding density in response to cedar encroachment was highest in plots with low encroachment for 9 of those species. For two breeding species, Louisiana Waterthrush and Painted Bunting, breeding density was highest in plots that were heavily invaded by redcedar. Breeding density of Great Crested Flycatcher varied by plots irrespective of redcedar cover. In addition, variance in breeding density was higher for Neotropical migrants between plots of low and high cedar encroachment (s = 0.58) than was variance in the breeding density of annual residents that bred in cross timbers forest (s = 0.27).

Together, the F1 & F2 axes of the PCA (Fig. 7) accounted for 49.37% of the variation in the environmental data. The largest, positive eigenvectors (F1 axis) were associated with the proportion of eastern redcedar stems and cedar canopy cover (Tab. 4; Fig. 7). Canopy cover and litter depth had the largest positive eigenvector values for the F2 axis (Tab. 4; Fig. 7). These four variables were determined to have the most explanatory power in terms of the F1 & F2 axes. The F1 & F2 axes of the CCA (Fig. 8) explained 47.96% of the variation in the data. The ordination analysis yielded the largest positive eigenvector values for the same two redcedar variables, while the negative F1 axis was driven by high shrub cover and grass cover (Tab. 5; Fig. 8). The F2 or vertical axis was driven by proportion of redcedar stems and high shrub cover on the positive F2 axis and canopy cover and litter depth on the negative F2 axis (Tab. 5; Fig. 8). Breeding landbird species sorted widely in ordination space, with separation among most generalist foraging resident species (e.g. Tufted Titmouse, Carolina Chickadee) occurring towards the center of the biplot and most canopy and shrub foragers (e.g. Red-eyed Vireo, Kentucky Warbler) being spatially opposed to redcedar metrics. In addition, three species, Brown-headed Cowbird, Louisiana Waterthrush, and Painted Bunting, were spatially associated with redcedar cover. These species were distributed in proximity to redcedar cover in quadrant IV (positive F1 and negative F2) of Figure 8. Black-and-white Warbler, a bark-probing insectivore, was closest to the resident species in ordination space (Fig. 8). Over the course of two field seasons, this species was present at 66% of survey plots including those with moderate to high degrees of redcedar encroachment. In addition to ordination analysis, Figure 9 displays the distribution of the twenty two most commonly encountered landbirds along two axes of forest cover (Fig. 9).

The winter assemblage in 2008 and 2009 was comprised of at least 33 species in cross timbers forest, or 77% of the hypothetical species pool of 43 species. Of the 33 species that occurred across all sites, 52% were Nearctic migrants that winter, but do not breed, in the study area. The top five most abundant birds wintering in the study area were American Robin, Cedar Waxwing, Yellow-rumped (Myrtle) Warbler, Dark-eyed Junco, and Blue Jay (Tab. 6). Winter sampling revealed important differences between 2008 and 2009, notably an irruption of Red-breasted Nuthatches in 2008 that was not repeated in 2009. Neither species richness (R^2=0.213, P=0.297) nor Shannon diversity indices (R^2=0.138, P=0.411) were significantly correlated with cedar cover. In addition, mean species abundances of American Robin ($F_{2,5}$=1.282, P=0.316), Cedar Waxwing ($F_{2,5}$=2.236, P=0.153), and Yellow-rumped Warbler ($F_{2,5}$=0.342, P=0.717), all species presumed to depend heavily on cedar during the winter, were not correlated with the degree of cedar component at the site level.

DISCUSSION

Several of the species I encountered in my survey plots occurred at comparable breeding densities to those previously recorded in much larger, less fragmented forests in the eastern U.S. For example, the Blue-gray Gnatcatcher occupies a wide variety of woodland habitats across much of the United States. Breeding density estimates for Blue-gray Gnatcatcher range from as high as 33.1 territorial males/10 ha in hardwood swamp forests in South Carolina (Strom 1983), to 7.1 territorial males/10 ha in blue oak woodland in central California (Williams 1979), to as low as 4.5 males/10 ha in pinyon-juniper woodlands in Utah (Salamacha 1984). The breeding density I estimated (4.34/10 ha) was similar to breeding density estimates from pinyon-juniper woodlands. However, breeding density of this species dropped off significantly in forests with intermediate to high degree of cedar encroachment (Figs. 3 & 4).

Heinen and O'Connell (*in press*) have demonstrated that a ground-nesting warbler species such as Kentucky Warbler and Black-and-white Warbler are occurring in cross timbers forests at comparable densities to those across the species' ranges but with variable responses in breeding densities in relation to increased redcedar cover. Likewise, canopy-nesting species such as Summer Tanager, Red-eyed Vireo, and Great Crested Flycatcher showed similar densities as elsewhere across the species' ranges. Again, responses in breeding density varied between species as eastern redcedar increased. James and Neal (1986) reported breeding density estimates for Summer Tanager across different regions of Arkansas, much nearer the center of this species breeding range. Estimates from upland habitats ranged from 0.75 to 2.5 males/10 ha, whereas estimates from bottomland forests ranged from 0.25 to 3.0 males/10 ha. I recorded an estimated 2.3 male Summer Tanagers per 10 ha in forests with low cedar encroachment versus only 0.6 males/10 ha in patches with intermediate to high degree of cedar encroachment. Breeding densities of Red-eyed Vireo have been shown to vary greatly by habitat type as well as over time. Densities as low as 0.2 pairs/ 10 ha have been recorded in pasture or shrub-dominated habitats with scattered trees (Graber et al. 1985), while densities as high as 16 pairs/10 ha have been recorded in New Hampshire (Robinson 1981) and 10 pairs/ha in oak-maple forests in Illinois (Kendeigh 1982). Kendeigh also noted a more than 3-fold difference between highest and lowest densities over a 50-year interval in forested habitats in Illinois. Upland forest densities over this time ranged from 1.8 to 6.2 pairs/10 ha, while densities from bottomland forests ranged from 1.7 to 5.9 pairs/10 ha. I encountered Red-eyed Vireos on 32% of survey plots in 2007 but in only 16% of surveys the following year. However, I estimated similar breeding densities of 1.7 territorial males/10 ha in forest with a low degree of cedar encroachment in 2007 and 1.4 territorial males/10 ha in 2008 (Fig 3; Fig. 4). These results suggest that if cedar has not significantly invaded the canopy, these forests may support healthy densities of Summer Tanager and Red-eyed Vireo. Great Crested Flycatcher densities, although comparable to elsewhere across the species' range, did not appear to be significantly influenced by the presence of cedar. This was surprising considering the species' preference for tall broadleaf forest throughout the rest of its range.

In contrast to the aforementioned Neotropical migrant songbird species, the cross timbers forests of central Oklahoma represent the core range of Painted Bunting breeding distribution. While this species is absent from much of the broadleaf forests of the eastern U.S., several

Breeding Bird Censuses from this species' disjunct breeding population in eastern Georgia and South Carolina have yielded a mean density estimate of 0.82 pairs/10 ha ± 2.8 SE (Hamel et al. 1982). A similar estimate of 0.75 males/10 ha was reported for individuals using clonal persimmon in northwest Arkansas (Shugart and James 1973), which is very near the core of this species' distribution. Over two breeding seasons and across all patches (n=50), I estimated a breeding density of 0.29 males/10 ha in forest with low cedar encroachment, 0.91 males/10 ha in forest with intermediate cedar encroachment, and 1.14 males/10 ha in forest with high cedar encroachment.

The use of cedar as food by wintering birds is also an important component in understanding the spread of this invasive tree. For example, Cedar Waxwing populations in the western U.S. displayed positive regional population trends attributed to winter exploitation of the fruiting invasive plant, Russian olive (*Elaeagnus angustifolia)* (Alcorn 1988, Witmer 1996a). Very little is known about the ecological effects of Cedar Waxwings as dispersers, but because they are a primary disperser of juniper fruits (Holthuijzen and Sharik 1985, Chavez-Ramirez and Slack 1994, Witmer 1996a) and are abundant winter residents in Oklahoma, waxwings may be significantly contributing to the spread of eastern redcedar. Previous research has also demonstrated that American Robins will often exhibit a foraging preference for invasive plant species over native plants (LaFleur et al. 2007). Germination rates of eastern redcedar seeds were 1.5-3.5 times higher when passing through the digestive tracts of Yellow-rumped Warblers and Cedar Waxwings than seeds that were manually stripped of their pulp (Holthuijzen and Sharik 1985).

Some over-wintering passerines may benefit from the spread of eastern redcedar. American Robin and Eastern Bluebird abundances have been shown to increase unimodally with highest abundances occurring at intermediate degrees of encroachment. Because I surveyed relatively intact forest patches, I was not able to adequately sample Eastern Bluebird, a species that tends to favor open spaces or forest edges. However, American Robin abundance across two winters and across all sites (n=14) showed highest abundances in patches heavily invaded by cedar. Cedar Waxwing, Ruby-crowned Kinglet, and Yellow-rumped Warbler have all been shown to depend heavily on cedar berries for sustenance during the winter. Although eastern redcedar may provide a vital food source for some species during the winter, recent findings suggest that some songbirds captured in oak-dominated cross timbers forest patches during the winter displayed higher body condition index based on fat scoring than those captured in cedar-dominated patches (Van Els 2009).

These results provide insight into the conservation value of the cross timbers forests. However, more demographic research needs to be done in order to quantify population statuses of these species, especially those that are listed as conservation concern species. Because these forests often represent the westernmost boundary of potential nesting habitat for eastern forest songbirds, it will be important to quantify nesting success, survivorship, return rates, etc. in order to determine if redcedar is in fact influencing these variables and to determine if these populations are acting as sources or sinks. Equally interesting is the potential positive influence cedar encroachment may be having on some over-wintering forest songbirds. Future conservation effort and decision-making within this highly diverse ecoregion must be sure to acknowledge the costs and benefits associated with issues related to both the breeding and wintering bird communities.

The “peripheral sink hypothesis” (Lomolino et al. 2006) predicts that populations near the edge of species distributions function as sinks (Pulliam 1988). Because the cross timbers currently represents the western-most limits of breeding distribution for several songbird species, it presents an opportunity to test this hypothesis and assess the degree to which local factors such as invasion by eastern redcedar may influence demographics. Due to potential range contraction for multiple species that could occur with forecast changes in climate and land cover, ecological investigations at the edge of species ranges take on greater prominence. For example, of the 35 species found breeding in cross timbers forests, at least 34% are predicted to experience significant range contractions as a result of global climate change (Price 2002). One model developed by the Canadian Climate Center predicted that several of the Neotropical migrant species we determined to be fairly common breeding residents of the cross timbers (i.e. Red-eyed Vireo, Kentucky Warbler, Louisiana Waterthrush, Summer Tanager, and Indigo Bunting) as well as some year-round resident species (i.e. Carolina Chickadee and Field Sparrow) could be extirpated from Oklahoma in the near future (Price 2002). Given the potential for rapid turnover in cross timbers bird communities, close monitoring of this unique forest resource, and the species it supports, is warranted.

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Table 1. Mean plot-level environmental variables included in the ordination analyses.

Environmental Variable	Abbreviation
Canopy Height (meters)	CanHt
Proportion of Canopy Cover	CanCvr
Proportion of Eastern Redcedar Stems	ERCstms
Proportion of Eastern Redcedar Canopy Cover	ERCcvr
Litter depth (cm)	LitDpth
Proportion of low understory cover (≤ 2 m)	LwShrb
Proportion of high understory cover (>2 m, ≤ 5 m)	HghShrb
Proportion of bare ground cover	Bare
Proportion of rock ground cover	Rock
Proportion of grass ground cover	Grass
Proportion of moss ground cover	Moss
Proportion of herbaceous ground cover	Herb
Proportion of wood ground cover	Wood
Proportion of leaf ground cover	Leaf

Table 2. Variance among patches and plots for each vegetation metric recorded in the field. Highest values for variance (marked with asterisks) are consistent among patches and plots for both of the metrics with the highest calculated variances.

Metric	Variance Among Patches	±Std Err	Variance Among Plots	±Std Err
Mean canopy cover	0.013	0.005	0.027	0.005
Mean ERC cover	*0.047	0.018	*0.077	0.015
Mean low shrub cover	0.017	0.006	0.033	0.007
Mean high shrub cover	0.005	0.002	0.013	0.003
Mean bare ground	0.002	0.001	0.006	0.001
Mean rock	0.001	0.000	0.003	0.001
Mean grass	0.010	0.004	0.022	0.004
Mean moss	0.001	0.000	0.003	0.001
Mean herbaceous	0.006	0.002	0.011	0.002
Mean wood	0.001	0.000	0.005	0.001
Mean leaf litter	*0.016	0.006	*0.038	0.008
Mean canopy height (m)	4.429	1.674	9.278	1.856
Mean litter depth (cm)	0.497	0.188	0.701	0.140

Table 3. Mean number of individuals per survey plot of the twenty-five most commonly recorded species during breeding season surveys.

Species	#/plot (2007)	#/plot (2008)	Avg #/plot (combined)
Northern Cardinal	0.97	1.12	1.04
Blue-gray Gnatcatcher	1.07	0.85	0.96
Tufted Titmouse	0.89	0.84	0.86
Carolina Chickadee	0.67	0.77	0.72
Black-and-white Warbler	0.55	0.51	0.53
Indigo Bunting	0.39	0.46	0.43
Field Sparrow	0.42	0.42	0.42
Red-bellied Woodpecker	0.31	0.33	0.32
Carolina Wren	0.22	0.35	0.28
Yellow-billed Cuckoo	0.15	0.35	0.25
Summer Tanager	0.27	0.23	0.25
Blue Jay	0.11	0.39	0.25
Great Crested Flycatcher	0.21	0.24	0.23
Painted Bunting	0.17	0.27	0.22
Kentucky Warbler	0.23	0.18	0.20
Louisiana Waterthrush	0.26	0.14	0.20
Red-eyed Vireo	0.19	0.19	0.19
Brown-headed Cowbird	0.16	0.13	0.15
White-eyed Vireo	0.11	0.17	0.14
Downy Woodpecker	0.11	0.13	0.12
Prothonotary Warbler	0.11	0.08	0.09
Northern Parula	0.06	0.09	0.07
Mourning Dove	0.04	0.05	0.04
Hairy Woodpecker	0.05	0.03	0.04
Brown Thrasher	0.03	0.03	0.03

Table 4. Eigenvector values for the first four explanatory axes (F1-F4) as generated during the PCA ordination analysis. Axes F1 and F2 are displayed in Figure 7. Eigenvectors for the F1 and F2 axes with the most positive and negativ values are marked with asterisks.

