CHARACTERISTICS OF AVIAN HABITAT WITHIN THE SOUTHERN MIXED PRAIRIE OF NORTHWESTERN OKLAHOMA

By

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I dedicate this work to the memory of my brother, Christopher Matthew Chapman.

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INTRODUCTION

This Thesis is composed of 2 manuscripts that are formatted for submission to scientific journals. Chapter II is formatted for submission to Ecological Applications, a publication of the Ecological Society of America. Chapter III is formatted for submission to the Journal of Wildlife Management, a publication of The Wildlife Society.

CHAPTER II

Juniperus Encroachment Influences Bird Assemblages of Southern Mixed Prairie, U.S.A.

ABSTRACT

Bird species associated with grasslands of southern mixed prairie have declined in abundance while species associated with shrub-stage woodland habitat have increased in abundance. Recent exponential increases in the extent of *Juniperus virginiana* L. may explain some of these trends in bird community composition on southern mixed prairie. The primary purpose of our study was to determine the influence of *J. virginiana* encroachment on avifaunal assemblages within southern mixed prairie. We examined characteristics of bird assemblages on patches of mixed prairie with various levels of *J. virginiana* encroachment in northwestern Oklahoma. Bird abundance was indexed using 50-m fixed-radius point counts, and mist nets were used to gather demographics on individual bird species. We found complete shifts from a grassland bird assembly to a shrub and woodland bird assembly at only 10% cover of *J. virginiana*. Species associated with grassland habitats declined rapidly in abundance and richness with as little as 3% cover of *J. virginiana*. Low abundances and poor representation of male and female grassland birds may indicate that habitat patches of mixed prairie with *J. virginiana* encroachment quickly develop into unsuitable habitat for grassland birds. Because of the narrow threshold in which *J. virginiana* cover changes bird communities on grasslands, the potential for rapid replacement by shrub and woodland bird assemblages exists. Our results indicate that encroachment of *J. virginiana* onto grasslands should be controlled to conserve habitat of declining grassland bird populations.

Key words: Canonical Correspondence Analysis; Detrended Correspondence Analysis; Eastern redcedar; Grassland birds; *Juniperus virginiana*

INTRODUCTION

Woody plant encroachment on grasslands, savannas, and shrub-steppe threatens the biological integrity of these ecosystems worldwide (Knopf and Samson 1995, Jeltsch et al. 1997, Archer 1989, Archer et al. 2000). Bird diversity on grassland ecosystems has increased as abundances of shrub and woodland associated avifauna increase along woody vegetation gradients within regional landscapes (Knopf 1986, Herremans 1998, Coppedge et al. in press). Although bird diversity has increased, faunal integrity of grassland ecosystems is threatened (Knopf 1992). Fragmentation of native grasslands by woodland expansion reduces breeding habitat available to endemic grassland avifauna and threatens to accelerate already precipitous declines of populations of grassland birds (Askins 1993, Knopf 1994). Studies across North America suggest that increasing woody cover results in declines in abundance of most species of grassland birds (Wiens 1969, Zimmerman 1988, Sample 1989, Askins 1993, Vickery 1996), but dynamics of woodland expansion onto habitat patches of native prairies and associated impacts on bird assemblages have received little attention.

Juniperus virginiana L. is increasing more rapidly than other woody plants on the central grasslands of North America (Schmidt and Kuhns 1990, Briggs and Gibson 1992, Johnson 1994, Schmidt and Leatherberry 1995, Engle and

Bidwell 2000) with exponential increases in distribution in portions of the southern Great Plains (Engle et. al 1995). Bird assemblages in mature stands of *J. scopulorum* in the northern Great Plains have been described (Hopkins et al. 1986, Sieg 1991a, 1991b), but effects of rapid encroachment of *Juniperus* on bird assemblages occupying habitat patches of native prairie are currently unknown. Previous studies investigating the relationship between birds and *J. virginiana* examined the role of birds as dispersal agents (Holthuijzen and Sharik 1985, Holthuijzen et al. 1987, Chavez-Ramirez and Slack 1994). Increasing density of *J. virginiana* in deciduous woodlands of central Texas, U.S.A., reduced available breeding habitat for the endangered black-capped vireo (*Vireo atricapillus*), a woodland associated bird (Grzybowski et al. 1994). *Juniperus virginiana* encroachment likewise threatens to reduce available breeding habitat for grassland birds.

Thresholds in habitat structure, including woody plant cover, have important management implications in the conservation of declining bird populations (Villard et al. 1999). Although the threshold of *J. virginiana* invasion that precipitates a change in assemblages of bird species in grasslands is unknown, woody canopy cover of as little as 18.5% represents a critical threshold where grassland rapidly converts to woodland (Loehle et al. 1996). Therefore, we sought to identify thresholds of *J. virginiana* cover at which bird a grassland bird assemblage shifts to an assemblage dominated by shrub and woodland avifauna. We also determined how individual bird species associate with varying amounts of *J. virginiana* cover.

STUDY AREA

Our study was conducted within the southern mixed prairie of northwestern Oklahoma, U.S.A. This region provided an ideal landscape to document effects of woody plant encroachment on bird communities because it is experiencing rapid widespread increases in *Juniperus*. *Juniperus virginiana* and *J. ashei* have increased in distribution nearly 80% during a 9-year period and now occupy almost 50% of Oklahoma's native grassland communities (Engle et al. 1995). Northwestern Oklahoma is characterized by gently sloping to steep uplands of silty to moderately sandy soils with natural vegetation dominated by mixed grasses (including *Andropogon hallii*, *Bouteloua* spp., *Buchloe dactyloides, Panicum virgatum, Schizachyrium scoparium*, and *Sorgastrum nutans*), numerous forb species, and occasional woody shrubs and trees (principally *Artemesia filifolia*, *Populus deltoides*, *Prunus angustifolia, Quercus* spp., *and Rhus* spp.; Fitzpatrick 1950, Steers et al. 1963). Climate of the region is sub-humid with a mean annual temperature of 15.3°C and mean annual precipitation of 62.7 cm (Oklahoma Climatological Survey 1997). Major land uses of the region include production of wheat (*Triticum aestivum*) and cattle (*Bos* spp.). Less than 5% of the total land area is enrolled in the Conservation Reserve Program (United States Department of Commerce 1992). Most grazing pastures, hayfields, and conservation-easement fields in the region are maintained as monocultures of *Bothriochloa ischaemum*, *Cynodon dactylon*, or *Eragrostis curvula*.

Study sites were located along three North American Breeding Bird Survey (BBS) routes: two in Woods County and one in both Dewey and Blaine Counties. Those counties have been identified as having areas of expanding populations of *J. virginiana*. The BBS designations for those routes were Eagle City (OK BBS route 19, Dewey and Blaine Counties), Tegarden (OK BBS route 30, Woods County), and Lookout (OK BBS route 31, Woods County; Figure 1). Those particular BBS routes were selected in order to cross reference habitat patch level data with landscape level information gathered in other studies (Coppedge et al. in press).

METHODS

Experimental Design

Twelve sites, 4 along each BBS route, were randomly selected as experimental units from patches of mixed prairie containing *J. virginiana*. Six of the selected sites, 2 per route, were sampled in 1998 and 6 were sampled in 1999. Each study site was permanently marked with 6 sample points in a 2 x 3 grid with 150 m spacing, for a 10-ha sampling area.

Bird species abundance was estimated using 50-m fixed-radius point counts. Point count data can be used to detect differences in relative bird abundance among habitat patches (Hutto et al. 1986). Savard and Hooper (1995) suggested a 100-m radius for point counts in open habitats, and Hutto et al. (1986) recommended a 25-m radius for point counts in more wooded habitats. A 50-m radius (0.79 ha) was selected as a compromise to standardize counts for comparisons between open and wooded habitats. Because of the propensity for elevated wind speeds in grasslands, a 50-m radius also allowed for easier detection of songs. Counts were not conducted during periods of heavy rain or wind speeds exceeding 8 km/hr. Counts were conducted once every 10 days during the breeding season from 1 May to 19 June (Ralph et al. 1993). Each point count was conducted between 0530 and 1000 hours CDT and was 8 min in duration. Eight-minute counts provided adequate data to detect differences in relative bird abundance among habitat patches (Savard and Hooper 1995). Counting began as the observer approached the edge of each 50-m radius plot. To reduce observer bias, 3 observers conducted counts and the same observer did not count each site more than 3 times nor on consecutive counts. Binoculars were used to verify bird identification when necessary.

Relative abundance was summarized from a mean of 5 counts and reported as a density of birds per 40 ha. Species recorded were placed into breeding habitat guilds following the Patuxent Wildlife Research Center (PWRC) guild delineations and included grassland, woodland, and shrub guilds (Peterjohn and Sauer 1993). Species selected for analysis included the mourning dove (see Table 1 for scientific names) and the 4 most abundant species in each of the grassland, shrub, and woodland breeding habitat guilds (Table 1). The mourning dove is classified by the PWRC as an urban bird, but on the Great Plains, the mourning dove is a habitat generalist because of its adaptability to changes in breeding habitat structure (Baskett and Sayre 1993). Species richness was the total number of all species observed from each guild on each study site.

Demographic parameters were determined from data collected using mist-net sampling. Mist nets can be used to detect differential use of subtly different habitat types in small geographical areas (Karr 1981). Each patch was netted once during each of 2 sampling periods. The first sampling period extended from 1 May to 1 June in 1998 and from 10 May to 25 May in 1999. The second sampling period began 10 days following the conclusion of the last mist-net day of the first period and extended from 10 June to 4 July in 1998 and 13 June to 30 June in 1999. Data from the first and second mist-net sampling periods were used to establish abundance of male and female adults. Data from the second mist-net sampling period were also used to determine abundance of juveniles to establish a relative measure of productivity (Peach et al. 1996). Two 12 x 2.6-m, 30-mm mesh, mist nets were placed around each of the 6 point-count centers in a location providing the best chance of capturing birds (Ralph et al. 1993) for a total of 12 nets. Nets were placed in approximately the same location for both sampling periods. Nets were opened one-half hour before dawn and remained opened for 3 hours, or 36 mist-net hours per study site per sampling period and 72 mist-net hours for each site. Mist netting was not conducted during heavy precipitation or with wind speeds >8 km/hr. Identification, age, and sex of each species was verified following Pyle (1997).

Canopy cover of *J. virginiana* on each study site was measured along 10-m transects at 30 random locations using the line-intercept method (Bonham 1989). *Juniperus virginiana* cover was expressed as a percentage and was estimated from the combined canopy distance measurements recorded from all transects within a site.