	F1	F2	F3	F4
ERCstms	*0.391	-0.191	-0.268	0.021
ERCcvr	*0.395	-0.084	-0.352	-0.176
CanHt	-0.273	0.030	-0.023	-0.625
CanCvr	-0.059	*0.529	-0.286	0.053
LitDpth	-0.072	*0.459	0.290	-0.081
LwShrb	*-0.379	-0.270	-0.054	-0.168
HghShrb	-0.220	*-0.389	0.272	-0.092
Bare	0.287	-0.278	0.109	0.078
Rock	0.162	-0.100	0.593	0.026
Grass	-0.227	-0.095	0.021	0.681
Moss	0.301	0.106	0.383	-0.209
Herb	*-0.291	*-0.310	-0.214	-0.085
Wood	-0.283	0.195	0.071	0.103

Table 5. Eigenvector values for the first four explanatory axes (F1-F4) as generated during the CCA ordination analysis and displayed in Figure 8. Eigenvectors for the F1 and F2 axes with the most positive and most negative values are marked with asterisks.

	F1	F2	F3	F4
ERCstms	*0.215	*0.089	-0.130	-0.037
ERCcvr	*0.239	0.052	-0.106	-0.021
CanHt	-0.067	-0.045	-0.017	0.029
CanCvr	-0.007	*-0.174	0.004	0.022
LitDpth	-0.012	*-0.111	-0.020	0.047
LwShrb	-0.108	0.013	0.031	-0.034
HghShrb	*-0.135	*0.133	0.044	0.054
Bare	0.196	0.021	-0.011	0.043
Rock	-0.107	0.042	-0.120	-0.011
Grass	*-0.151	-0.056	0.028	-0.132
Moss	-0.106	0.012	-0.085	0.067
Herb	-0.066	0.061	-0.024	0.031
Wood	-0.121	-0.004	0.007	0.068
Leaf	0.172	0.015	0.040	0.056

Table 6. Mean number of individuals of the twenty-five most commonly encountered landbird species during winter surveys, sorted by decreasing combined average abundance.

Species	**#/survey (2007–2008)**	**#/survey (2008–2009)**	**combined average (2007–2009)**
American Robin	32.10	24.67	28.38
Cedar Waxwing	12.78	15.00	13.89
Yellow-rumped Warbler	11.76	15.90	13.83
Dark-eyed Junco	8.19	10.52	9.36
Blue Jay	3.86	3.90	3.88
Carolina Chickadee	2.33	3.71	3.02
Tufted Titmouse	2.52	3.43	2.98
Northern Cardinal	1.95	2.81	2.38
American Crow	1.62	2.44	2.03
Carolina Wren	1.48	2.05	1.76
White-throated Sparrow	1.05	1.81	1.43
Spotted Towhee	0.81	1.52	1.16
Northern Flicker	0.90	1.29	1.10
Red-breasted Nuthatch	1.76	0.33	1.05
Red-bellied Woodpecker	1.00	0.95	0.98
Hermit Thrush	0.71	1.14	0.93
Downy Woodpecker	0.95	0.62	0.79
Ruby-crowned Kinglet	0.86	0.48	0.67
White-breasted Nuthatch	0.43	0.38	0.41
Yellow-bellied Sapsucker	0.38	0.29	0.34
Red-headed Woodpecker	0.10	0.52	0.31
American Tree Sparrow	0.24	0.29	0.27
Fox Sparrow	0.19	0.33	0.26
Hairy Woodpecker	0.24	0.20	0.22
Golden-crowned Kinglet	0.05	0.19	0.12

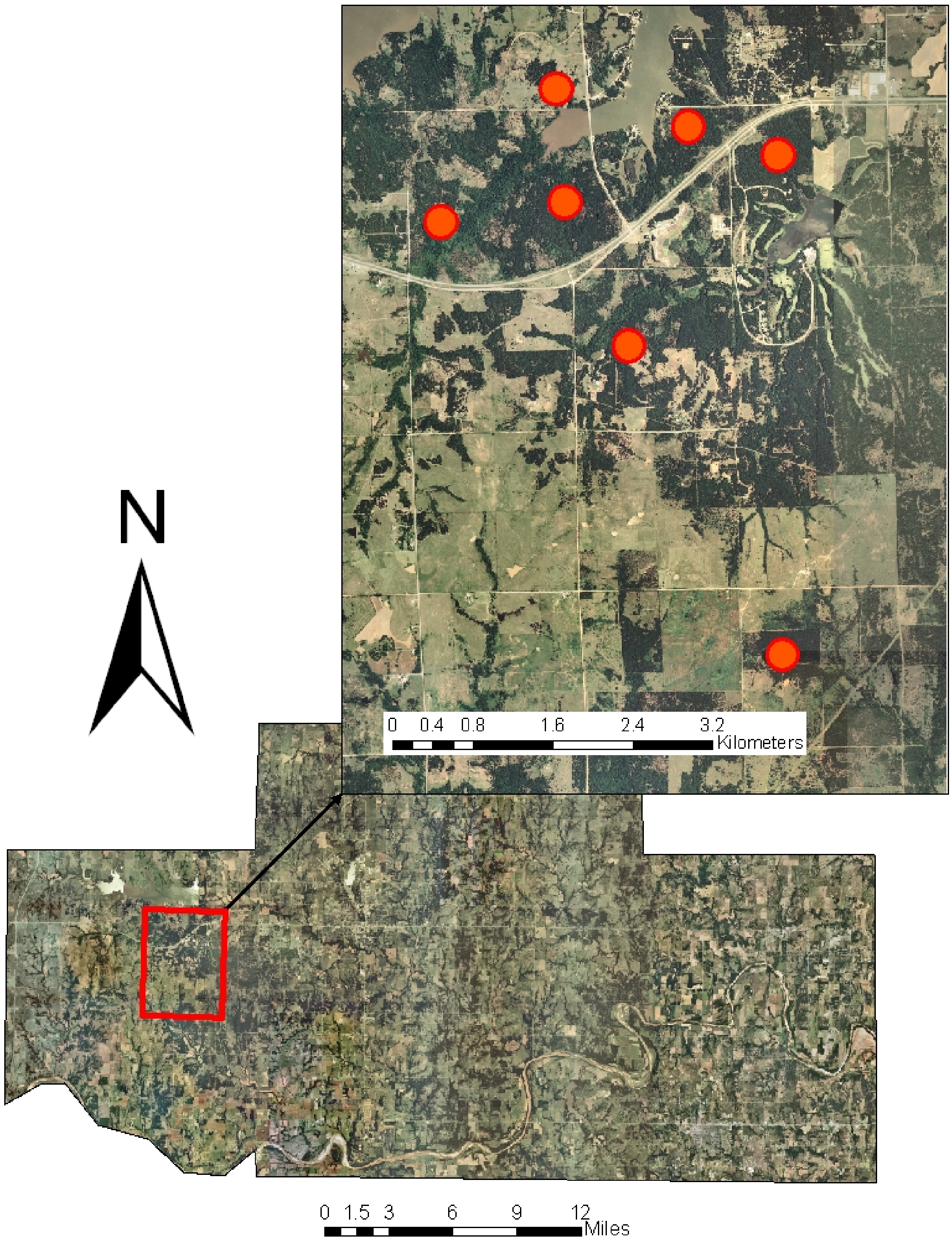

Figure 1. Survey locations for study of cross timbers songbirds in Payne County, OK.

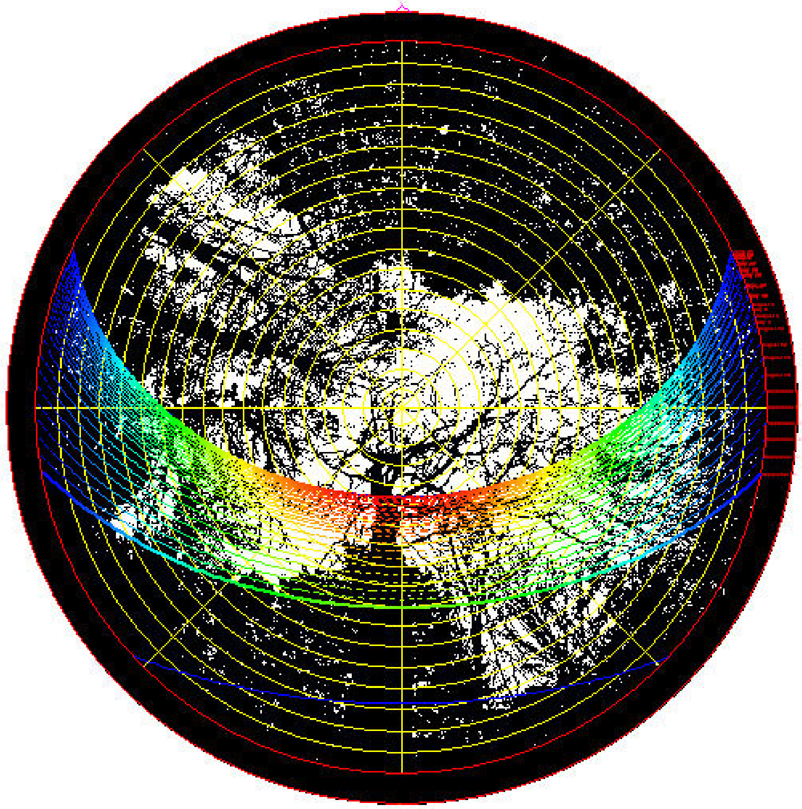

Figure 2. Example of hemispherical canopy photography used to quantify eastern redcedar cover in the forest canopy. In program WinSCANOPY, color photographs are converted to high contrast black and white to facilitate quantification of total leaf cover.

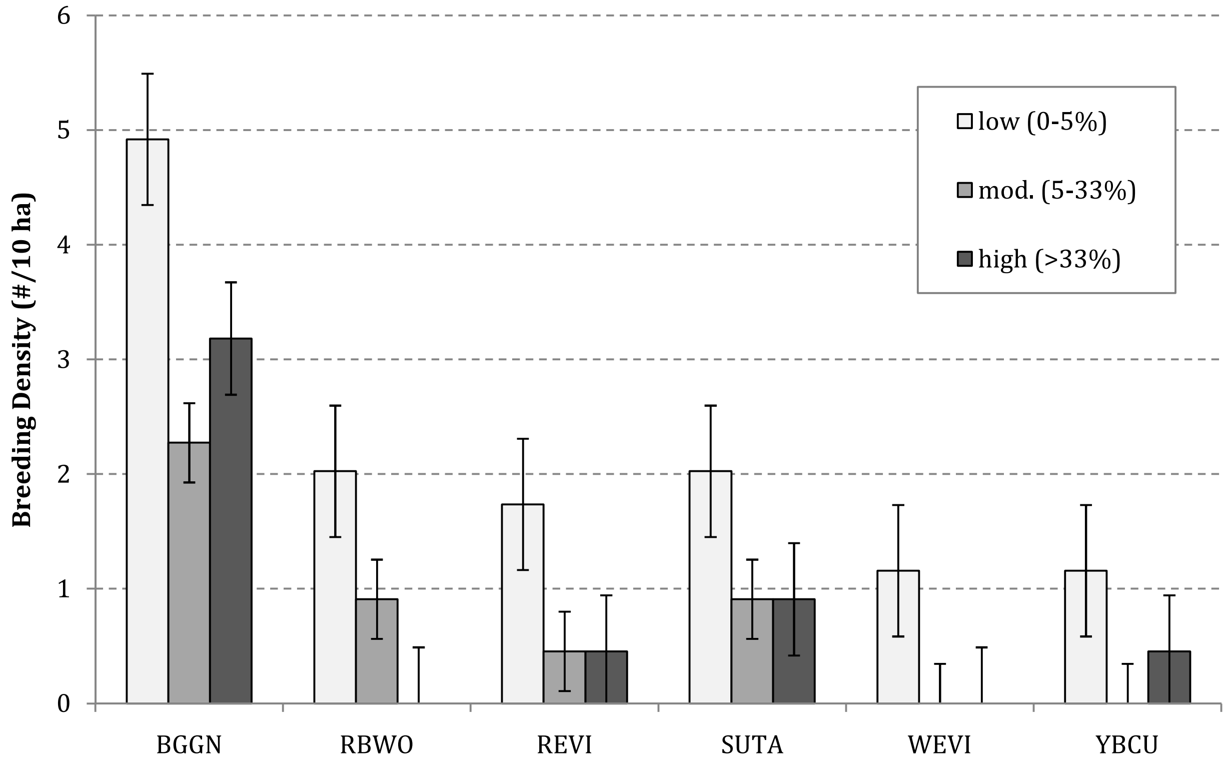

Figure 3. Estimated breeding densities (mean±SE) for six landbird species within 3 broad categories of cedar encroachment within cross timbers forest survey plots in 2007. Cedar encroachment was based on mean proportion of redcedar stems relative to all other tree species present at the survey plot.

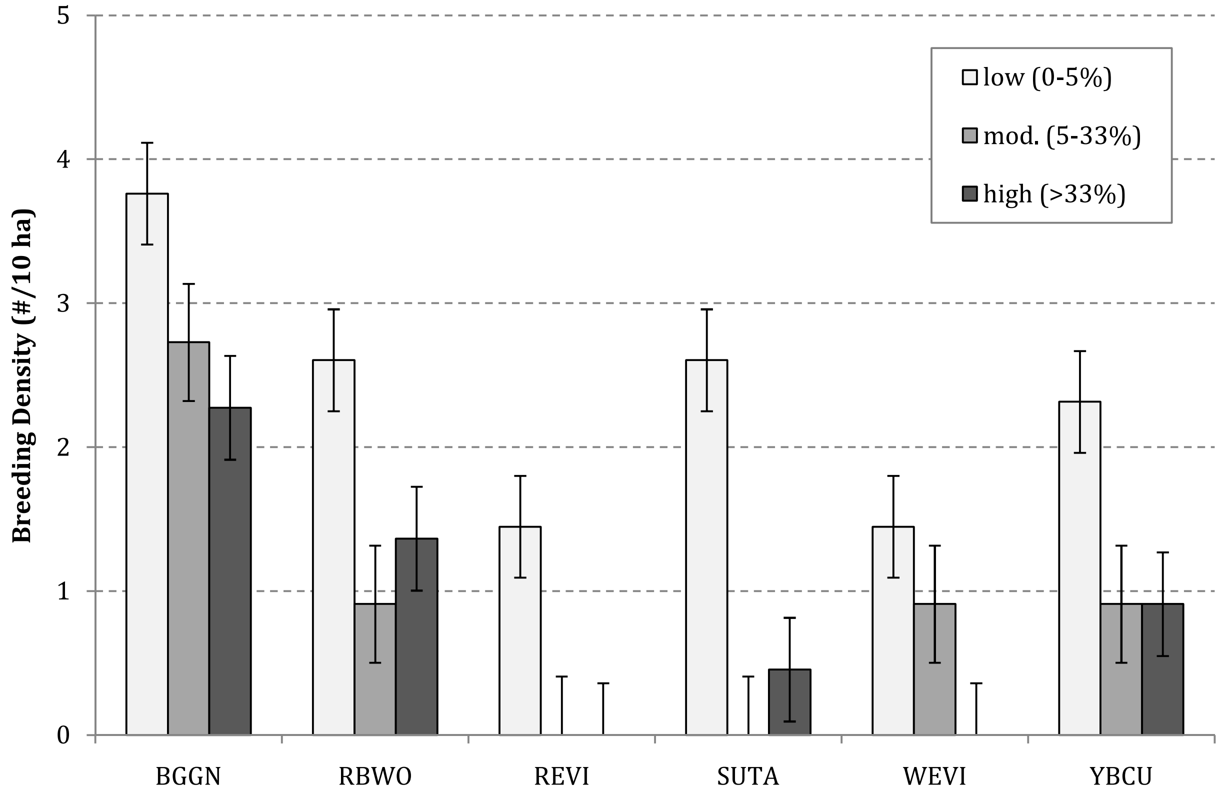

Figure 4. Estimated breeding densities of six landbird species within 3 broad categories of cedar encroachment within cross timbers forest survey plots in 2008. Cedar encroachment was based on mean proportion of redcedar stems relative to all other tree species present at the survey plot.

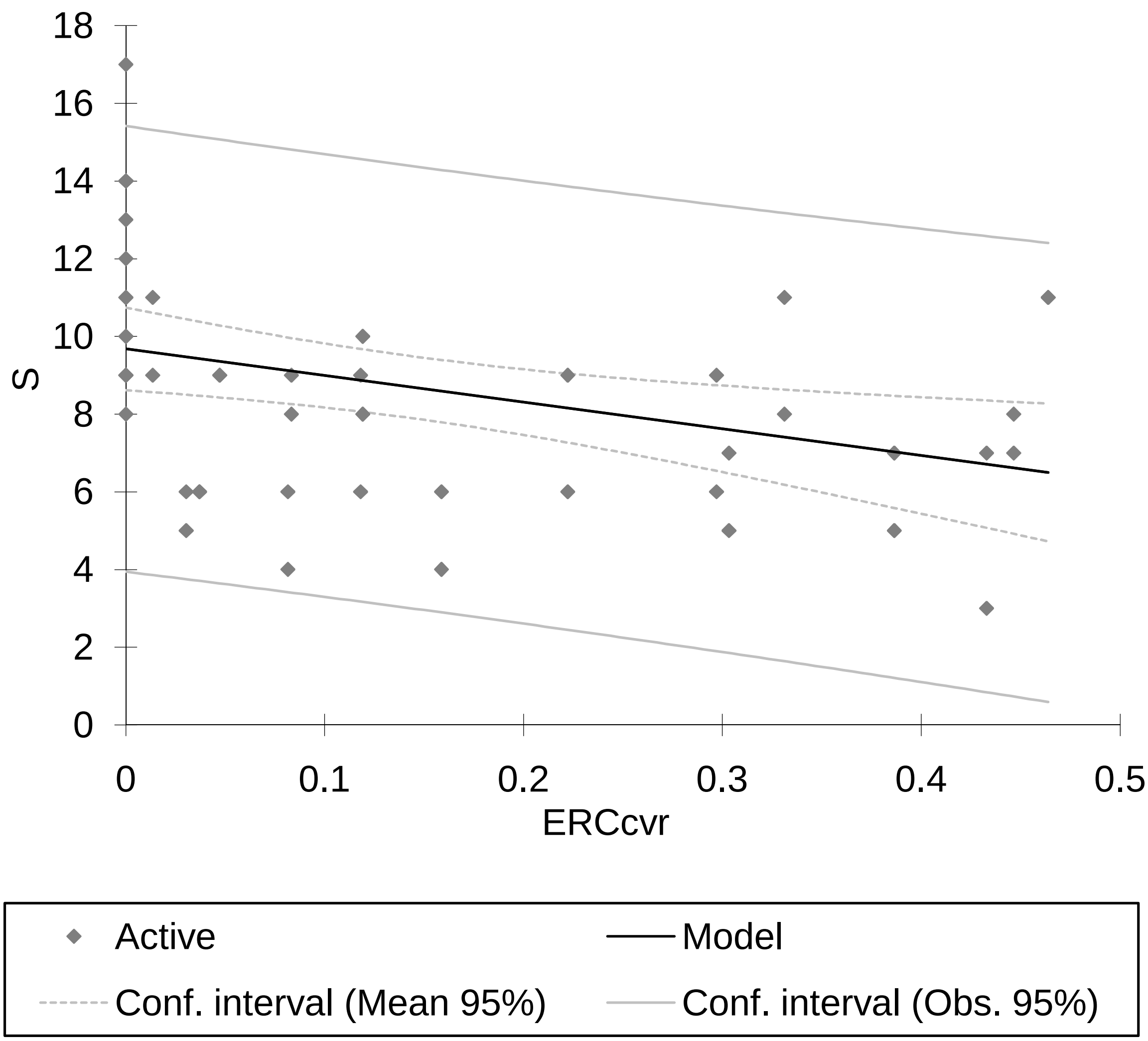

Figure 5. Linear regression of landbird richness (S) by mean proportion of canopy cover at survey plots attributed to eastern redcedar (ERCcvr). R^2=0.140, P<0.008.

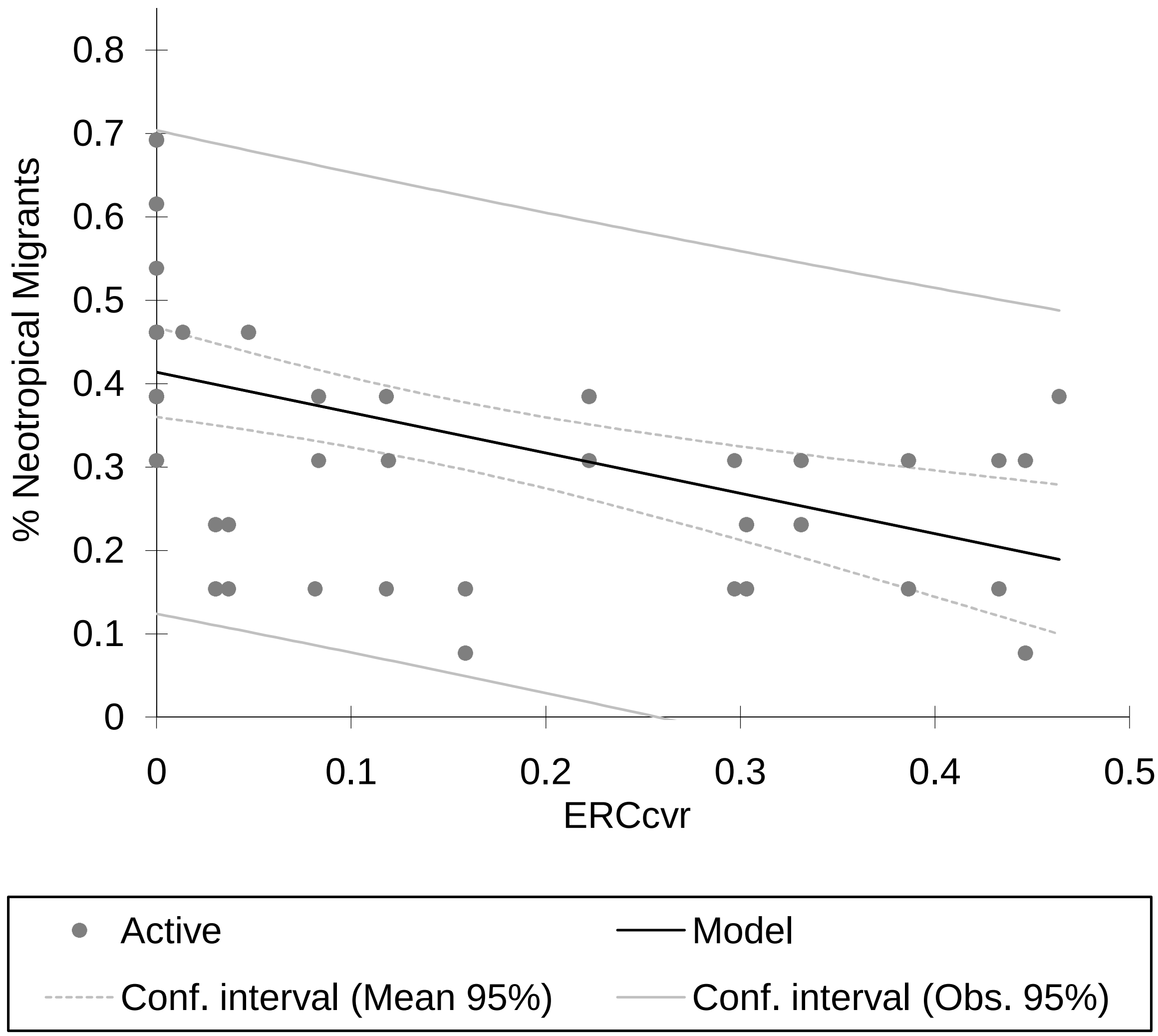

Figure 6. Linear regression of % Neotropical migrant species by mean proportion of canopy cover at survey plots attributed to eastern redcedar (ERCcvr). R^2=0.241, P<0.001.

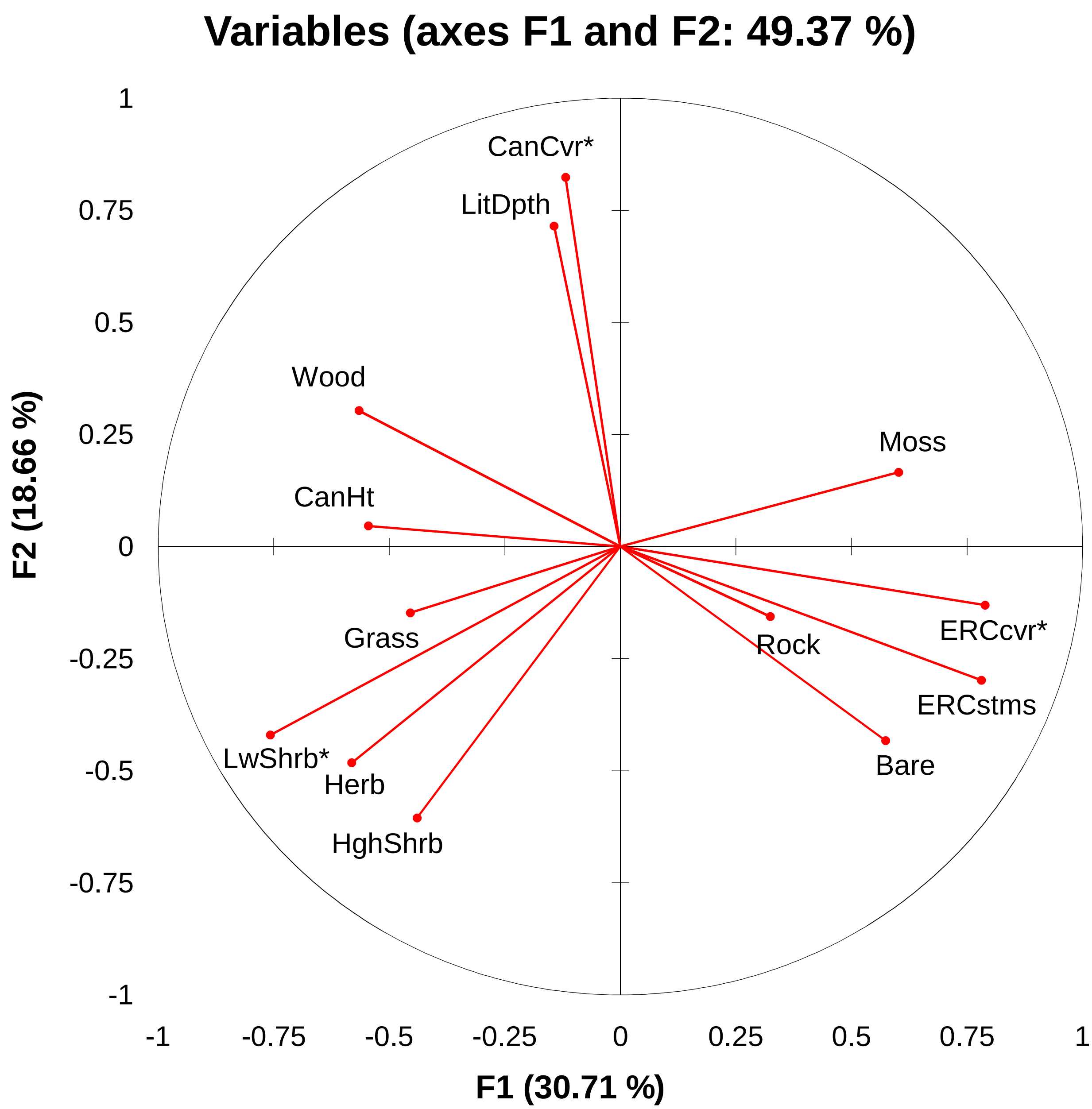

Figure 7. Principle Components Analysis of the thirteen environmental variables recorded at the sub-plot levels of all 25 survey plots in cross timbers forests. Variables with the most explanatory power are marked with asterisks.