Data Analysis

We used detrended correspondence analysis (DCA) within CANOCO v4.0 (ter Braak and Smilauer 1998) and linear regression to determine relationships of *J. virginiana* cover to composition of bird assemblages. Detrended correspondence analysis is an indirect gradient analysis technique used to identify factors influencing characteristics of communities that vary along compositional gradients (Peet et al. 1988, Palmer 1993). The DCA used in this analysis was a partial DCA (pDCA) as year and route were included as covariables. To determine how bird composition shifts with change in cover of *J. virginiana*, we regressed axis 1 site scores from the pDCA against *J. virginiana* cover. We interpret a significant regression of the pDCA axis 1 site scores as a change in bird composition with increasing levels of *J. virginiana* cover ≤25%. A regression with slope = 0 would indicate no change in bird composition.

The relationship of breeding bird guilds to cover of *J. virginiana* was determined by regressing relative abundance and richness of breeding bird guilds against cover of *J. virginiana*. Relationships of the most abundant bird species from each guild also were determined through regression of relative abundance against cover of *J. virginiana*. Heteroscedasticity was reduced by square-root transformation of pDCA axis-1 site scores, bird guild abundance, and bird species richness. Significance of the model was determined by analysis of variance (PROC GLM; SAS Institute Inc. 1989).

We related number of males and females of each bird species from mist-net data to *J. virginiana* cover using canonical correspondence analysis (CCA), a direct gradient analysis that presents linear combinations of explanatory environmental or habitat variables as ordination axes (ter Braak 1986, 1987) with CANOCO v4.0 (ter Braak and Smilauer 1998). The arrangement of a species in ordination space relative to a vector identified by an environmental variable indicated how strongly associated a species was to that environmental variable (Palmer 1993). Cover of *J. virginiana* was selected as a lone environmental variable. Species aligned in the direction of the vector were correlated positively with increasing cover of *J. virginiana*, whereas those aligned opposite the vector origin were correlated negatively with cover of *J. virginiana*. A partial CCA (pCCA) was used because year and route were included as covariables. Uncommon species, those that occurred on ≤4 study sites, were removed to eliminate stochastic influences these species may have on the analysis (Hill and Gauch 1980). Monte Carlo permutations were used to test for significance of the relationship of bird species and *J. virginiana* cover.

RESULTS

We found evidence that avifaunal composition on southern mixed prairie shifts along a *J. virginiana* cover gradient. Canopy cover of *J. virginiana* on our 12, 10-ha, study sites ranged from 0% to 26% (Table 2). Regression of axis 1 site scores from the pDCA of breeding bird abundances against *J. virginiana* cover indicate that avifaunal composition changed at <5% *J. virginiana* cover, and the change continued as cover of *J. virginiana* increased (Figure 2). That change in bird assemblages reflected a decline in grassland birds and a concurrent increase of shrub and woodland associated birds.

Grassland bird abundance and richness approached zero at only 25% cover of *J. virginiana* (Figure 3). Few grassland birds were observed on sites with high levels of *J. virginiana* cover (Table 2). Two species of grassland birds were observed in sites with >25% *J. virginiana* cover (Figure 3b), the grasshopper sparrow and the eastern meadowlark, both of which had abundances under 7 individuals/ 40 ha (Table 2). Dickcissels and western meadowlarks were found only on sites with <10% cover of *J. virginiana* (Table 2). The negative association of grassland birds to *J. virginiana* cover was reflected in the rapid decline of grasshopper sparrows with increasing cover of *J. virginiana* (Figure 4). That grassland birds were negatively associated with *J. virginiana* cover was also reflected in the arrangement of male and female grassland birds in the pCCA (Figure 5). For example, male and female grasshopper sparrows were aligned closely together along axis 1 opposite the origin of the *J. virginiana* vector. Male dickcissels displayed the greatest aversion to *J. virginiana*, and no female dickcissels were captured on mixed prairie sites with *J. virginiana* encroachment. Male grasshopper sparrows and dickcissels represented the majority of grassland birds captured and most captures of all grassland birds were on sites with <5% cover of *J. virginiana* (Table 3). Only 6 juvenile grassland birds, all grasshopper sparrows, were captured in the 2 years of the study (Table 3).

Shrub-affiliated bird species increased in richness and abundance with increasing cover of *J. virginiana*, reaching a density of >42 birds/40 ha at 25% *J. virginiana* cover (Table 2; Figure 6). Shrub birds also displayed the greatest variability to *J. virginiana* cover. For example, lark sparrows had a slightly negative correlation, and northern cardinals and field sparrows were positively correlated with increasing *J. virginiana* cover (Figure 5). Lark sparrows were abundant throughout all study sites (Table 2). The northern cardinal showed the most rapid increase in abundance with increasing cover of *J. virginiana* (Figure 7) and was the most abundant bird species occupying stands of *J. virginiana* with >25% cover (Table 2). Northern cardinal males were more positively correlated with increasing cover *J. virginiana* than females (Figure 5). Most captures of lark sparrows were on sites with <10% cover of *J. virginiana*, whereas all other shrub birds captured were on sites with >12% *J. virginiana* cover (Table 3). As in the grassland guild, only 6 juvenile shrub birds, representing 5 species, were captured (Table 3).

Abundance and richness of woodland associated bird species increased steadily with increasing cover of *J. virginiana* (Figure 8) and were greatest on study sites with >15% cover of *J. virginiana* in our study (Table 2). Of all increasing bird species, Carolina chickadees demonstrated the most rapid increase in abundance with increasing cover of *J. virginiana* (Figure 9). Likewise Carolina chickadees were the most abundant woodland species occupying habitat patches with >25% cover of *J. virginiana* (Table 2). Woodland species were arranged by the pCCA biplot in the direction of increasing *J. virginiana* cover and, thus, are positively associated with increasing cover of *J. virginiana* (Figure 5). Female Carolina chickadees and Bewick's wrens were more associated with *J. virginiana* cover than males of the 2 species (Figure 5). The majority of species of woodland birds were captured on sites with >12% cover of *J. virginiana* (Table 3). Four Bewick's wrens represented the only captures of juvenile woodland birds (Table 3).

DISCUSSION

Avifaunal Community

Less than 1% cover of *J. virginiana* invading a habitat patch of southern mixed prairie initiates a change in the bird assemblage inhabiting the patch (Figure 2). The shift in bird species composition resulted directly from an immediate and rapid decline in the abundance and richness of grassland birds (Figure 3) and concurrent increases in abundances and richness of shrub and woodland associated bird species (Figures 6 and 8). Similar changes in bird assemblages have been observed with woody plant invasion into other grassland ecosystems such as desert grasslands of Arizona, U.S.A. (Lloyd et al. 1998) and grasslands of the Kalahari Basin in Botswana (Herremans 1998). The change in bird assemblage on our study sites was gradual, indicated by the shallow slope of Figure 2, as *J. virginiana* cover increased to 25%. This result is similar to changes in bird assemblages in forested landscapes. As forest canopy cover declines, bird assemblages gradually shift from species of birds associated with mature forest interior to bird species associated with earlier stages of forest succession (Villard et al. 1999).

Grassland Birds

Juniperus virginiana encroachment into grassland habitat patches may provide differential visual cues to grassland birds that indicate unsuitable habitat. *Juniperus virginiana* reduces standing herbaceous biomass and forb density (Engle and Stritzke 1992, Gehring and Bragg 1992), which could reduce the capacity of grasslands experiencing *J. virginiana* encroachment to provide critical habitat requirements. Indeed, in our study, abundance and richness of grassland birds declined with increasing cover of *J. virginiana* (Figure 3). Although individual species of grassland birds have varying habitat requirements, most species of grassland birds share an aversion to extensive woody vegetation (Wiens 1969, Best et al. 1981 Zimmerman 1988, Askins 1993). Even at spatial scales larger than the habitat patch (>10 ha), grassland birds in the southern Great Plains decline as woody vegetation increases (Coppedge et al. in press).

Because grassland birds have specific habitat requirements, early stages of shrub and tree invasion may represent the development of unsuitable habitat (Askins 1993). The basic configuration of a bird species' ecological niche assumes that predictable relationships exist between occurrence of a bird and its characteristic vegetation requirements (James 1971). An individual bird of any species selects habitat based on visual cues from the structural attributes of the vegetation required by the species (James 1971). The magnitude of change in the bird community caused by *J. virginiana* invasion into grassland patches is remarkable given that grassland birds are sensitive to size and shape of habitat patches and structural attributes of herbaceous vegetation within a patch (Herkert 1994, Helzer and Jelinski 1999, Coppedge et al. in press).

Our results suggest that invasion by *J. virginiana* results in habitat conversion rather than creating sink habitat for grassland birds. A sink habitat is defined as habitat of relatively poor quality in which recruitment of a species occupying a habitat patch does not compensate for loses of individuals (Donovan et al. 1995). If patches of mixed prairie experiencing *J. virginiana* encroachment are to be considered sink habitat, then abundance of grassland birds would not decline as rapid as in our study. Patches with <5% *J. virginiana* cover may indeed serve as sink habitat to grassland birds where low levels of *J. virginiana* cover are maintained. As *J. virginiana* cover increases, however, the patch may become less suitable and may be avoided by grassland birds.

The grasshopper sparrow prefers open habitat with low densities of herbaceous vegetation and little or no shrub cover (Whitmore 1981, Vickery 1996, Dechant et al. 1998). The grasshopper sparrow was most abundant on our study sites where *J. virginiana* cover was <10% (Table 2). Grasshopper sparrows did occur in low abundances on one site with >25% *J. virginiana* cover, but individuals appeared to be using *J. virginiana* as song perches as they moved between the study site with *J. virginiana* and an adjacent patch with no *J. virginiana*. Densities of grasshopper sparrows in the Piedmont of Georgia, U.S.A., were similar in cultivated grasslands with <10% shrub cover to open grasslands. But, grasshopper sparrows were absent on sites where shrub cover reached 35%, even though suitable habitat remained in over one-half of the total area (Johnston and Odum 1956). Perhaps the upper tolerance limit of grasshopper sparrows to shrub cover may occur from 25-35% cover. Grasshopper sparrows and dickcissels were abundant on mowed and burned fields of northwestern Arkansas, U.S.A., but none were found in stands with woody vegetation (Shugart and James 1973).

Dickcissels prefer open areas of structurally heterogeneous habitat with tall herbaceous vegetation and higher percentages of forb cover (Zimmerman 1971, 1982). We did not observe dickcissels on habitat patches with >5% cover of *J. virginiana*, a reflection of their aversion to woody vegetation (Table 2; Best et al. 1981). Zimmerman (1971) reported low sex ratios and lower male densities of dickcissels on a 21-ha site containing *J. virginiana* compared with pastures and old fields, but he did not quantify cover of *J. virginiana*. Dickcissel abundance was correlated negatively with wooded field perimeters and wooded area surrounding Conservation Reserve Program (CRP) fields in Kansas, U.S.A. (Hughes et al. 1999), although they will use wooded edges as song perches (Zimmerman 1966, Hughes et al. 1999). Absence of dickcissels on a site with no recorded *J. virginiana* cover in our study (Table 2) may have resulted from a lack of tall grasses and sparse herbaceous cover (Zimmerman 1971).

Neither of the 2 species of meadowlark was observed on many of our study sites (Table 2) because they typically prefer areas with little or no woody vegetation (Dechant et al. 1999b, Sample 1989), although they will use shrubs as song perches (Knick and Rotenberry 1997). The eastern meadowlark was one of the most abundant species of grassland birds in our study area, and western meadowlarks were abundant along both the Tegarden and Lookout BBS routes (Chapman et al. unpublished data). The western meadowlark was not observed on the Eagle City route in our study, nor has it been recorded in more recent BBS counts (United States Geological Survey, Patuxent Wildlife Research Center 2000). The Eagle City route also experienced the most expansive landscape-level increase of *J. virginiana* in the study area.

Western Meadowlarks were most abundant along the Lookout route, which has been least affected by landscape-level increases in J. virginiana cover (Coppedge et al. in press). Eastern meadowlarks were present in low abundance on only one *J. virginiana* patch, which contained >25% cover (Table 2), and were observed using the *J. virginiana* as song perches while flying to and from an adjacent patch with no *J. virginiana*. No eastern meadowlarks occupied sites where shrub cover reached 35% in the Piedmont region of Georgia, U.S.A., although suitable habitat remained in over one-half of the total area (Johnston and Odum 1956). Inferences about the relationship in numbers of male and female meadowlark species to *J. virginiana* cover can not be made from Figure 5 because the mesh size of the mist nets was not adequate for capture of birds their size.

The response mechanism involved in the decline of grassland bird as *J. virginiana* invades grassland patches is undoubtedly multi-dimensional. In addition to changing factors such as size and shape of habitat patches and structural attributes of vegetation, *J. virginiana* encroachment may result in an increase in brood parasitism. Brown-headed cowbirds, a common nest parasite of grassland birds (Johnson and Temple 1990), were abundant at intermediate levels of *J. virginiana* cover (Table 2). Increases in *J. virginiana* cover may result in increasing abundances of mammalian and bird predators and nest predators associated with woody vegetation. Raccoons (*Procyon lotor*) and gray foxes (*Urocyon cinereoargenteus*) seem to display an affinity for grasslands fragmented with a woody shrub component (Bradley and Fagre 1988).

Shrub and Woodland Birds

Bird species typical of eastern forests and successional habitats are increasing across the landscape of southern mixed prairie (Coppedge et al. in press). Our results confirm this increase on habitat patches as northern cardinals and Carolina chickadees displayed almost exponential growth rates in abundance with increasing cover of *J. virginiana* (Figures 7 and 9). These birds were the most abundant species on habitat patches with the greatest amount of *J. virginiana*. Their abundance may be more a response to structure of woody vegetation than a response to *J. virginiana* specifically. Most species of forest birds select breeding habitat by structure of woody vegetation more than by composition of tree species and coniferous forests generally support a lower density and diversity of breeding birds because of their structural simplicity (Dickson et al. 1993). *J. virginiana* may provide visual cues of suitable habitat required by the shrub and woodland bird species observed in our study.

Lark sparrows were abundant across all levels of *J. virginiana* cover and exhibited the most consistent abundance across habitat patches with low cover of *J. virginiana* (Table 2). Lark sparrows range widely across North America but evolved on the Great Plains (Knopf and Samson 1995). Because they breed in areas with a substantial shrub component (Rising 1996, Dechant et al. 1999a), lark sparrows are considered shrub birds by the Patuxent Wildlife Research Center (Peterjohn and Sauer 1993). Small *J. virginiana* trees may be perceived by lark sparrows to be structurally similar to *Artemesia filifolia* and *Prunus angustifolia*, both of which are common in this region, thus accounting for their abundance throughout all study sites.

Source-sink dynamics of shrub and woodland birds may be difficult to determine in early stages of *J. virginiana* encroachment onto patches of native prairie. Females of both Carolina chickadees and Bewick's wrens displayed a stronger correlation to increasing cover of *J. virginiana* than did males of the 2 species. We may be observing early stages of dispersal of these species onto patches of mixed prairie as *J. virginiana* increases.

Implications and Conclusions

Avifaunal mixing on Great Plains grasslands and shrub-steppe occurs when bird species associated with eastern woodland habitats expand along riparian corridors of increasing cover of woody vegetation (Knopf 1986). Encroachment of *Juniperus virginiana* extends this mixing of bird species out of riparian zones and onto the more expansive prairie uplands. Encroachment of *Juniperus virginiana* enhanced bird diversity on our mixed prairie study sites that, like other central grasslands of North America, were historically low in diversity of bird species (Cody 1966, Wiens 1973). Bird diversity also has increased on native grasslands of north-central North Dakota, U.S.A., as woodland associated avifauna has increased with encroachment of *Populus* spp. (Grant and Berkey 1999). Although some species of shrub and woodland birds were historically encountered in wooded "islands" of the Great Plains (Faanes 1984, Rumble et al. 1998), current increases in bird species associated with woody vegetation outnumber declining species of grassland birds. As a result, bird diversity on the Great Plains of North America is increasing at the expense of those few endemic species of grassland birds.

Encroachment of woody vegetation threatens biological integrity of grassland ecosystems and associated vertebrate assemblages worldwide (Knopf and Samson 1995, Bogan 1997, Archer et al. 2000). Implementation of government conservation easement programs, such as the Conservation Reserve Program, has helped in slowing grassland bird declines in North America (Johnson and Schwartz 1993). However, these programs do not protect grasslands that are not enrolled from encroachment by woody plants. Invasions of woody plants into grassland ecosystems reduce availability of grassland habitats (Knopf 1994) and threaten to accelerate declines of grassland birds, especially area-sensitive species (Herkert 1994). Area of encroachment by *J. virginiana* is increasing 4% annually in Oklahoma (Engle et al. 1995). Fragmentation caused by this rapid increase in *J. virginiana* cover reduces quantity of available habitat for grassland birds (Coppedge et al. in press).

Our study indicates that encroachment of *J. virginiana*, especially in the early stages, degrades quality of grassland bird habitat and reduces abundance of grassland birds within invaded patches. Fire was a keystone process in the development of the central grasslands of North America (Axelrod 1985), and reintroduction of fire through prescribed burning could conserve remaining grassland bird habitat while slowing the influx of *J. virginiana*. The future of grassland vertebrates requires conservation of their native habitats and ecological niches (Knopf and Samson 1995). Therefore, conservation efforts on grassland ecosystems should include control of woodland expansion (Herkert 1994). Such efforts will slow the decline of avifauna endemic to grasslands and preserve the biological integrity of the central grasslands of North America and grassland ecosystems worldwide.

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Table 1. Breeding habitat guild, common names, scientific names, and American Ornithological Union species codes of common bird species of the southern mixed-prairie.

Breeding Habitat Guild Common Name	Scientific Name	Species Code
Grassland		
Dickcissel	Spiza americana	DICK
Eastern Meadowlark	*Sturnella magna*	EAME
Grasshopper Sparrow	*Ammodramus savannarum*	GRSP
Western Meadowlark	*Sturnella neglecta*	WEME
Shrub		
Brown-Headed Cowbird	*Molothrus ater*	BHCO
Field Sparrow	*Spizella pusilla*	FISP
Lark Sparrow	*Chondestes grammacus*	LASP
Northern Cardinal	*Cardinalis cardinalis*	NOCA
Woodland		
Bewick's Wren	*Thryomanes bewickii*	BEWR
Carolina Chickadee	*Parus carolinensis*	CACH
Great-crested Flycatcher	*Myiarchus crinitus*	GCFL
Yellow-billed Cuckoo	*Coccyzus americanus*	YBCU
Generalist		
Mourning Dove	*Zenaida macroura*	MODO

Table 2. Mean (± SE) cover of *Juniperus virginiana* (%), and mean (± SE) relative abundance (birds/40 ha) of common bird species and species richness by breeding habitat guild on 12, 10-ha sites of southern mixed prairie in Oklahoma.

	Oklahoma Breeding Bird Survey Route					
	31	30	31	31	19	30
Juniper Cover	0.0	0.4 (0.4)	3.4 (2.6)	9.0 (5.0)	9.6 (3.6)	12.8 (5.1)
Grassland Birds						
GRSP	5.1 (5.1)	84.9 (11.7)	11.9 (4.3)	8.5 (4.7)	0.0	15.3 (6.2)
DICK	0.0	6.8 (6.8)	6.8 (4.2)	0.0	0.0	0.0
EAME	0.0	0.0	0.0	0.0	0.0	0.0
WEME	5.1 (5.1)	0.0	28.9 (22.7)	22.1 (7.9)	0.0	0.0
Abundance	5.1 (5.1)	30.6 (9.7)	23.8 (15.3)	10.2 (6.0)	0.8 (0.8)	7.6 (0.8)
Richness	5	5	6	3	2	5
Shrub Birds						
BHCO	8.5 (6.6)	10.2 (6.8)	11.9 (9.9)	3.4 (3.4)	23.8 (9.8)	27.2 (9.1)
FISP	0.0	6.8 (6.8)	0.0	0.0	1.7 (1.7)	0.0
LASP	20.4 (6.9)	20.4 (6.9)	20.4 (12.48)	23.8 (9.8)	10.2 (3.2)	8.5 (3.8)
NOCA	0.0	6.8 (6.8)	0.0	1.7 (1.7)	17.0 (3.8)	6.8 (4.2)
Abundance	17.8 (2.5)	18.7 (2.9)	17.8 (4.2)	9.6 (4.8)	29.7 (9.3)	22.9 (0.8)
Richness	6	6	7	8	9	10
Woodland Birds						
BEWR	0.0	0.0	0.0	0.0	3.4 (3.4)	1.7 (1.7)
CACH	0.0	0.0	0.0	0.0	3.4 (3.4)	0.0
GCFL	3.4 (2.1)	10.2 (10.2)	3.4 (3.4)	0.0	0.0	0.0
YBCU	1.7 (1.7)	0.0	5.1 (3.4)	5.1 (2.1)	1.7 (1.7)	0.0
Abundance	2.5 (0.8)	4.0 (3.2)	4.2 (4.2)	1.7 (1.0)	4.2 (2.5)	0.0
Richness	7	2	3	3	5	3
Generalist						
MODO	1.7 (1.7)	0.0	5.1 (3.4)	1.7 (1.7)	0.0	0.0