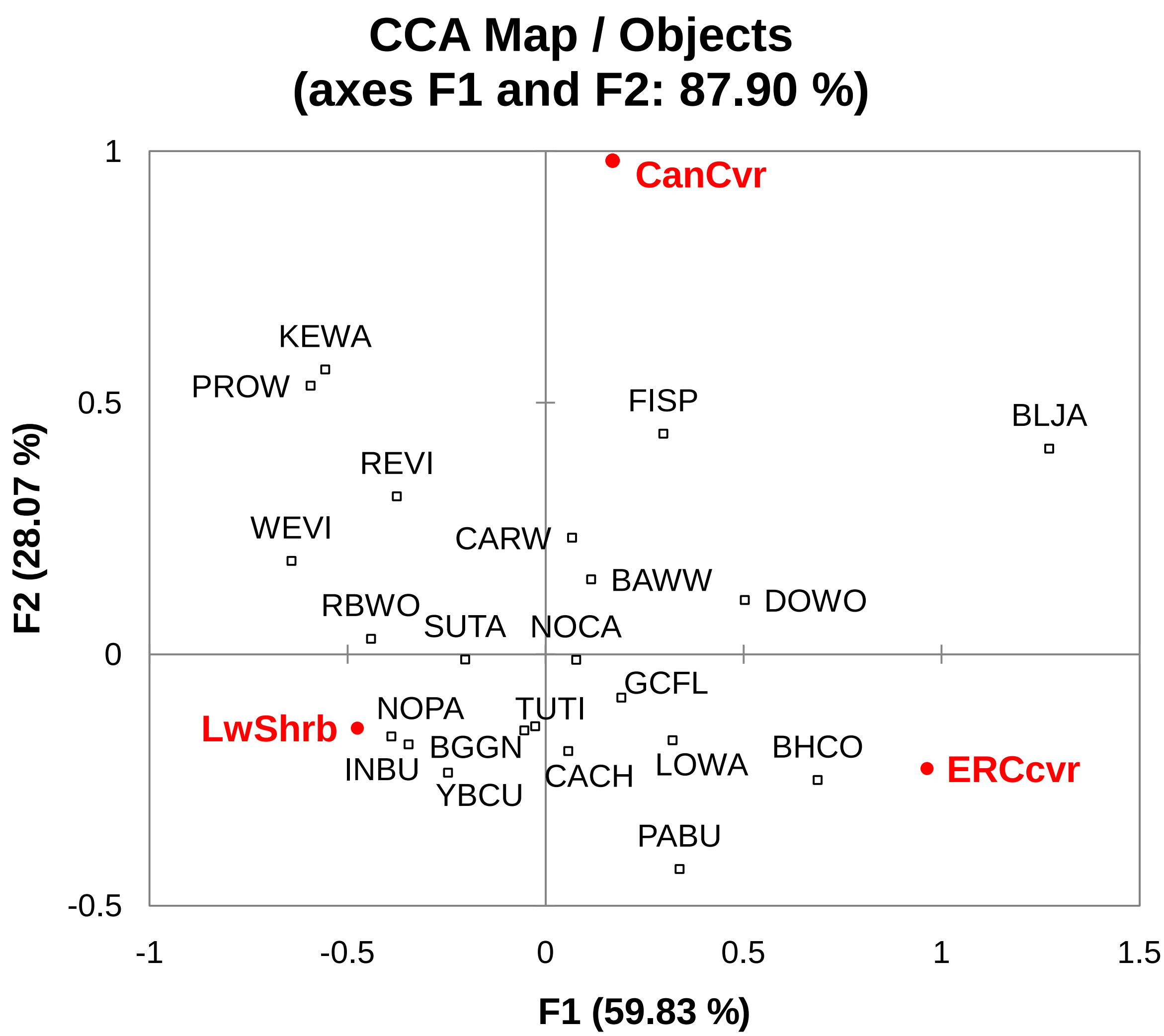

Figure 8. Canonical Correspondence Analysis of 3 environmental variables (proportion of canopy cover, proportion of eastern redcedar cover, and proportion of low shrub cover) related to abundance of 20 breeding birds in cross timbers forest.

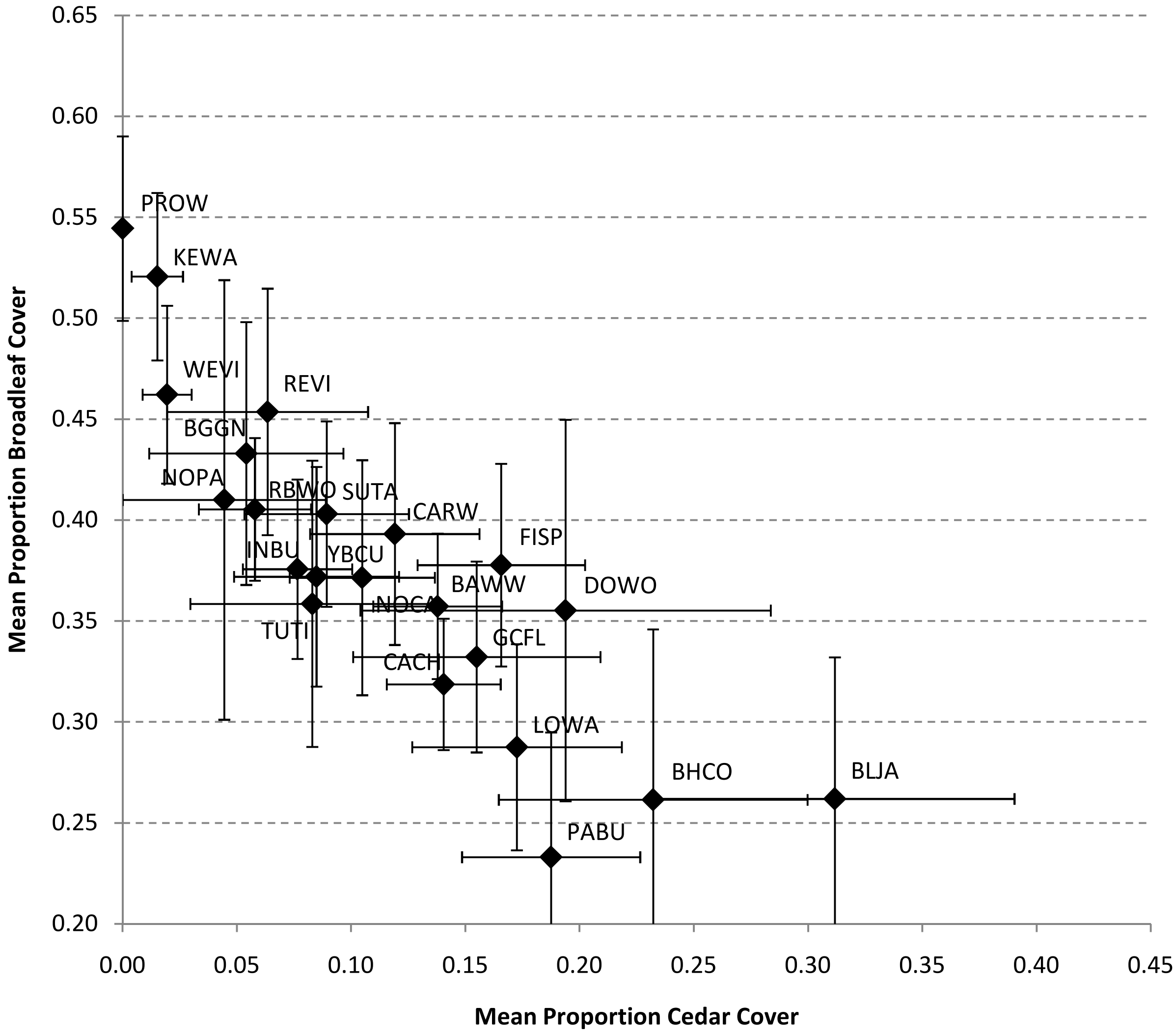

Figure 9. Twenty two of the most commonly encountered landbirds plotted along two axes of forest cover. Horizontal error bars represent the range of redcedar cover over which the species occurred at greater than its mean density among all plots; vertical error bars represent the range of broadleaf cover over which the species occurred at greater than its mean density among all plots.

CHAPTER III

SONGBIRD ASSEMBLAGES ACROSS A GRADIENT OF FOREST IN THE CROSS TIMBERS REGION

INTRODUCTION

Stressors associated with urbanization can influence distribution and abundance of native birds (Pidgeon et al., 2007). For example, urbanization often results in a net loss of native vegetation, an increase in habitat fragmentation, and a decrease in vertical stratification (Crooks et al. 2001, Blewett and Marzluff 2005, Zanette et al. 2005). As a result, synanthropic species (e.g., European Starling [*Sturnus vulgaris*]) that might have otherwise found native forest patches unsuitable will colonize newly disturbed areas (Gering and Blair, 1999). Blair (2004) demonstrated an overall decline in nest predation rate for tree-nesting species such as Northern Cardinal (*Cardinalis cardinalis*) and American Robin (*Turdus migratorius*) along an increasing urban gradient, and relatively high nest success for these species may contribute to populations of synanthropic species in urban areas (Gering and Blair, 1999). In contrast, native habitat specialists (e.g., forest ground-nesting species) are often eliminated completely from urban forests (O'Connell et al. 2000).

In addition to structural and compositional changes, native ecosystem processes can also be disrupted in urban environments. In the U.S. Southern Plains, for example, humans have largely eliminated fire in urbanizing landscapes, and this has led to the proliferation of eastern redcedar (*Juniperus virginiana*) in remnant cross timbers forest patches and upland grasslands (Coppedge et al. 2001, Chapman et al. 2004, Brooks 2008, McKinley and Blair 2008). This native, though invasive, juniper has degraded habitat for grassland birds by converting tallgrass and mixed-grass prairies to shrublands (Brown and Archer 1999, Rosenstock and Riper 2001, Barth 2002, Engle et al. 2008). Redcedar encroachment in the mid-story of forest patches has also become widespread, potentially influencing the abundance and distribution of wintering birds (Van Els 2009). At least one study (Heinen and O'Connell, *in press*) also demonstrated that the density of some forest-breeding songbirds was negatively correlated with eastern redcedar cover in cross timbers forest.

Across much of central Oklahoma, a broad, fire-dependent mosaic of cross timbers forest and tallgrass prairie marks the transition between forest and grassland biomes (Duck and Fletcher 1943). Cross timbers forest patches are dominated by a low (< 18 m), continuous canopy of post (*Quercus stellata*) and blackjack oak (*Q. marilandica*). Additional canopy species include eastern redcedar, pecan (*Carya illinoensis*), hackberry (*Celtis occidentalis*), and cottonwood (*Populus deltoides*), the latter largely limited to riparian areas. Understory cover in these forest patches varies with the frequency and intensity of fire (Clark et al. 2005), and may include buckbrush (*Symphoricarpos orbiculatas*), briars (*Smilax* spp.), and poison ivy (*Toxicodendron radicans*) as well as regenerating canopy species.

Over the past century, dramatic changes have occurred across the cross timbers landscape in Oklahoma, resulting primarily from fire suppression and agricultural and urban development. To monitor ongoing changes in this landscape and promote conservation management for native birds, Partners in Flight has identified the Oaks & Prairies Bird Conservation Region (BCR; Fig. 1) as a management region extending from southeastern Kansas to central Texas (Panjabi et al. 2005).

Modern human settlement of the Oklahoma portion of the Oaks and Prairies BCR reflects the rapid population influx associated with the land openings of 1889-1907 (USGenWeb Project). In addition to thousands of farms and ranches established immediately following the Land Runs, rapid urban development also occurred. For example, Oklahoma City and Guthrie are estimated to have grown in population from zero to 10,000 on the day of their founding (Howard 1889).

Despite Oklahoma's relatively low human population density (approx 20/km^2 versus a national average of 33/km^2; US Census Bureau 2008) and importance for agricultural production, cities in Oklahoma have rapidly increased in population size and area in recent years. For example, 15 of 20 counties contained within or partially overlapping (>10% coverage) the Oaks & Prairies BCR have experienced population increases since 2000. Of the 15 counties, 10 increased by at least 5%, and in 6 of the 10, the increase was at least 10%. In these urbanizing areas, development typically occurs on cleared fields previously used for farming and ranching. Thus, land cover has been dynamic over the past century: the original widespread conversion of cross timbers to agricultural land uses (Farley et al. 2002) has, in urbanizing areas, largely given way to conversion from agricultural to residential land uses. This pattern of development has most likely resulted in a net gain of forest cover in cities in the Oaks and Prairies BCR, as tree species uncommon in or absent from native cross timbers forests (e.g., red oak [*Quercus rubra*], sweetgum [*Liquidambar styraciflua*], tuliptree [*Liriodendron tulipifera*], silver maple [*Acer saccharinum*], loblolly pine [*Pinus taeda*], etc.) have been widely planted in residential areas. These now mature trees in many residential areas provide a leafy canopy that is attractive to some forest-breeding songbirds.

In contrast to the typical scenario of habitat loss and fragmentation due to urbanization, the broad scale conversion of former cross timbers forest and prairie mosaic to relatively full canopies of eastern broadleaf forest types has provided breeding habitat for forest canopy birds such as Great Crested Flycatcher and Red-eyed Vireo. While forest canopy may have increased in urban areas, native understory vegetation remains limiting, potentially barring colonization of ground-nesting and ground-foraging native birds (Jokimaki and Huhta 2000). These urban forests represent a newly realized habitat type uncharacteristic of the region's native forests.

To begin to understand the ecological relationships of songbirds in urban forests within the Oaks and Prairies BCR, I surveyed bird species assemblages and obtained demographic data on select species from 28 plots in and around Stillwater, a city of medium size (2008 pop. est. 47,653; U.S. Census Bureau) in Payne County, OK. The plots were selected along a gradient characterized by increasing impervious surface cover and decreasing canopy cover. My specific objectives were to (1) quantify use of urban forest by breeding songbirds, especially native cross timbers species, (2) assess the degree to which proportions of impervious surface and canopy cover influence use of urban forests by breeding species, and (3) identify other vegetation and site parameters that play an important role in the distribution of these species.