Table 2. Continued

	Oklahoma Breeding Bird Survey Route					
	19	19	19	30	30	30
Juniper Cover	13.3 (5.0)	14.7 (4.8)	16.2 (5.7)	25.2 (7.3)	25.4 (6.6)	25.9 (5.8)
Grassland Birds						
GRSP	0.0	0.0	10.2 (8.2)	0.0	0.0	3.4 (2.1)
DICK	0.0	0.0	0.0	0.0	0.0	0.0
EAME	0.0	0.0	0.0	0.0	6.8 (6.8)	0.0
WEME	0.0	0.0	0.0	0.0	0.0	0.0
Abundance	0.0	0.0	5.1 (3.4)	0.0	3.4 (3.4)	1.7 (1.7)
Richness	0	0	2	1	2	1
Shrub Birds						
BHCO	17.0 (7.1)	11.9 (5.1)	11.9 (9.9)	15.3 (11.2)	3.4 (2.1)	13.6 (6.9)
FISP	17.0 (3.8)	8.5 (3.8)	1.7 (1.7)	1.7 (1.7)	0.0	8.5 (3.8)
LASP	42.4 (19.5)	13.6 (5.1)	6.8 (4.2)	5.1 (3.4)	27.2 (8.7)	17.0 (8.1)
NOCA	13.6 (5.8)	8.5 (3.8)	27.2 (8.2)	40.7 (6.8)	13.6 (7.9)	6.8 (3.2)
Abundance	65.4 (7.6)	32.3 (0.0)	28.9 (3.4)	42.4 (13.6)	29.7 (12.7)	22.9 (11.0)
Richness	13	8	8	9	9	10
Woodland Birds						
BEWR	0.0	17.0 (7.6)	1.7 (1.7)	10.2 (5.0)	5.1 (2.1)	0.0
CACH	10.2 (10.2)	3.4 (3.4)	8.5 (6.6)	28.9 (15.1)	13.6 (7.8)	6.8 (3.2)
GCFL	0.0	0.0	1.7 (1.7)	1.7 (1.7)	3.4 (3.4)	1.7 (1.7)
YBCU	0.0	0.0	5.1 (3.4)	1.7 (1.7)	0.0	1.7 (1.7)
Abundance	5.1 (5.1)	1.7 (1.7)	11.0 (7.6)	24.6 (0.8)	9.3 (7.6)	9.3 (4.2)
Richness	3	6	7	9	4	6
Generalist						
MODO	10.2 (8.2)	0.0	1.7 (1.7)	5.1 (3.4)	1.7 (1.7)	3.4 (3.4)

Table 3. Mean (± SE) cover of *Juniperus virginiana* (%) and number of males (M), females (F), and juveniles (J) of common bird species captured by breeding habitat guild on 12, 10-ha sites of southern mixed prairie in Oklahoma.

	Oklahoma Breeding Bird Survey Route																	
	31			30			31			31			19			30		
Juniper Cover	0.0			0.4 (0.4)			3.4 (2.6)			9.0 (5.0)			9.6 (3.6)			12.8 (5.1)		
	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J
Grassland Birds																		
GRSP	0	0	0	6	1	4	3	1	0	1	0	0	0	0	0	2	3	2
DICK	0	0	0	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0
EAME	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
WEME	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0
Shrub Birds																		
BHCO	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	3	1	0
FISP	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
LASP	1	1	0	1	0	0	9	0	0	3	3	0	0	0	0	0	1	0
NOCA	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Woodland Birds																		
BEWR	0	0	0	1	0	0	0	0	0	0	0	0	1	2	0	0	0	1
CACH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCFL	1	2	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
YBCU	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Generalist																		
MODO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3. Continued

	Oklahoma Breeding Bird Survey Route																	
	19			19			19			30			30			30		
Juniper Cover	13.3 (5.0)			14.7 (4.8)			16.2 (5.7)			25.2 (7.3)			25.4 (6.6)			25.9 (5.8)		
	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J
Grassland Birds																		
GRSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DICK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EAME	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WEME	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Shrub Birds																		
BHCO	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
FISP	2	1	1	4	1	1	3	2	0	1	0	0	1	1	0	2	1	0
LASP	2	0	0	0	2	0	2	0	0	0	0	1	1	1	0	1	1	0
NOCA	0	1	1	0	1	0	1	0	0	3	1	0	2	1	0	0	0	0
Woodland Birds																		
BEWR	0	0	1	0	1	0	0	1	1	0	0	1	1	2	0	1	1	0
CACH	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	1	1	0
GCFL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
YBCU	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
Generalist																		
MODO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Figure 1

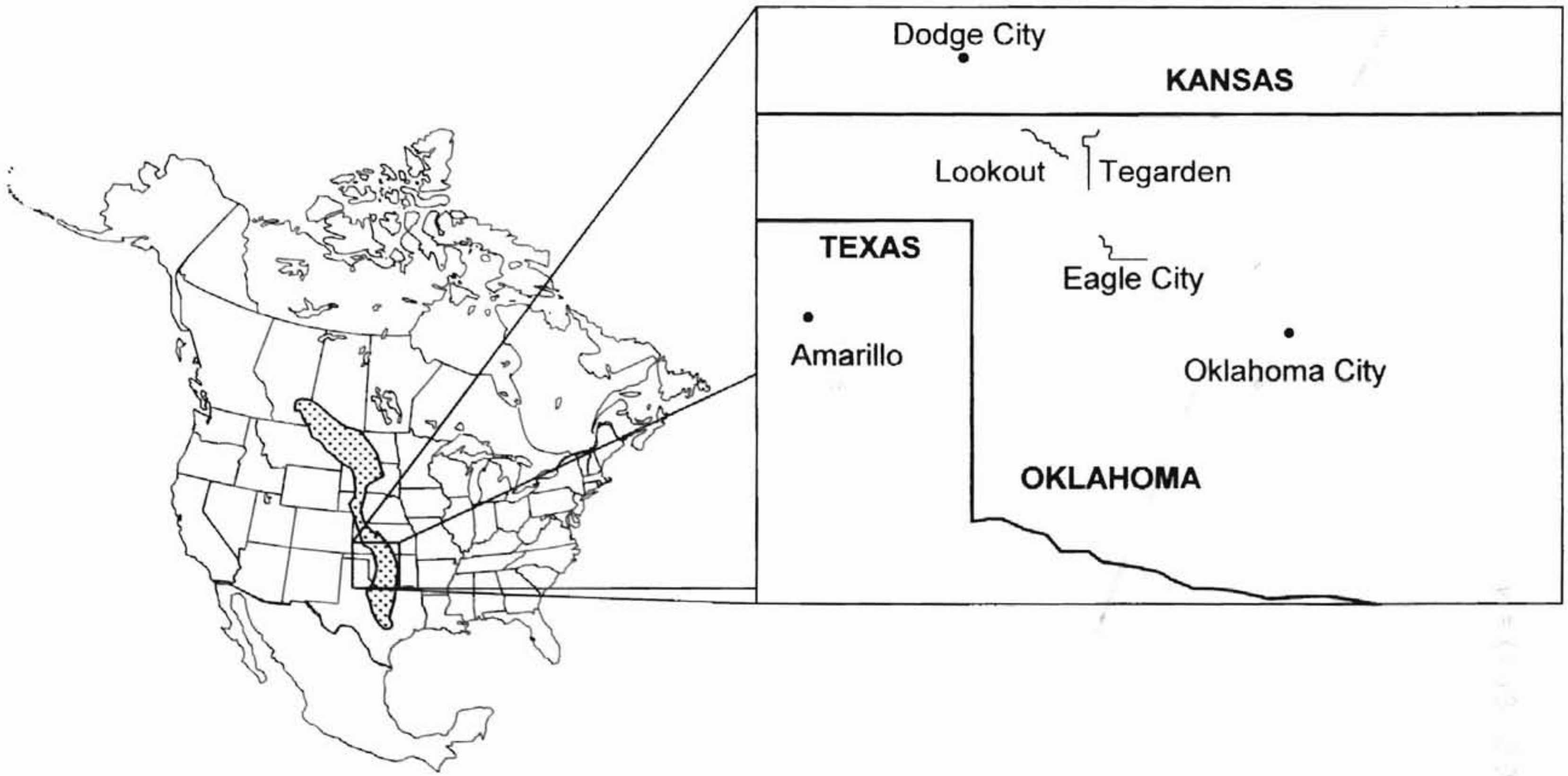
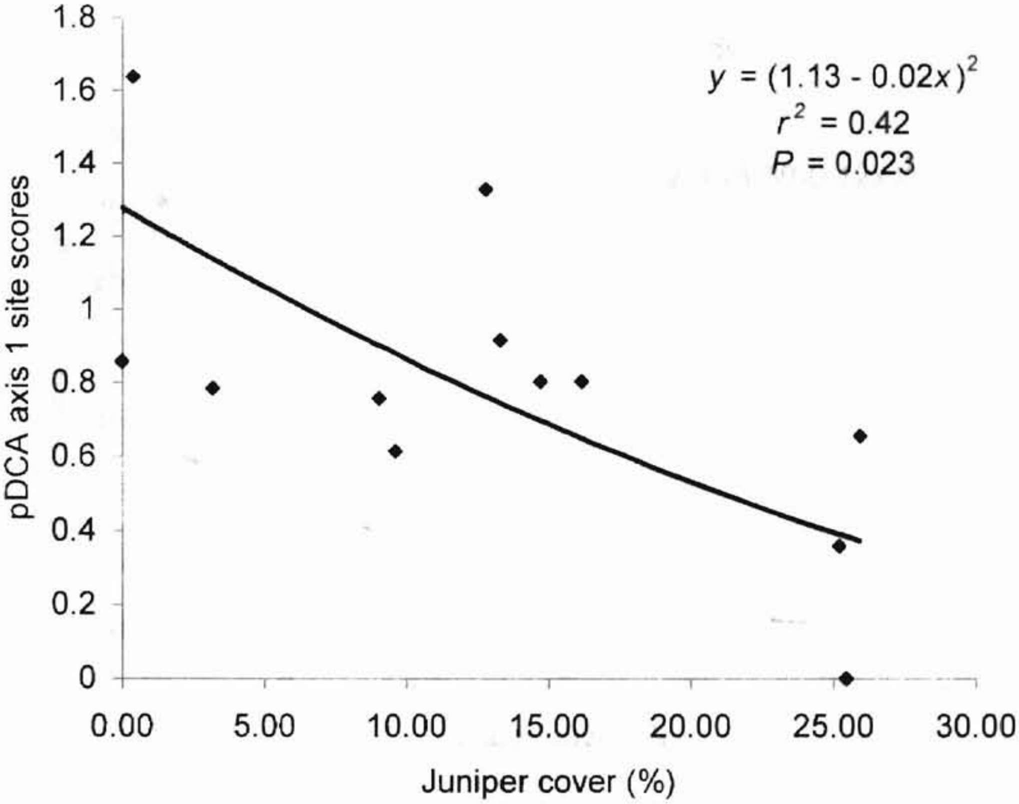

Dodge City
KANSAS
Lookout
Tegarden
TEXAS
Eagle City
Amarillo
Oklahoma City
OKLAHOMA

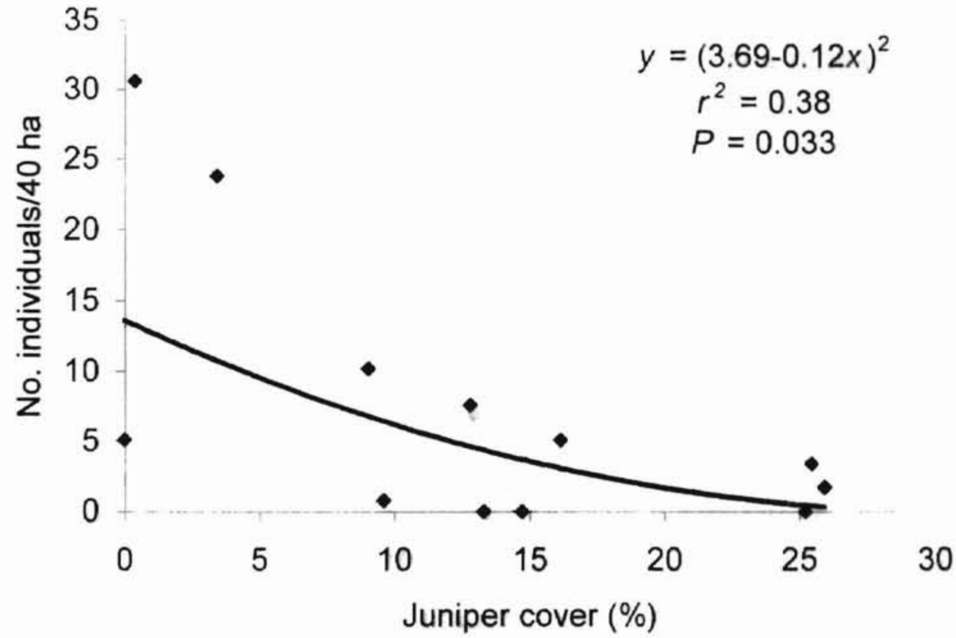
Figure 2



$y = (1.13 - 0.02x)^2$
$r^2 = 0.42$
$P = 0.023$
pDCA axis 1 site scores
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0.00
5.00
10.00
15.00
20.00
25.00
30.00
Juniper cover (%)

Figure 3

a) Abundance of grassland birds



b) Richness of grassland birds

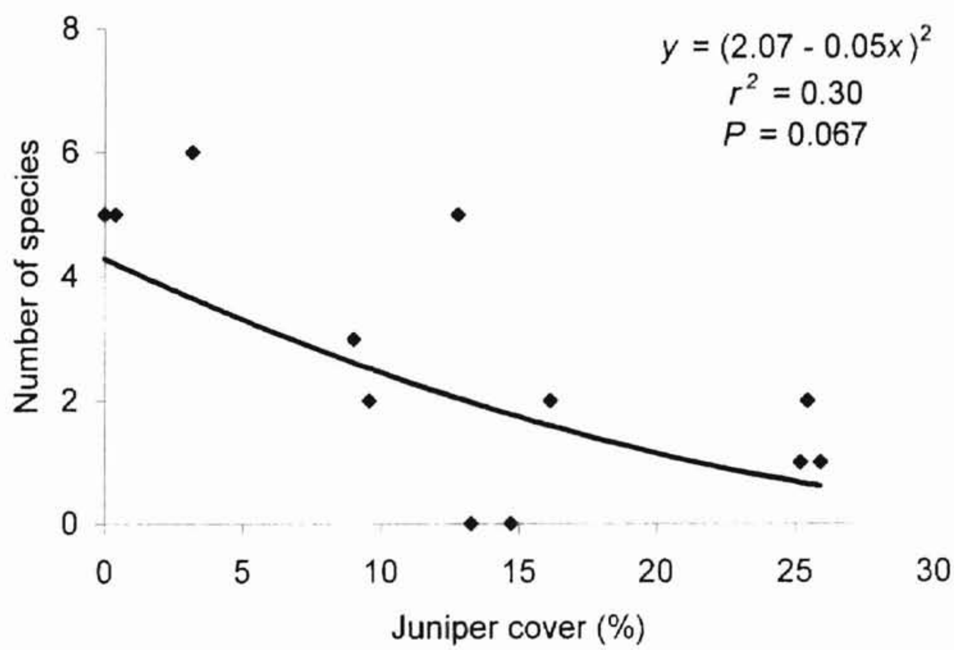
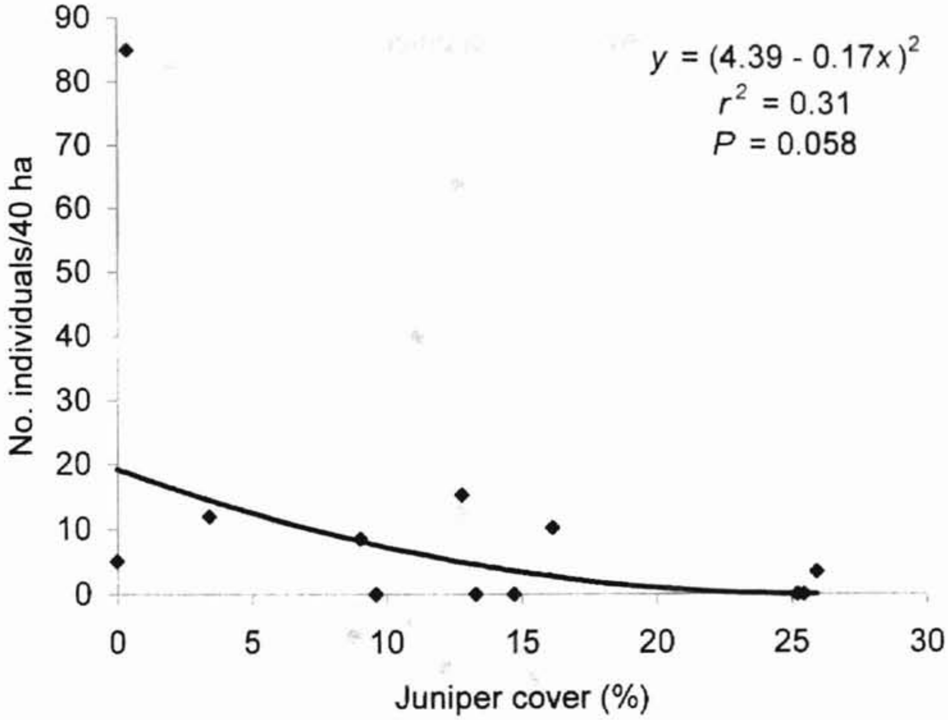


Figure 4



$y = (4.39 - 0.17x)^2$
$r^2 = 0.31$
$P = 0.058$
No. individuals/40 ha
Juniper cover (%)
0
5
10
15
20
25
30
10
20
30
40
50
60
70
80
90

Figure 5

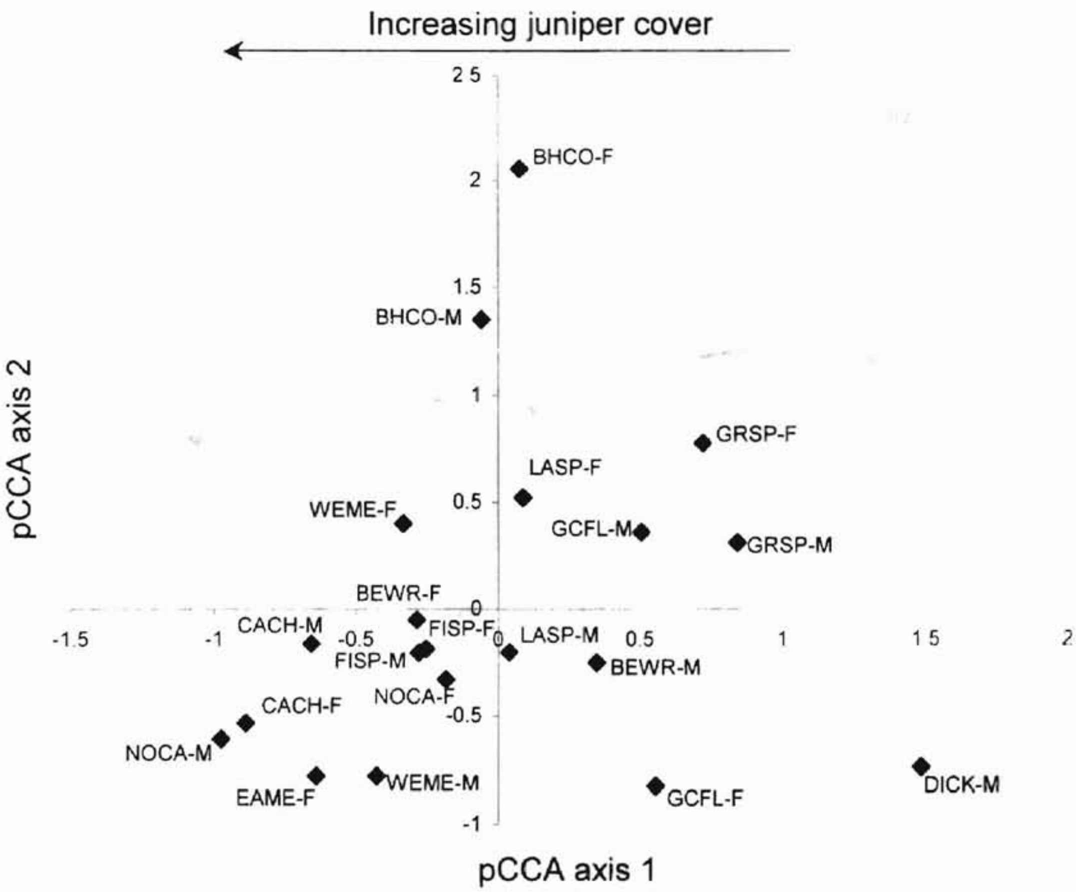

Increasing juniper cover
BHCO-F
BHCO-M
GRSP-F
LASP-F
WEME-F
GCFL-M
GRSP-M
BEWR-F
CACH-M
FISP-F
LASP-M
FISP-M
BEWR-M
NOCA-F
CACH-F
NOCA-M
EAME-F
WEME-M
GCFL-F
DICK-M
pCCA axis 1
pCCA axis 2