METHODS

Study Area

This study took place within the incorporated limits of Stillwater, Payne County, OK (36° 05' N 97° 12' W). The city of Stillwater encompasses approximately 70 km^2 (US Census Bureau), entirely contained within the Oaks and Prairies BCR. Land cover in Stillwater was approximately 30% herbaceous, 22% low intensity development, 18% developed open space, 10% deciduous forest, 7% medium intensity development, 5% cultivated cropland, 4% high intensity development, and 2% or less each hay/pastureland, open water, and evergreen forest (NLCD 2001).

Study Design

I established 28 sampling plots covering an estimated geographic area of 1200 ha. To sample from the complete gradient of forest cover within Stillwater, I used aerial photographs from the National Agriculture Imagery Program (NAIP; USDA 2003) to identify areas of high, intermediate, and low forest cover. I clustered sampling plots in areas with similar forest cover, road density, and housing density. Within each area, I selected 4 survey plots so that plot centers were separated by at least 250 m. All plots contained multiple classifications of land cover. I surveyed mostly developed open space, deciduous forest, and low-medium intensity development (all included deciduous trees > 5m in height). Approximate forest patch sizes ranged from 1 to 15 ha, and forests were generally dominated by oaks. Plots represented a gradient of urban forest with minimal surrounding urbanization to urban forest patches heavily influenced by urbanization (Fig. 2). I defined urbanization as a ratio of impervious surface per pixel from Multi-Resolution Land Cover data (NLCD 2001) to the sum proportion of all vegetative cover in plots visually estimated in the field.

Breeding Bird Surveys

I sampled birds from the plot centers of each of the 28 sampling plots using repeated point counts. I conducted point counts during early morning hours (0530–0930 CDT) of May and June 2008 under dry conditions with relatively light winds. I followed standard songbird sampling procedures for counts of singing males (Ralph et al. 1995) with some modifications. I counted only those singing males judged to be within 100 m of the plot center and using the habitat, excluding flyovers. I visited survey plots six times during the sampling period and used the average raw abundance per survey as the estimate of abundance for the season. I omitted from analysis all species detected on two or fewer surveys, assuming that species detected on at least three surveys represented individuals on breeding territories.

Vegetation Sampling and Analysis

To quantify vegetation structure and composition at the plots, I established 10m radius subplots, 15m from plot center at 0, 120, and 240º. In these subplots, I made visual estimates of percent ground cover in leaves, grasses, forbs, mosses, rocks, woody debris, and bare soil. I also estimated shrub cover up to 5m (low <2m, high >2m) and total tree canopy cover, and identified to species all trees and shrubs within the subplots. I used both a clinometer and a digital rangefinder to estimate canopy height and an angle gauge from plot center to estimate stand basal area (Stoddard and Stoddard 1987).

GIS Characterization and Analysis

I recorded UTM coordinates for plot centers in the field using a hand held GPS (Garmin Geko 201, Garmin International, Olathe, KS, USA). I used an optical rangefinder to judge distances from the plot center in the field. Using the NAIP photograph (USDA 2003) as a base map in a GIS (ArcMap 9, ESRI, Redlands, CA, USA), I delineated plot boundaries by adding 28 separate polygon feature classes. Within each feature class, I added the previously created 100 m radius circle (polygon shape file) and snapped the center of the circle to the appropriate survey center-point. I then used these polygon features as the input zone features and the degree of canopy and impervious surface data (NLCD 2001) as the input value rasters for performing Zonal Statistics for each plot (ArcToolbox> Spatial Analyst Tools > Zonal > Zonal Statistics). I also specified 'MEAN' as the statistic type in order to generate the average degree (0-100) of canopy cover and impervious surface cover for each of the plots (Fig. 3).

Statistical Analysis

I began statistical analysis of breeding bird data by computing percent abundance and density at the plot level for the most frequent species, as well as for several species of conservation concern. I used multivariate analyses (principle components [PCA; Fig. 4] with canonical correspondence [CCA; Fig. 5]), as well as analysis of variance (ANOVA), Spearman's rank correlation, and linear regression to explore relationships among multiple site and vegetation characteristics (Tab. 1) and various avian response variables. All statistical analyses were conducted using the XLSTAT 2009 statistics software add-in for Microsoft Excel.

RESULTS

During May–June of 2008, I found 43 total species and 34 species of passerines, doves, woodpeckers, and cuckoos using urban forests within the study area (*Appendix*, Tab. 2). The five most abundant species were European Starling (7.2/10 ha), House Sparrow (6.8/10 ha), American Robin (4.0/10 ha), Northern Cardinal (2.8/10 ha), and Blue Jay (2.0/10 ha), respectively. In addition to these abundant, synanthropic species, I discovered multiple forest birds using urban forest patches in Stillwater. These included Red-eyed Vireo, Great Crested Flycatcher, Northern Parula, and Yellow-billed Cuckoo. Among breeding birds, I encountered 22 species frequently enough for comparative analysis of density (territories/plot).

Breeding landbirds sorted predictably in ordination space, with wide separation between synanthropic species (e.g. European Starling) and native forest birds (e.g., Yellow-billed Cuckoo; Fig. 5). Canonical Correspondence Analysis yielded six environmental variables (Tab. 2) that together accounted for approximately 77.5% of the variability in breeding densities. Eigenvalues for both axes 1 and 2 explained 60.06% of the variability (Fig. 5). This relatively high degree of explanatory power indicates close association between species densities and the environmental variables correlated with the first two axes. I interpret axis 1 as positively correlated with amount of impervious surfaces within the plot. This axis illustrates a near polar relationship between imperviousness and an abundance of mature, forest cover on the plot. Axis 2 is correlated positively with woody cover, primarily in small trees and shrubs. From Figure 5, this indicates that native forest species such as Northern Parula and Great Crested Flycatcher used areas with tall trees and open understories (e.g., lawns and other herbaceous vegetation), while others such as Blue-Gray Gnatcatcher and Red-eyed Vireo were associated with tall trees and a well developed woody understory (e.g., increased structural complexity of woody vegetation). The cluster of truly urban-associated species in the study (Western Kingbird, European Starling, Mourning Dove, Northern Mockingbird, House Finch, and House Sparrow) primarily used plots with high degrees of impervious surfaces, few trees, and relatively small amounts of herbaceous and woody cover. These species frequently made use of anthropogenic structures for roosting (e.g., Western Kingbirds perching on utility poles) and/or nesting (e.g., House Sparrows in storm gutters).

Analysis of variance for species' mean territories/plot in 3 categories of % impervious surface yielded significant (P<0.05) differences between groups in over 40% of species (Tab. 3). Analysis of variance for species' mean territories/plot in 3 categories of % canopy cover yielded significant (P<0.05) differences between groups in over 45% of species (Tab. 4). Adjusted breeding species richness was highest among plots with low impervious surface cover (11.67±0.39) and was significantly different and higher ($F_{2,26}$=2.491, P=0.006) than plots with a high degree of impervious surfaces (6.75±0.32; Fig.6). Conversely, adjusted species richness estimates were highest among plots with high % canopy cover (11.20±0.53) and were significantly higher ($F_{2,26}$=5.64, P=0.01) than plots with low % canopy cover (7.33±0.46; Fig. 7). Figure 8 shows the distribution of species along two important axes of habitat cover (impervious surface vs. leaf litter ground cover) as determined by ordination analysis (Tab. 2, Figs. 4 & 5).

DISCUSSION

In total, I observed 43 species of which I judged 22 to be breeding residents. These numbers are similar to urban/residential bird surveys conducted in other parts of North America. For example, Melles et al. (2003) recorded a total of 42 species in Vancouver and Burnaby, British Columbia, with 25 being commonly encountered. Other studies that have focused on native forest patches as islands in a matrix of urban or developed habitat have found greater numbers of breeding residents. For example, Tilghman (1987) encountered 77 species occupying forest patches in Springfield, MA with forest patch size accounting for 77 and 75% of the variability in richness and diversity indices. Considering this, it is not surprising that these very small forest patches within a matrix of urban/residential habitat located along the westernmost limits of most eastern songbird's ranges would not support a high number of species.

Cross timbers forests support a variety of generalist species as well as several specialists. Heinen and O'Connell (*in press*) reported 27 breeding landbird species in cross timbers forest patches near Stillwater, OK. Although species richness estimates for Stillwater's urban forests were comparable to those of the cross timbers forest patches, the avian communities associated with these urban forests were missing some conspicuous elements. For example, foraging and breeding specialists such as Black-and-white Warbler, Louisiana Waterthrush, and Prothonotary Warbler did not occur in urban forests probably due to the lack of continuous understory habitat. The F1 axis of the PCA (Fig. 4) suggests that ground cover (e.g., leaf litter, herbaceous plants, and downed wood) and the amount of understory development (both low and high shrub layers) may be as important as determining community make-up as is canopy cover or proportion of impervious surface. These metrics were the most negatively related to impervious surfaces and bare ground (Tab. 3), and may be important determinants in the probability of use by ground nesting and foraging forest birds. Patches with continuous canopy and understory growth could have also been depauperate of specialists due to relatively small patch sizes. Urban forest patches ranged in size from approximately 1 to 15 ha versus approximately 15 to 150 ha for cross timbers forest patches.

Annual resident species in urban forests varied in their abundance and density relative to rural, cross timbers forest. Differences in breeding densities of notable resident species as compared to those estimated by Heinen (this volume) included densities in urban forests 1.5x lower for Carolina Chickadee (2.02 vs. 2.99/10 ha), 2x higher for Carolina Wren (2.02 vs. 1.02/10 ha), 2.5x higher for Downy Woodpecker (1.12 vs. 0.45/10 ha), 1.3x lower for Northern Cardinal (2.80 vs. 3.57/10 ha), 1.5x lower for Red-bellied Woodpecker (1.01 vs. 1.46/10 ha), and 3.7x lower for Tufted Titmouse (0.90 vs. 3.31/10 ha) than comparable density estimates from cross timbers forests.

In addition to the predictable occurrence of annual residents in Stillwater's urban forest patches, I encountered Neotropical migrants such as Red-eyed Vireo (0.07/survey), Northern Parula (0.11/survey), and Great Crested Flycatcher (0.10/survey) with some consistency, although only at plots with minimal impervious surfaces. Red-eyed Vireo density (0.22/10 ha) was approximately 3.7x lower than was estimated in nearby, rural, cross timbers forest patches. Great Crested Flycatcher density (0.45/10 ha) was 2.1x lower than in rural, cross timbers forests. Other Neotropical migrants encountered in urban forests, such as Blue-gray Gnatcatchers (0.45/10 ha) and Yellow-billed Cuckoos (0.34/ 10 ha) occurred at much lower densities than typical in rural, cross timbers forest. For example, Heinen and O'Connell (in press) estimated a breeding density of Blue-Gray Gnatcatcher in cross timbers forest more than 7.5 times greater than I observed in urban forests.

My results suggest that city parks, forested residential neighborhoods, and other tracts of urban forest can support increased diversity at local scales, and provide habitat for native forest species that use leafy canopies during the breeding season. This leads to questions regarding whether, from a conservation standpoint, such species should be using these habitats. In other words, are these habitats ecological traps? Or are these habitats yielding source or sink populations? While we now know that certain canopy species (e.g., Yellow-billed Cuckoo) will hold territories in urban forest patches, we do not know to what degree these patches are providing quality habitat for those species. Do urban-nesting forest birds have ample foraging opportunities? Are they subject to high rates of nest predation? Relative to territories in rural, cross timbers forests, is cowbird parasitism a greater problem?

The question of whether or not urban habitats are ecological traps is just beginning to receive serious attention in the literature. For example, Leston and Rodewald (2006) showed that Northern Cardinals were attracted to microclimatic features of urban forests, for example, locally increased temperatures during winter associated with dense understory along urban riparian zones. They concluded, however, that while breeding density of Northern Cardinals increased in urban habitats, their populations did not function as ecological traps because the number of nesting attempts, young fledged, and survival rates did not differ between rural and urban forest patches. My data suggest that Northern Cardinal may be a species whose local populations may be functioning as ecological traps, as breeding density was slightly lower (1.3x) in urban forests than rural forests.

Similar work is warranted in urban cross timbers forests. Basic demographic and reproductive success data are needed to determine the quality of urban forest patches for native forest birds. In addition, the possibility (among some species) of attraction to urban forests due to the full canopies often exhibited by urban trees relative to trees in more dense forest should be explored. Better information on the quality of urban forest tracts for native forest birds can provide insight into the conservation and management of forest birds in general, and potentially lead to specific management recommendations that could help urban forests provide a broader spectrum of resources attractive to native species.

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Table 1. Plot- and site-level environmental variables included in ordination analyses.

Environmental Variable	Abbreviation
Canopy Height (meters)	CanHt
Percent Canopy Cover	CanCvr
% Tree Canopy*	Cnpy
% Imperviousness*	Imprvs
Proportion of low understory cover (≤ 2 m)	LwShrb
Proportion of high understory cover (>2 m, ≤ 5 m)	HghShrb
Proportion of bare ground cover	Bare
Proportion of rock ground cover	Rock
Proportion of grass ground cover	Grass
Proportion of moss ground cover	Moss
Proportion of herbaceous ground cover	Herb
Proportion of wood ground cover	Wood
Proportion of leaf ground cover	Leaf

*Mean percent tree canopy and impervious cover plot-level metrics were obtained by MRLC data analysis in ArcGIS. All other metrics were obtained by taking the average of the 3 subplot field estimates.

Table 2. Eigenvalues for environmental variables correlated with the first two axes of Canonical Correspondence Analysis with mean abundance for 22 landbirds in urban forest plots. Eigenvectors for the F1 and F2 axes with the most positive and most negative values are marked with asterisks.

Environmental Variable	Axis 1	Axis 2
Canopy Height (meters)	-0.196	-0.104
Percent Canopy Cover	-0.382*	-0.060
% Imperviousness	0.420*	0.044
Percent low understory cover (≤ 2 m)	-0.335	0.141*
Percent high understory cover (>2 m, ≤ 5 m)	-0.365	0.126
Percent grass ground cover	0.069	-0.124*
Percent bare ground cover	0.360*	-0.010
Percent rock ground cover	0.163	0.032
Percent moss ground cover	-0.265	-0.222*
Percent wood ground cover	-0.381	0.058
Percent leaf ground cover	-0.466*	0.136*
Percent herbaceous ground cover	-0.360	0.068

Table 3. Analysis of Variance results for comparison of landbird breeding density in urban forests in 3 categories of impervious surface cover by plot as calculated using MRLC data in ArcGIS.