Figure 6

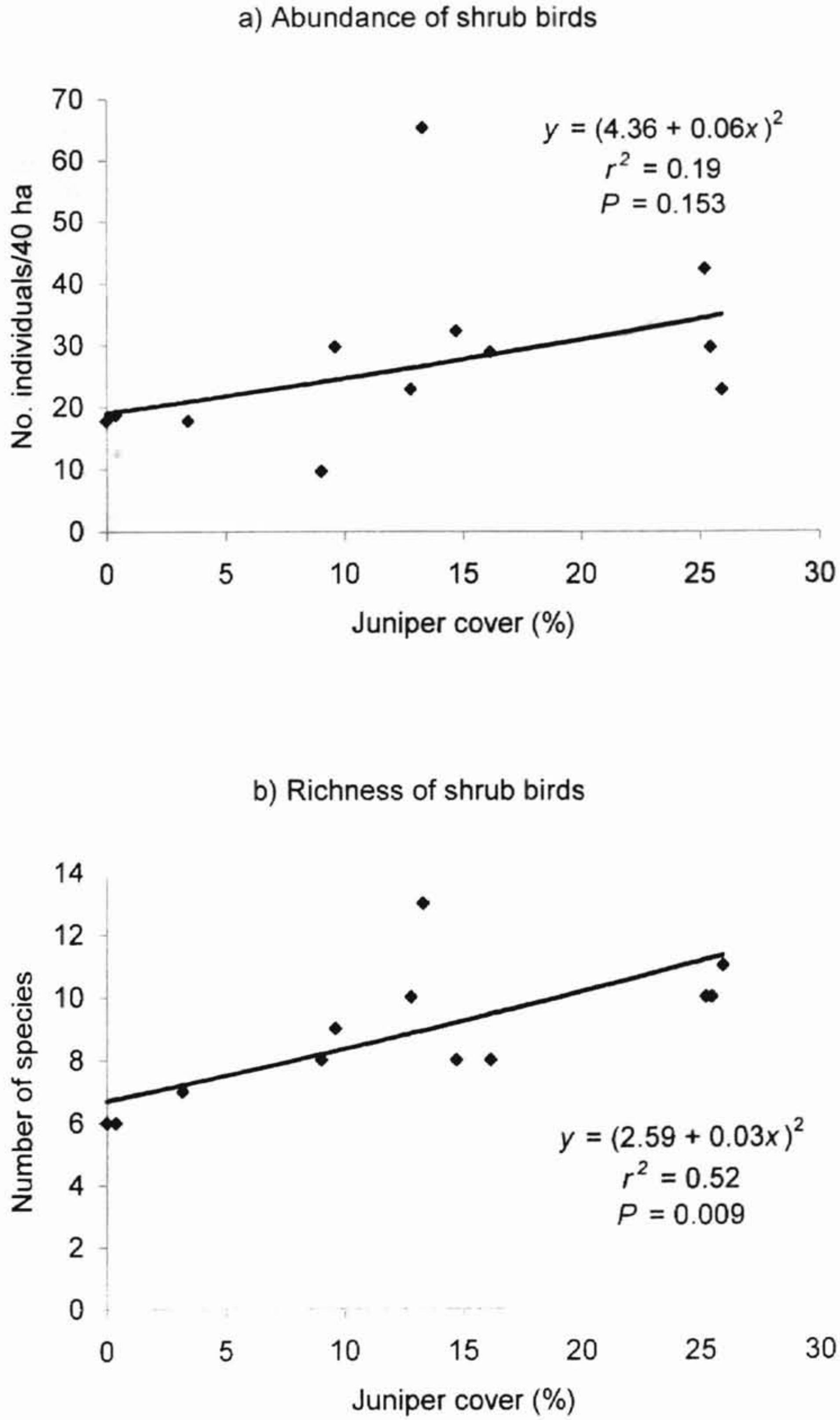
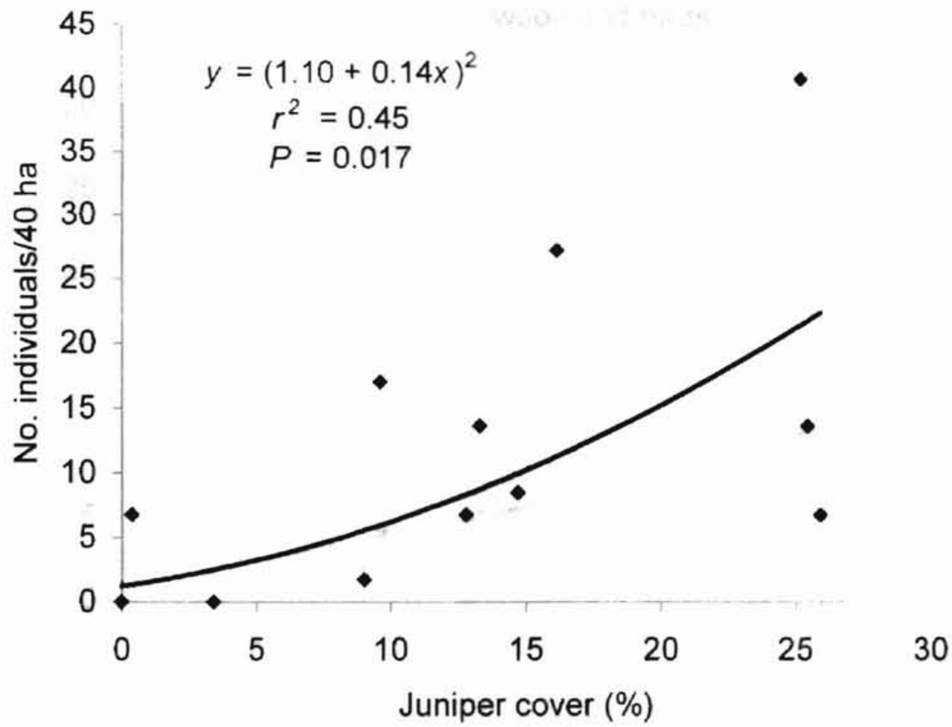

a) Abundance of shrub birds
y = (4.36 + 0.06x)^2
r^2 = 0.19
P = 0.153
No. individuals/40 ha
70
60
50
40
30
20
10
0
0
5
10
15
20
25
30
Juniper cover (%)
b) Richness of shrub birds
y = (2.59 + 0.03x)^2
r^2 = 0.52
P = 0.009
Number of species
14
12
10
8
6
4
2
0
0
5
10
15
20
25
30
Juniper cover (%)

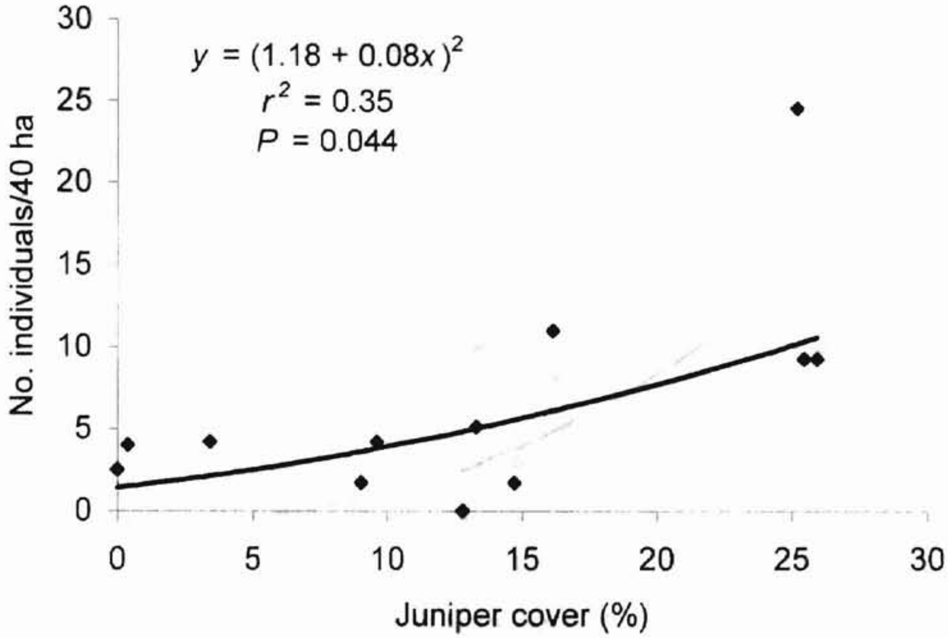
Figure 7



$y = (1.10 + 0.14x)^2$
$r^2 = 0.45$
$P = 0.017$
No. individuals/40 ha
Juniper cover (%)
0
5
10
15
20
25
30
35
40
45