			Territories/plot LS Means^{Grp}		
Species	$F_{2,26}$	*P*	Low (0-20%)	Int. (20-40%)	High (>40%)
American Robin	1.162	0.329	1.667	1.250	1.143
Blue-gray Gnatcatcher	7.857	0.002	0.667^{A}	0.000^{B}	0.000^{B}
Blue Jay	2.032	0.152	0.833	0.786	0.250
Brown Thrasher	1.411	0.263	0.333	0.214	0.000
Carolina Chickadee	10.612	< 0.001	1.500^{A}	0.571^{B}	0.125^{B}
Carolina Wren	3.247	0.056	0.833	0.786	0.250
Downy Woodpecker	2.319	0.119	0.667	0.357	0.125
Eastern Phoebe	4.911	0.016	0.333^{A}	0.000^{A,B}	0.000^{B}
European Starling	2.901	0.074	1.500	2.214	3.000
Great Crested Flycatcher	1.563	0.229	0.333	0.143	0.000
Gray Catbird	1.411	0.263	0.167	0.286	0.000
House Finch	1.034	0.370	0.167	0.500	0.500
House Sparrow	8.443	0.002	1.000^{A}	2.214^{A,B}	3.000^{B}
Mourning Dove	1.968	0.161	0.500	0.786	1.125
Northern Cardinal	1.705	0.202	1.167	0.929	0.625
Northern Mockingbird	2.562	0.097	0.500	0.714	1.125
Northern Parula	1.563	0.229	0.333	0.143	0.000
Red-eyed Vireo	4.911	0.016	0.333^{A}	0.000^{A,B}	0.000^{B}
Red-bellied Woodpecker	4.287	0.025	0.667^{A}	0.357^{A,B}	0.000^{B}
Tufted Titmouse	4.545	0.021	0.667^{A}	0.286^{B}	0.000^{B}
Western Kingbird	2.787	0.081	0.000	0.071	0.375
Yellow-billed Cuckoo	9.821	0.001	0.500^{A}	0.000^{B}	0.000^{B}

Table 4. Analysis of Variance results for comparison of landbird breeding density in urban forests in terms of estimated number of territories/plot relative to 3 categories of tree canopy cover by plot as calculated using MRLC data in ArcGIS.

			Territories/plot LS Means^{Grp}		
Species	$F_{2,26}$	P	Low (0-20%)	Int. (20-40%)	High (>40%)
American Robin	0.314	0.733	1.444	1.222	1.200
Blue-gray Gnatcatcher	2.922	0.072	0.000	0.000	0.400
Blue Jay	4.531	0.021	0.333^{A}	0.444^{A,B}	1.100^{B}
Brown Thrasher	0.194	0.825	0.111	0.222	0.200
Carolina Chickadee	4.391	0.023	0.222^{A}	0.556^{A,B}	1.100^{B}
Carolina Wren	4.432	0.023	0.333^{A}	0.556^{A,B}	1.000^{B}
Downy Woodpecker	2.081	0.146	0.222	0.222	0.600
Eastern Phoebe	2.009	0.155	0.000	0.000	0.200
European Starling	5.142	0.013	3.222	1.667	2.000
Great Crested Flycatcher	1.839	0.180	0.000	0.111	0.300
Gray Catbird	0.739	0.488	0.111	0.111	0.300
House Finch	0.597	0.558	0.444	0.556	0.300
House Sparrow	4.561	0.020	3.000^{A}	1.889^{A,B}	1.700^{B}
Mourning Dove	3.537	0.044	1.222	0.556	0.700
Northern Cardinal	2.732	0.085	0.556	1.000	1.100
Northern Mockingbird	5.488	0.011	1.222^{A}	0.667^{A,B}	0.500^{B}
Northern Parula	5.357	0.012	0.000^{A}	0.000^{A}	0.400^{B}
Red-eyed Vireo	0.477	0.626	0.000	0.111	0.100
Red-bellied Woodpecker	4.850	0.017	0.000^{A}	0.333^{A,B}	0.600^{B}
Tufted Titmouse	5.558	0.010	0.000^{A}	0.222^{A,B}	0.600^{B}
Western Kingbird	1.276	0.297	0.222	0.222	0.000
Yellow-billed Cuckoo	0.953	0.399	0.000	0.111	0.200

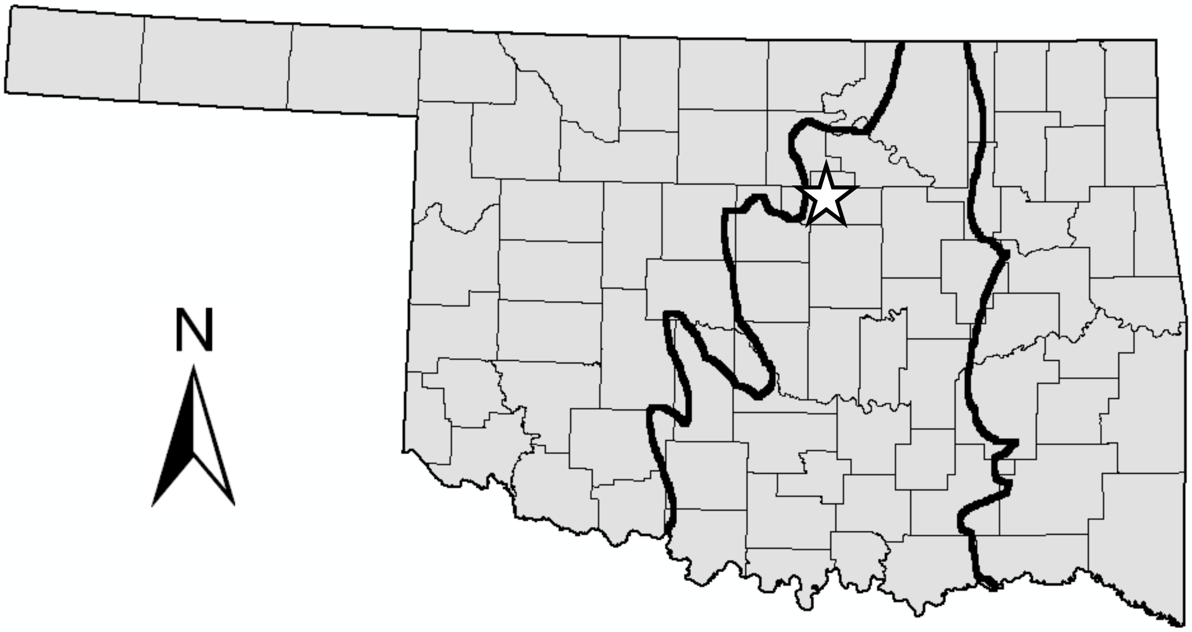

Figure 1. Approximate boundary of the Oaks & Prairies Bird Conservation Region in Oklahoma. The study area in Payne County is indicated by a star.

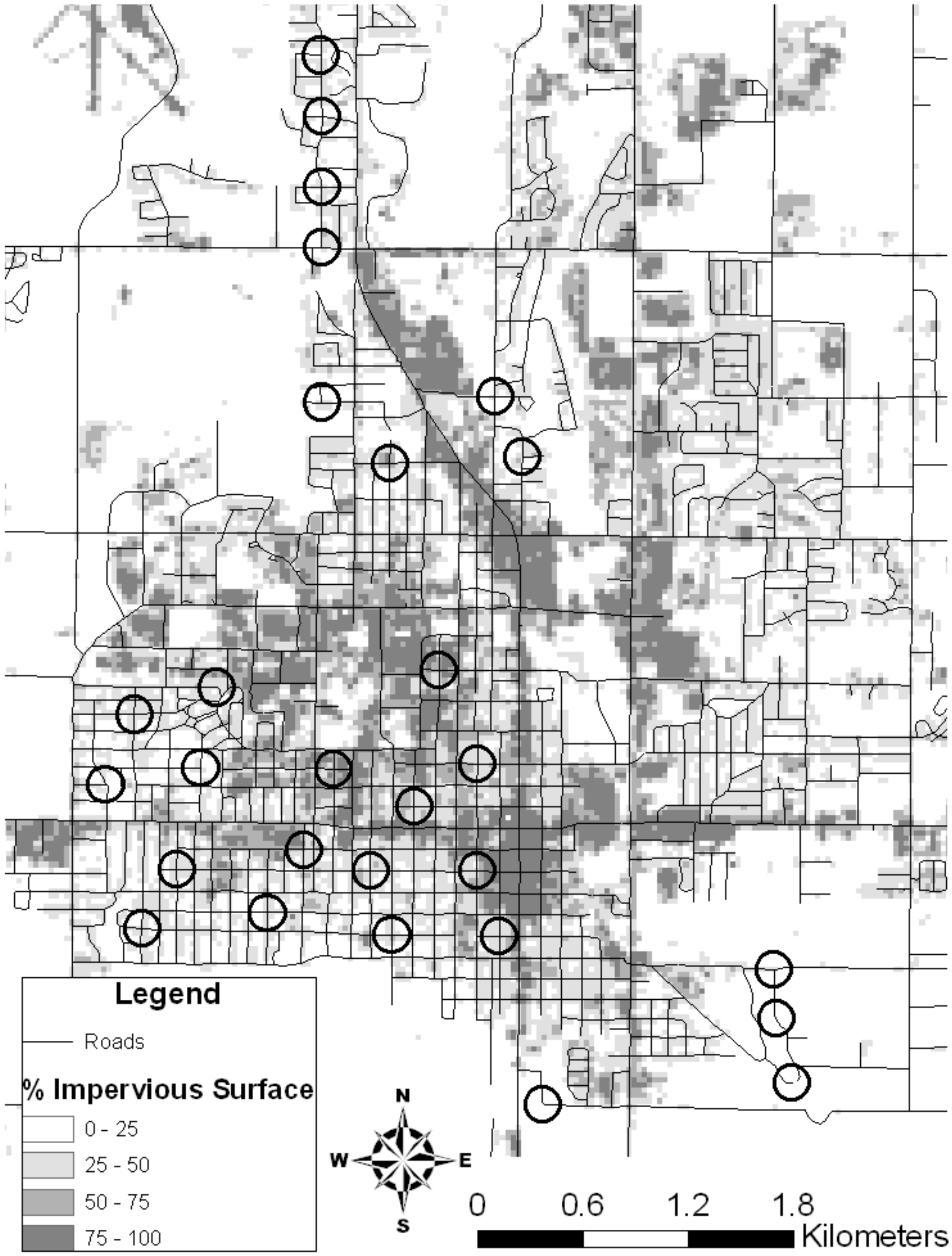

Figure 2. Multi-resolution Land Cover (NLCD 2001) for Stillwater, OK illustrating four categories of impervious surface cover at 30 m resolution. The distribution of 28 sampling plots for breeding birds is indicated.

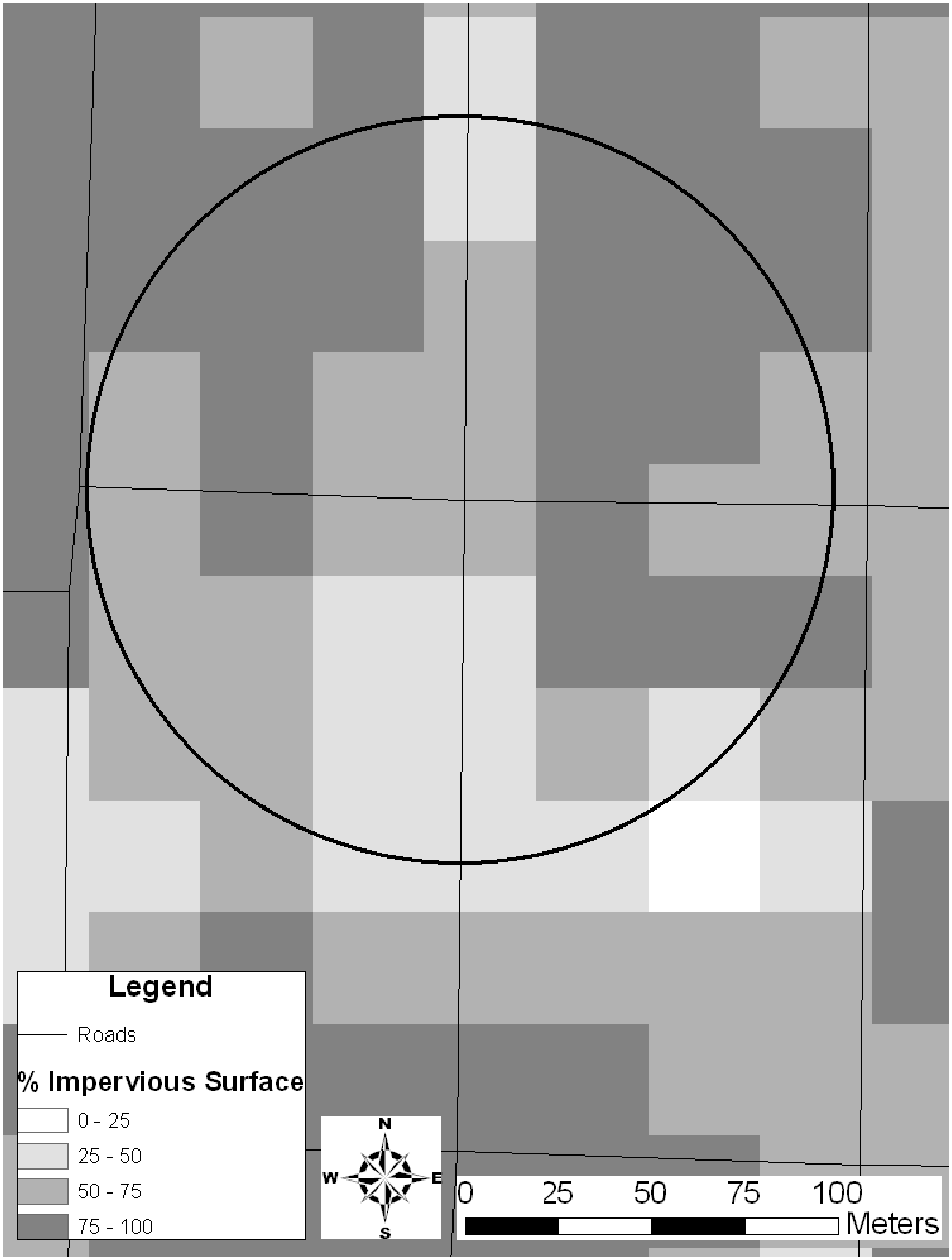

Figure 3. Spatial distribution of four categories of impervious surface cover within a single bird sampling plot.

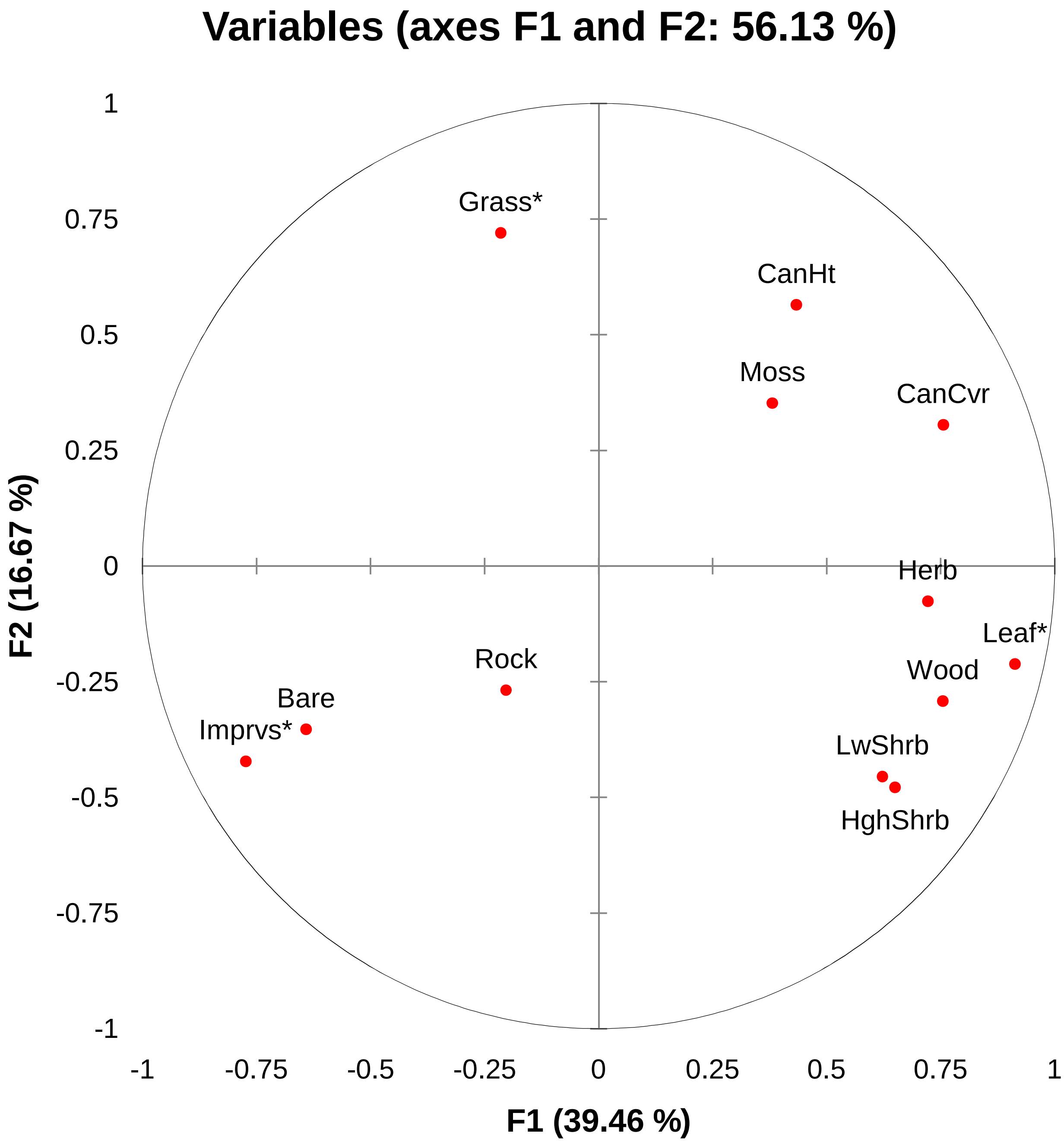

Figure 4. Principle Components Analysis of the thirteen environmental variables recorded at the sub-plot levels of all 25 survey plots in Stillwater's urban forests. Variables with the most explanatory power are marked with asterisks.

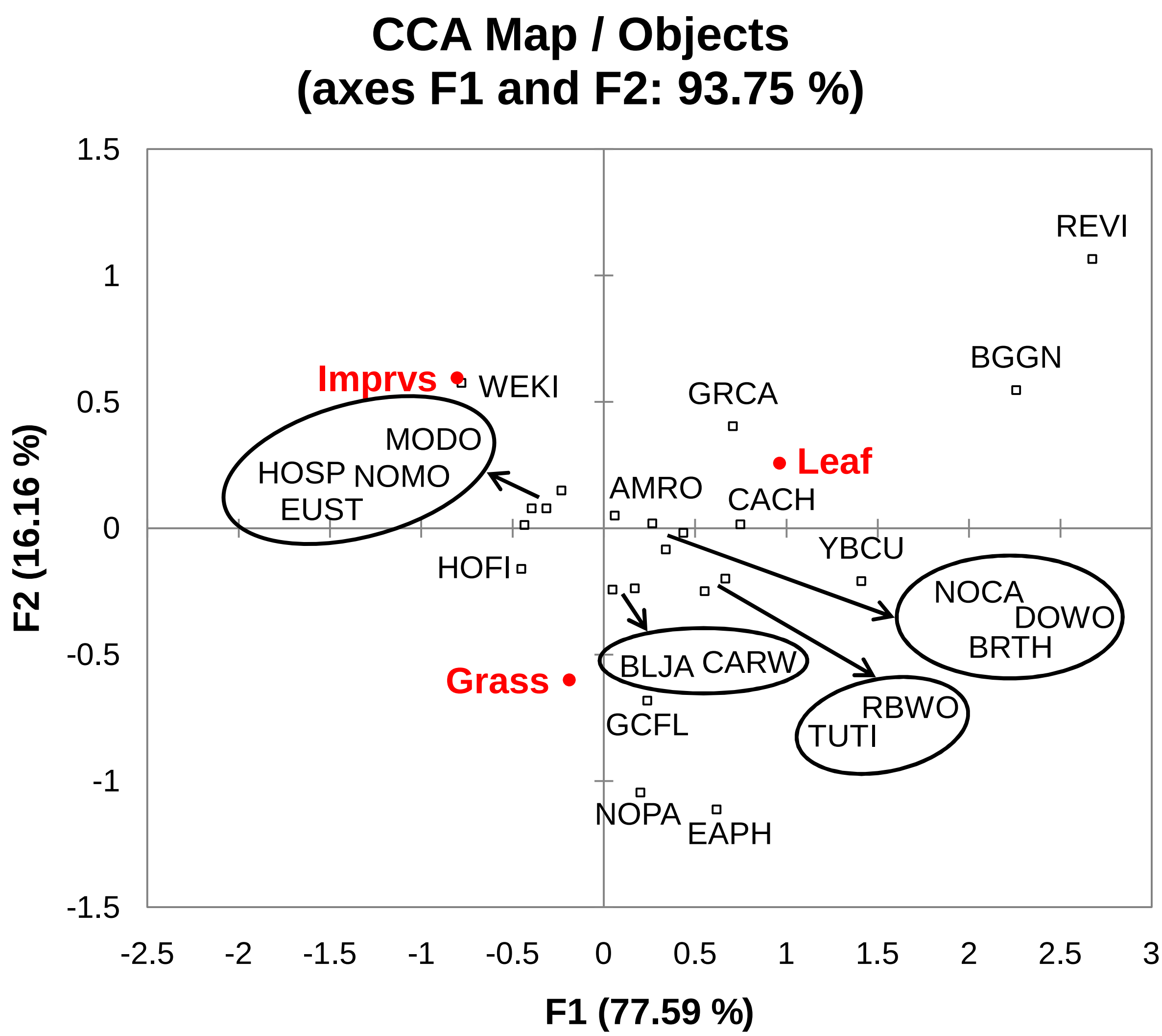

Figure 5. Canonical Correspondence Analysis biplot of 3 environmental variables (% Impervious surface, % Grass ground cover, and percent Leaf ground cover) and 22 breeding landbirds in urban forest plots. Cumulative axes 1 and 2 explained 93.75% of the variability in breeding bird density.

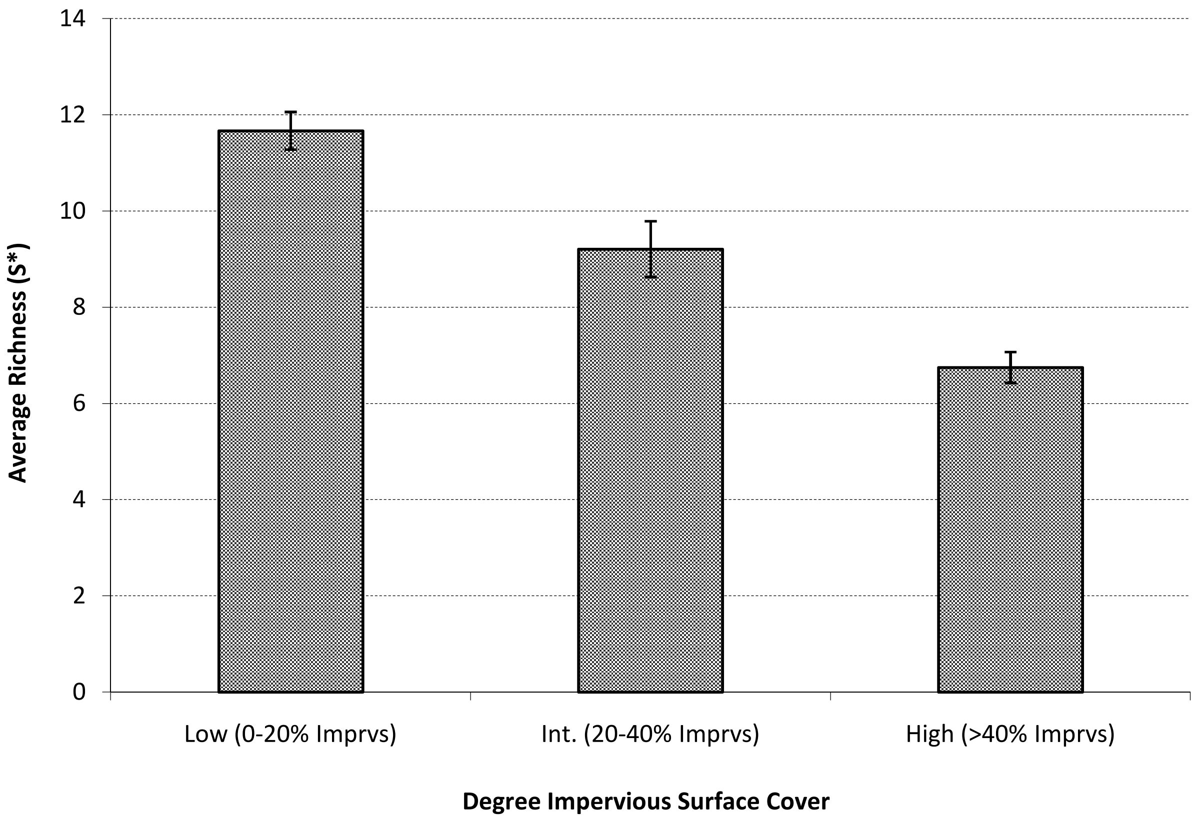

Figure 6. Mean adjusted species richness (S*) estimates (±SE) for survey plots with 3 classifications of urbanization based on proportion of impervious surface (Imprvs).

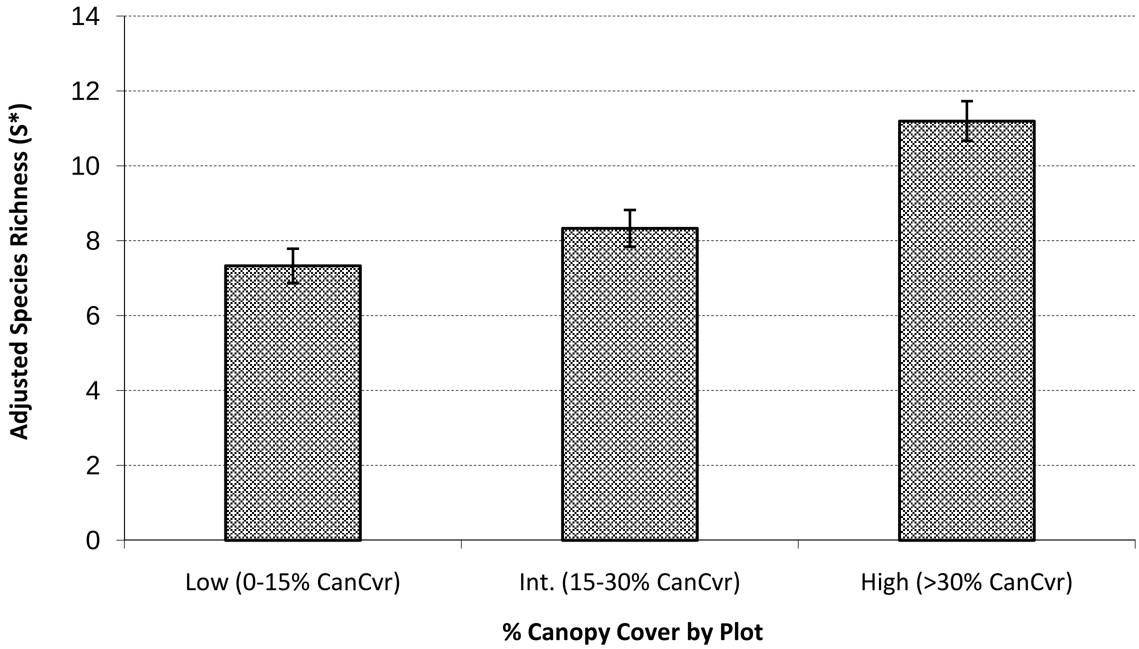

Figure 7. Mean adjusted species richness (S*) estimates (±SE) for survey plots with 3 classifications of urbanization based on % tree canopy cover by plot (CanCvr).