Figure 8

a) Abundance of woodland birds



b) Richness of woodland birds

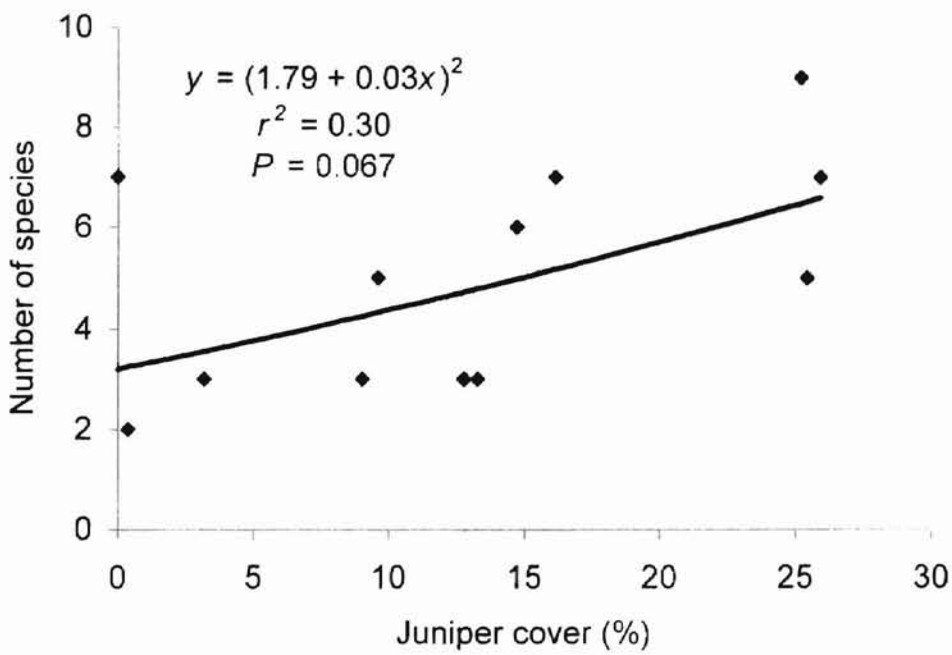
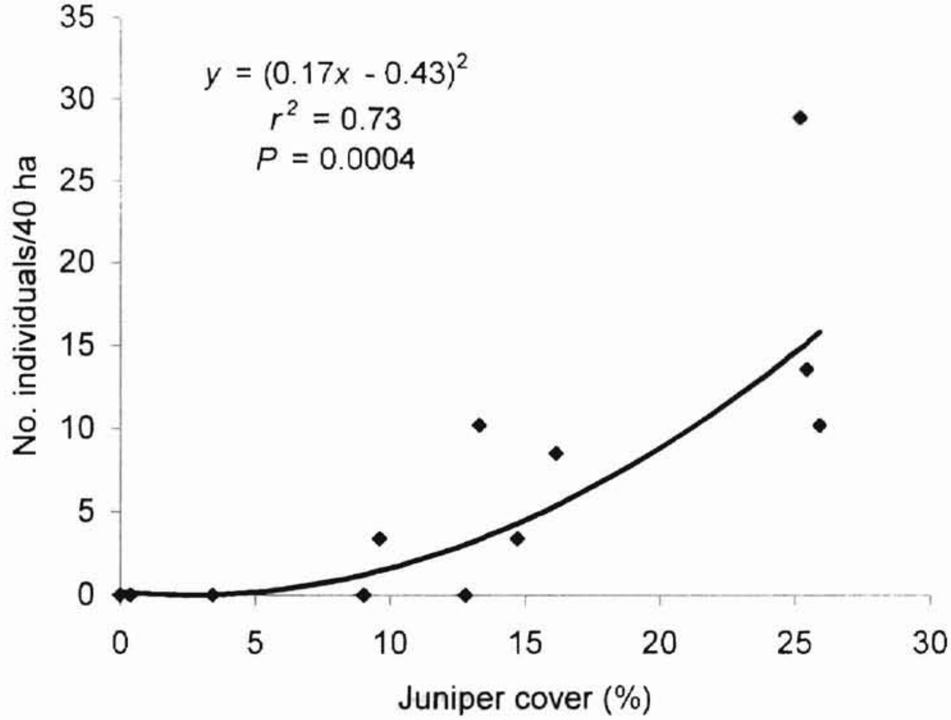


Figure 9



$y = (0.17x - 0.43)^2$
$r^2 = 0.73$
$P = 0.0004$
No. individuals/40 ha
35
30
25
20
15
10
5
0
0
5
10
15
20
25
30
Juniper cover (%)

CHAPTER III

Habitat Attributes Influencing Bird Assemblages within Southern Mixed Prairie

Abstract: Composition and structure of vegetation within a habitat patch are key factors influencing the dynamics of bird assemblages in grasslands. However, relatively little is known about how differences in habitat attributes between native grasslands and grasslands of introduced monocultures influence bird assemblages. Composition of plant species, vegetation structure, and abundance of breeding birds were compared on introduced grasslands of Old World Bluestem (*Bothriochloa ischmaeum*) to grasslands of native vegetation within the southern mixed prairie of northwestern Oklahoma. We determined relative abundance of birds in introduced and native grasslands over 2 years using fixed-radius point counts. Influence of gradients in composition and structure of vegetation on bird assemblages was determined using canonical correspondence analysis. Percent composition of plant species of introduced and native grasslands was distinctly different. However, neither habitat structure (e.g., horizontal heterogeneity and vertical structure) nor bird assemblage differed between the 2 grassland types. Although percent composition of plant species influenced the assemblage of birds occupying grasslands, our data suggest that habitat structure influenced bird assemblages in grasslands more than percent composition of plant species. Assemblages of grassland birds were arranged along gradients of structure of vegetation that are influenced by type and intensity of disturbances associated with land management. Herbivory may be a major factor influencing horizontal and vertical structure of grassland habitat and therefore bird assemblages occupying these grasslands. Programs and policies that encourage restoring grasslands, either native or introduced, and that

do not allow for suitable disturbance regimes will selectively benefit a narrow suite of birds.

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Key words: canonical correspondence analysis, grassland birds, habitat attributes, habitat management, introduced grasslands, Oklahoma, southern mixed prairie.

Structural and compositional characteristics of vegetation influence abundance and diversity of bird assemblages in grassland habitat (Cody 1968; Wiens 1973*b*, 1974*b*; Rotenberry and Wiens 1980*a*; Wiens and Rotenberry 1981). Recent comparisons of Conservation Reserve Program (CRP) fields to cropland espouse structure as the critical element governing habitat selection by bird species of North America's central grasslands (Johnson and Schwartz 1993*b*, King and Savidge 1995, Granfors et al. 1996, Millenbah et al. 1996, Patterson and Best 1996, Best et al. 1997, Hughes et al. 1999). This perspective suggests that presence of perennial herbaceous cover alone provides sufficient habitat for bird assemblages in fields revegetated with perennial grasses when compared with cropland.

Relatively little is known about how differences in habitat attributes between grasslands with native vegetation and grasslands of introduced monocultures potentially influence bird populations. In fact, we found few studies that compared abundance of bird species on native and introduced grasslands, and in these studies on northern mixed prairies, bird abundance was not influenced by kind of grassland (Renken and Dinsmore 1987, Wilson and Belcher 1989, Sutter et al. 1995, Sutter and Brigham 1998, Davis and Duncan 1999). In studies that quantified structure of vegetation, native and introduced grasslands were found to be structurally similar (Renken and Dinsmore 1987, Wilson and Belcher 1989, Sutter and Brigham 1998, Davis and Duncan 1999).

Because different taxa of plants vary in growth form diverse mixtures of plants should contribute more to habitat structure than simple mixtures of plants (Rotenberry 1985). Habitat structure should be heterogeneous on southern mixed prairies where the vegetation is dominated by a mixture of short, mid, and tall grasses. Furthermore, forbs can comprise ≥25% of the total standing herbaceous crop, and small trees and shrubs on some soils add further to the compositional and structural complexity of the vegetation (Bragg and Steuter 1995, Vinton and Collins 1997). In contrast, introduced grasslands (including lands enrolled in the CRP) of southern mixed prairie usually were established as monocultures of introduced grasses (Engle and Bidwell 2000) and are often managed intensively to reduce structural heterogeneity (McMurphy et al. 1990). The central grasslands of North America contain several million hectares of introduced grasslands (Berlinger and Knaap 1991, Bjerke 1991).

Thus, we hypothesize that plant species composition influences structure of vegetation and therefore habitat selection by birds of grasslands in which plant compositional and growth-form complexity vary widely. Moreover, variation in climate, soils, and disturbance (e.g., haying, mowing, herbivory, and fire) contributes to this complexity, thus creating gradients in composition and structure of vegetation (Vinton and Collins 1997, Coppedge et al. 1998). Gradients in composition and structure of vegetation influence bird assemblages in shrub-steppe and forested ecosystems (Rotenberry and Wiens 1980*a*, Mehlhop and Lynch 1986, Schieck et al. 1995, Schulte and Niemi 1998). Influence of compositional and structural gradients of vegetation on bird assemblages of native and introduced grasslands has been documented in few grassland regions of the world. Therefore, in addition to comparing the influence of discrete cover type (native vs. introduced) on bird assemblages of southern mixed prairie, our objective was to determine the relative influence of gradients of habitat attributes on bird assemblages within 2 grassland cover types. Specifically, we determined the influence of gradients in vegetation composition and structure on bird assemblages occupying native and introduced grasslands.

STUDY AREA

This study was conducted within the southern mixed prairie of northwestern Oklahoma. The region is characterized by gently sloping to steep uplands of silty to moderately sandy soils (Fitzpatrick 1950). Natural vegetation is dominated by grasses (notably little bluestem [*Schizachyrium scoparium*], sand bluestem [*Andropogon hallii*], buffalo grass [*Buchloe dactyloides*], and grama grasses [*Bouteloua* spp.]), but forb species are diverse and occasional woody shrubs and trees (principally sand sagebrush [*Artemesia filifolia*], sand plum [*Prunus angustifolia*], small oaks [*Quercus* spp.], and sumacs [*Rhus* spp.]) are locally abundant in native grasslands. The climate of the region is sub-humid with a mean annual temperature of 15.3 C and mean annual precipitation of 62.7

cm (Oklahoma Climatological Survey 1997). Major land uses of the region include cattle and small grain (e.g., wheat and sorghum) production. Less than 5% of the total land area is enrolled in the CRP (United States Department of Commerce 1992). Introduced grasslands are a common land cover type and are established as monocultures of nonnative forage grasses (McCoy et al. 1992).

METHODS

Study sites were located along 2 North American Breeding Bird Survey (BBS) routes in Woods County, Oklahoma. The BBS designations for those routes were Tegarden (OK BBS route 30; 36°50'N, 99°00' W) and Lookout (OK BBS route 31; 36°58'N, 99°13'W; Fig. 1). Those BBS routes were selected to cross reference community level data with landscape level information gathered in other studies (Coppedge et al. in press). We identified habitat patches of 2 grassland types on each BBS route: i) patches composed primarily of Old World bluestem (*Bothriochloa ischmaeum*), an introduced grass, and ii) patches composed primarily of native plant species. Four sites of each of 2 grassland types (introduced and native) were selected at random from each of the 2 BBS routes for a total of 16 study sites. Eight of the selected sites, 2 per grassland type per route, were sampled in 1998 and the remaining 8, 2 per grassland type per route, were sampled in 1999. A 10-ha sampling area was established within each habitat patch to denote a study site. Grazing use on each site was estimated ocularly by the Deming method and classified as no use, light use, moderate use, or heavy use (Deming 1939). Of the 8 introduced grassland sites selected, 3 were enrolled in the CRP (ungrazed), 2 were heavily grazed, 2 were hay fields, and 1 was neither hayed or grazed (Table 1). Seven of the 8 native grassland sites were grazed continuously at light to moderate stocking rates and 1 site had received long-term rest from grazing (Table 1).

Vegetation Measurements

Data on vegetation were collected from 50 random sampling points per study site during the last week of May and the first week of June 1998 and 1999. Horizontal structure and vegetation composition were estimated within a 20- x 50-cm frame placed at each sample point (Daubenmire 1959). Within each frame, canopy cover by species (Appendix A) was classified as 0-5%, 6-25%, 26-50%, 51-75%, 76-95%, and >95% from which the midpoints were used in the analysis. Cover of vegetation was estimated on an overlapping basis allowing for cover to exceed 100% at any given sample point. To assess vertical structure of the vegetation, we estimated visual obstruction from a distance of 4 m and a height of 1 m using a Robel pole (Robel et al. 1970).