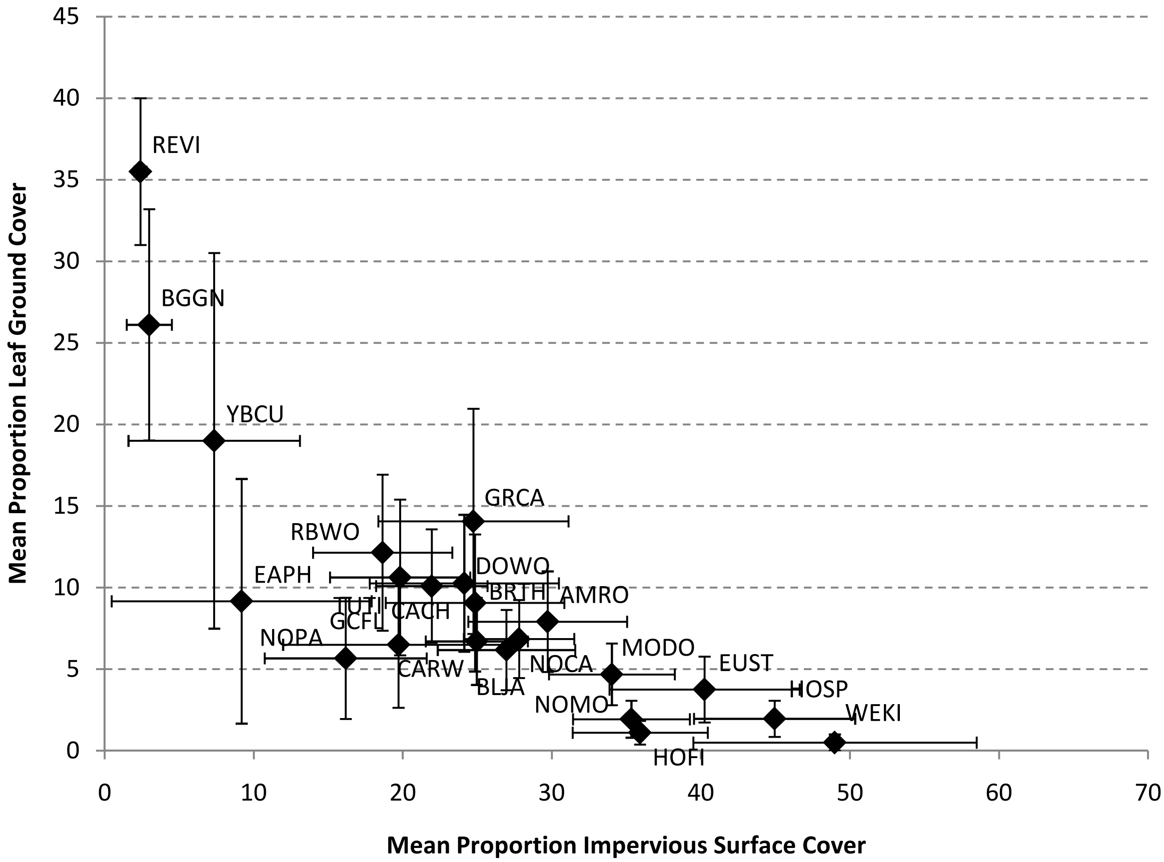

Figure 8. Twenty two of the most commonly encountered landbirds are plotted along two axes of urban habitat cover. Horizontal error bars represent the range of impervious surface cover over which the species occurred at greater than its mean density among all plots; vertical error bars represent the range of leaf litter ground cover over which the species occurred at greater than its mean density among all plots.

APPENDICES

Table 1. All commonly encountered landbird species included in Chapters 1 & 2 data analysis, arranged alphabetically by common name.

Alpha Code	Common name	*Scientific name*
AMCR	American Crow	*Corvus branchyrhynchos*
AMRO	American Robin	*Turdus migratorius*
AMTS	American Tree Sparrow	*Spizella arborea*
BAWW	Black-and-white Warbler	*Mniotilta varia*
BLJA	Blue Jay	*Cyanocitta cristata*
BGGN	Blue-gray Gnatcatcher	*Polioptila caerulea*
BRTH	Brown Thrasher	*Toxostoma rufum*
BHCO	Brown-headed Cowbird	*Molothrus ater*
CACH	Carolina Chickadee	*Poecile carolinensis*
CARW	Carolina Wren	*Thryothorus ludovicianus*
CEDW	Cedar Waxwing	*Bombycilla cedrorum*
DEJU	Dark-eyed Junco	*Junco hyemalis*
DOWO	Downy Woodpecker	*Picoides pubescens*
EAPH	Eastern Phoebe	*Sayornis phoebe*
EUST	European Starling	*Sturnus vulgaris*
FISP	Field Sparrow	*Spizella pusilla*
FOSP	Fox Sparrow	*Passerella iliaca*
GCKI	Golden-crowned Kinglet	*Regulus satrapa*
GRCA	Gray Catbird	*Dumetella carolinensis*
GCFL	Great Crested Flycatcher	*Myiarchus crinitus*
HAWO	Hairy Woodpecker	*Picoides villosus*
HETH	Hermit Thrush	*Catharus guttatus*
HOFI	House Finch	*Carpodacus mexicanus*
HOSP	House Sparrow	*Passer domesticus*
INBU	Indigo Bunting	*Passerina cyanea*
KEWA	Kentucky Warbler	*Oporornis formosus*
LOWA	Louisiana Waterthrush	*Seiurus motacilla*
MODO	Mourning Dove	*Zenaida macroura*
NOCA	Northern Cardinal	*Cardinalis cardinalis*
NOFL	Northern Flicker	*Colaptes auratus*
NOMO	Northern Mockingbird	*Mimus gundlachii*
NOPA	Northern Parula	*Parula americana*
PABU	Painted Bunting	*Passerina ciris*
PROW	Prothonotary Warbler	*Protonotaria citrea*
RBWO	Red-bellied Woodpecker	*Melanerpes carolinus*
RBNU	Red-breasted Nuthatch	*Sitta canadensis*

REVI	Red-eyed Vireo	*Vireo olivaceus*
RHWO	Red-headed Woodpecker	*Melanerpes erythrocephalus*
RCKI	Ruby-crowned Kinglet	*Regulus calendula*
SPTO	Spotted Towhee	*Pipilo maculatus*
SUTA	Summer Tanager	*Piranga rubra*
TUTI	Tufted Titmouse	*Baelophus bicolor*
WEKI	Western Kingbird	*Tyrannus verticalis*
WBNU	White-breasted Nuthatch	*Sitta carolinensis*
WEVI	White-eyed Vireo	*Vireo griseus*
WTSP	White-throated Sparrow	*Zonotrichia albicollis*
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*
YBCU	Yellow-billed Cuckoo	*Coccyzus americanus*
YRWA	Yellow-rumped Warbler	*Dendroica coronata*

Table 2. All species (43) detected May–June at urban forest plots in Stillwater, OK, 2008.

Common name (Alpha Code)	Scientific name
American Goldfinch (AMGO)*	*Carduelis tristis*
American Robin (AMRO)	*Turdus migratorius*
Baltimore Oriole (BAOR)*	*Icterus galbula*
Barred Owl (BAOW)*	*Strix varia*
Belted Kingfisher (BEKI)*	*Megaceryle alcyon*
Blue Jay (BLJA)	*Cyanocitta cristata*
Blue-Gray Gnatcatcher (BGGN)	*Polioptila caerulea*
Brown Thrasher (BRTH)	*Toxostoma rufum*
Brown-headed Cowbird (BHCO)*	*Molothrus ater*
Carolina Chickadee (CACH)	*Poecile carolinensis*
Carolina Wren (CARW)	*Thryothorus ludovicianus*
Chimney Swift (CHSW)*	*Chaetura pelagica*
Chipping Sparrow (CHSP)*	*Spizella passerina*
Common Grackle (COGR)*	*Quiscalus quiscula*
Cooper's Hawk (COHA)*	*Accipiter cooperii*
Downy Woodpecker (DOWO)	*Picoides pubescens*
Eastern Phoebe (EAPH)	*Sayornis phoebe*
Eurasian Collared-Dove (ECDO)*	*Streptopelia decaocto*
European Starling (EUST)	*Sturnus vulgaris*
Gray Catbird (GRCA)	*Dumetella carolinensis*
Great Crested Flycatcher (GCFL)	*Myiarchus crinitus*
House Finch (HOFI)	*Carpodacus mexicanus*
House Sparrow (HOSP)	*Passer domesticus*
Mississippi Kite (MIKI)*	*Ictinia mississippiensis*
Mourning Dove (MODO)	*Zenaida macroura*

Nashville Warbler (NAWA)*	*Vermivora ruficapilla*
Northern Cardinal (NOCA)	*Cardinalis cardinalis*
Northern Mockingbird (NOMO)	*Mimus polyglottos*
Northern Parula (NOPA)	*Parula americana*
Red-bellied Woodpecker (RBWO)	*Melanerpes carolinus*
Red-eyed Vireo (REVI)	*Vireo olivaceus*
Red-shouldered Hawk (RSHA)*	*Buteo lineatus*
Red-tailed Hawk (RTHA)*	*Buteo jamaicensis*
Rock Pigeon (ROPI)*	*Columba livia*
Ruby-throated Hummingbird (RTHU)*	*Archilochus colubris*
Scissor-tailed Flycatcher (STFL)*	*Tyrannus forficatus*
Tufted Titmouse (TUTI)	*Baeolophus bicolor*
Turkey Vulture (TUVU)*	*Cathartes aura*
Western Kingbird (WEKI)	*Tyrannus verticalis*
White-breasted Nuthatch (WBNU)*	*Sitta carolinensis*
Yellow-billed Cuckoo (YBCU)	*Coccyzus americanus*
Yellow Warbler (YEWA)*	*Dendroica petechia*

*Species encountered on fewer than 50% of surveys at every plot encountered (these included species such as migrants which were only encountered in the first one or two weeks of surveys or species not encountered regularly or perhaps accidentally), species only encountered as fly-overs, and/or species not considered ‘landbirds’ (that is, species not belonging to the Passerines or their allies).

VITA

Jason R. Heinen

Candidate for the Degree of

Master of Science

Thesis: SONGBIRD COMMUNITY STRUCTURE IN CROSS TIMBERS FOREST: INFLUENCE OF JUNIPER INVASION AND URBANIZATION

Major Field: Natural Resource Ecology & Management

Biographical:

Personal Data: Born in Tulsa, Oklahoma, February 4, 1981.

Education: Completed the requirements for the Master of Science in Natural Resource Ecology & Management at Oklahoma State University, Stillwater, Oklahoma in December, 2009; completed the requirements for the Bachelor of Science in Fisheries & Wildlife Ecology at Oklahoma State University, Stillwater, Oklahoma in December, 2006.

Experience: Bird Keeper Intern, Tulsa Zoo & Living Museum, August/2009 – December/2009; Teaching Assistant, Oklahoma State University, January/2007 – May/2009; Research Assistant, Oklahoma State University, January/2008 – December/2008; Field Technician, Oklahoma Fish & Wildlife Cooperative Unit, May/2006 – August/2006.

Professional Memberships: Oklahoma Chapter of the American Fisheries Society, 2004 – Present; O.S.U. Chapter of The Wildlife Society, 2005 – Present; Payne County Audubon Society, 2007 – Present; Oklahoma Ornithological Society, 2008 – Present; National Audubon Society, 2009 – Present.

Name: Jason R. Heinen Date of Degree: December, 2009

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: SONGBIRD COMMUNITY STRUCTURE IN CROSS TIMBERS FOREST: INFLUENCE OF JUNIPER INVASION AND URBANIZATION

Pages in Study: 83 Candidate for the Degree of Master of Science

Major Field: Natural Resource Ecology and Management

Scope and Method of Study: Several species of North American songbirds with population centers in the eastern U.S. reach the southwestern limit of their breeding range in Oklahoma cross timbers forest. Historically, the cross timbers was dominated by post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*), but increasingly, these patches are influenced by eastern redcedar (*Juniperus virginiana*) encroachment, as well as urbanization. We investigated the influence of eastern redcedar and urbanization on both breeding and over-wintering songbird communities. During the breeding season (May–July) and peak of winter (Dec-Feb) in 2007-'08 and 2008-'09, we surveyed 7 cross timbers forest patches in Payne County, Oklahoma. The study plots within these patches represented a gradient of condition from low to high prevalence of redcedar. In addition, we established survey plots (n=28) along a gradient of urbanization (as defined by the proportion of impervious surfaces) within Stillwater city limits and conducted surveys of these plots during May-July of 2008. We used repeated samples of a modified spot-mapping approach during breeding surveys, and a modified area search method during winter surveys.

Findings and Conclusions: During May–June of 2007 and 2008, I found at least 35 species of landbirds (songbirds, woodpeckers, cuckoos, doves, etc.) breeding in cross timbers forest in the study area and at least 33 landbird species, or 77% of the hypothetical species pool during winter. The breeding bird assemblage included approximately 12 species (34% of total) that reach a western limit of their global breeding range in the cross timbers, of which 9 were Neotropical migrants. Species richness (R^2=0.140, P<0.008) and proportion of Neotropical migrants (R^2=0.241, P<0.001) were both higher among plots with low cedar encroachment than those with heavy encroachment. In winter, neither species richness (R^2=0.213, P=0.297) nor Shannon diversity indices (R^2=0.138, P=0.411) were significantly correlated with cedar cover. Analysis of variance for species' mean territories/plot in 3 categories of % impervious surface yielded significant (P<0.05) differences between groups in over 40% of species. Analysis of variance for species' mean territories/plot in 3 categories of % canopy cover yielded significant (P<0.05) differences between groups in over 45% of species.