Bird Abundance

Relative abundance of bird species within each study site was estimated using point counts of 50-m radius (0.79 ha) on 6 permanently marked sampling points spaced at 150 m (Savard and Hooper 1995). Counts were conducted 5 times, once within each of 5 10-day intervals during the breeding season from 1 May through 19 June in 1998 and 1999 (Ralph et al. 1993). Counts were not conducted during periods of heavy rain or wind speeds exceeding 8 km/hr. Each point count was conducted between 0530 and 1000 hours CDT and was 8 min in duration. Eight-minute counts provided adequate data to detect differences in relative bird abundance among habitat patches (Savard and Hooper 1995). Counting began as the observer approached the edge of each 50-m radius plot. To reduce observer bias, 3 observers conducted counts and the same observer did not count each site more than 3 times nor on consecutive counts. Binoculars were used to verify bird identification when necessary.

Data Analyses

We related habitat attributes to assemblages of breeding birds within patches of introduced and native grasslands. Habitat attributes were percent composition of plant species, horizontal heterogeneity (patchiness) of vegetation, and vertical structure (density of visual obstruction) of vegetation, which have been identified as important habitat attributes affecting assemblages of birds in grassland habitats (Wiens 1973*b*, 1974*b*; Rotenberry and Wiens 1980a, 1980b; Patterson and Best 1996). To represent percent composition of plant species (COMP) of each study site, we subjected percent canopy cover of plant species to detrended correspondence analysis within CANOCO (v4.0; ter Braak and Smilauer 1998). Detrended correspondence analysis (DCA) is a multivariate technique for representing patterns in communities composed of species that vary unimodally along underlying compositional gradients (Peet et al. 1988). We used a partial DCA (pDCA) because year and route were included as covariables. To represent horizontal heterogeneity of vegetation we created an index by calculating the coefficient of variation of percent cover of grass (CVGRASS; Wiens 1974, Roth 1976), the dominant plant cover. Vertical structure of vegetation was summarized as the mean height (cm) of visual obstruction (VOB) within a site (Robel et al. 1970). Differences in habitat attributes (COMP, CVGRASS, VOB) between types of grassland (native and introduced) were determined with the Wilcoxon signed-rank test (PROC NPAR1WAY; SAS Institute Inc. 1989).

Relative abundance of bird species was summarized from the data recorded within point count plots and was extrapolated to number of individuals per 40 ha. Effects of the interaction between year and grassland type on relative abundance of individual species of birds were tested using a Kruskal-Wallis 1-way analysis of variance (PROC GLM; SAS Institute Inc. 1989). In the absence of a significant interaction, differences in bird abundance across grassland type were determined using the Wilcoxon signed-rank test (PROC NPAR1WAY; SAS Institute Inc. 1989).

To assess the effects of gradients of composition and structure of vegetation on bird assemblages, we related relative abundance of the most common bird species (those that occurred on ≥10% of sites) to the 3 habitat attributes (COMP, CVGRASS, VOB) using canonical correspondence analysis within CANOCO (v4.0; ter Braak and Smilauer 1998). Canonical correspondence analysis (CCA) is a direct gradient analysis that presents linear combinations of explanatory environmental (habitat) variables as ordination axes (ter Braak 1986, 1987). The arrangement of a species in ordination space relative to a vector identified by an environmental variable indicated how strongly correlated a species was to that environmental variable (Palmer 1993). Year and route were included as covariables (pCCA) and Monte Carlo permutations (n =

199) were used to test for significance. We subjected the site scores of the pCCA to the Wilcoxon signed-rank test (PROC NPAR1WAY; SAS Institute Inc. 1989) to determine if bird assemblages on introduced grasslands differed from bird assemblages in native grasslands along habitat gradients identified by inter-set correlations in the pCCA.

RESULTS

Percent composition of plant species of introduced and native grasslands was distinct because the 2 grassland types were separated along axis 1 in the plot of site scores in the pDCA of cover of plant species (Fig. 2a). Separation of grassland types was reflective of differences in species richness between types of grassland (Fig. 2a and 2b). Nonnative grasses typical of introduced grasslands had low scores on axis 1 of the species scatter plot of the pDCA, whereas native grasses and the majority of forb species had high scores on axis 1 (Fig. 2b). Therefore, site scores from axis 1 of the pDCA were interpreted as an index to the percent composition of vegetation within our study sites. Traditional indices to composition of vegetation (e.g., richness, evenness, or diversity) may obscure taxonomic information of the plant community (Rotenberry 1985). For example, 2 sites may yield identical indices of diversity but may share no species in common. Because we analyzed percent cover of each plant species in the pDCA, site scores from axis 1 of the pDCA represented floristic variability of the plant communities occupying our study areas.

The difference in composition of vegetation between sites of introduced and native grasslands was confirmed by the Wilcoxon signed-rank test of the site scores (P = 0.001; Table 2). However, dissimilarity in habitat attributes among introduced and native grasslands was restricted to composition of vegetation. Vertical structure (VOB) and horizontal structure (CVGRASS) did not differ between introduced and native grasslands (P = 0.16 and 0.08, respectively; Table 2).

A relationship between the bird assemblage and habitat attributes was indicated by the Monte Carlo permutation test within the pCCA (Table 3; Fig. 3). The first pCCA axis was correlated with horizontal heterogeneity of vegetation (CVGRASS; Table 3). Vertical structure of vegetation (VOB) was correlated with axis 2 of the pCCA (Table 3). Axis 3 of the pCCA was correlated with vegetation composition (COMP; Table 3).

Results of the pCCA indicated the 2 structural attributes (VOB, CVGRASS) represented more important habitat gradients to bird assemblages than composition of plant species (COMP) on grasslands that we studied (Table 3). Assemblages of birds occupying introduced grasslands differed along the gradient of composition of plant species from bird assemblages occupying native grasslands, but this gradient explained only 18% of the variance between abundance of bird species and habitat attributes (Table 3, Fig. 3a). Although no difference was detected in bird assemblages between introduced and native grasslands along the gradient of horizontal heterogeneity (CVGRASS) or along the gradient of visual obstruction of vegetation (VOB), the 2 gradients explained most of the variance between bird abundance and habitat attributes (Table 3, Fig. 3a).

No interaction between year and grassland type on abundance of individual species of birds was detected ($P > 0.05$). Pooled across years, no species of bird differed ($P > 0.05$) in abundance between introduced and native grasslands (Table 4).

Individual species of birds displayed expected relationships with the gradients in habitat structure (VOB, CVGRASS) and composition of vegetation (COMP) identified by the pCCA (Fig. 3b). Species such as the northern bobwhite (see Table 4 for scientific names) and killdeer aligned in the direction of increased horizontal patchiness whereas western meadowlark and grasshopper sparrow aligned toward decreased horizontal patchiness (Fig. 3b). Western meadowlark and grasshopper sparrow were also more associated with low levels of vertical structure (Fig. 3b). Northern mockingbirds, brown-headed cowbirds, dickcissels, and eastern meadowlarks favored sites with high levels of vertical structure and more richness of plant species (Fig. 3b).

DISCUSSION

Habitat Composition and Structure

Introduced and native grasslands were characterized as having 2 distinct compositional communities of plants. Our study confirms previous findings that indicate native grasslands are compositionally richer in plant species than introduced grasslands (Wilson and Belcher 1989, Sutter and Brigham 1998). The composition of plant species on native grasslands is often associated with soils, type and extent of disturbance, and amount of precipitation during the growing season (Collins and Barber 1985, Collins et al. 1987, McIntyre and

Lavorel 1994). The compositional gradient evident from axis 1 of the pDCA (Fig. 2a) is most likely a response of land management given the separation of grassland types and that precipitation during the growing season was similar for both years of our study. Introduced grasslands are established and often maintained as a monoculture of a nonnative species of grass (McCoy et al. 1992, Engle and Bidwell 2000), and therefore, low diversity of plant species can be expected. Composition of vegetation, even within native grasslands, can fluctuate with natural and anthropogenic disturbance. For example, forbs in grasslands generally demonstrate a positive relationship with low to moderate intensity of grazing resulting in an increase in plant richness (Collins and Barber 1985, Coppedge et al. 1998, Rambo and Faeth 1999).

Different taxa of plants have different growth forms and thus should contribute differently to development of structure of vegetation (Rotenberry 1985). Thus, we expected native grasslands to be more structurally complex than introduced grasslands given the greater species richness of native grasslands. Moreover, shrubs, which are largely absent from introduced grasslands, also increase structural complexity of native grasslands (Collins et al. 1987). However, no discernable difference was detected in either horizontal patchiness or vertical structure between native and introduced grasslands in our study. This was surprising given the diverse growth forms of plants within the native grasslands of our study that included sod-forming grasses and bunchgrasses (of short, mid, and tall stature), forbs, and woody plants.

Herbivory, a major driver in creating variability in grassland habitat structure (Vinton and Collins 1997), was also an apparent factor in our study area. Livestock grazing at low to moderate stocking rates creates patches of lightly grazed and heavily grazed vegetation that produces heterogeneous horizontal structure of vegetation. In contrast, more homogeneous levels of vertical structure are achieved with heavy grazing pressure that results from uniform, close utilization of forage (Holechek et al. 1998). The absence of herbivory also results in homogeneous horizontal structure of vegetation. Study sites of both introduced and native grasslands contained a range of grazing use from no grazing, such as on CRP and hay fields, to heavy grazing (Table 1).

Bird Assemblage – Habitat Relationship

Despite large compositional differences of plant species between native and introduced grasslands, bird assemblages did not differ between the 2 grassland types (Table 4). Neither in previous studies (Renken and Dinsmore 1987, Wilson and Belcher 1989, Sutter et al. 1995, Sutter and Brigham 1998, Davis and Duncan 1999) nor in our study (Table 4) did abundance of individual bird species, total bird abundance, and richness of birds differ between discrete classification of grasslands as native or introduced. However, we expected abundance of some birds to be greater on native grasslands because complexity of vegetation afforded by greater forb abundance is thought to be beneficial to some species of grassland birds (Wiens 1969, 1973*a*; Zimmerman 1971). Forb abundance apparently does not influence bird assemblages where structural heterogeneity is low, such as within revegetated grasslands (see Hull et al. 1996).

Habitat structure appears to be more important than composition of plant species in determining composition of bird assemblages over a broad array of habitat compositional and structural settings. Individual bird species respond to habitat structure rather than composition of plant species (Zimmerman 1971, Wiens 1973a; Sutter et al. 1995; Herkert 1997), and our study indicates that bird assemblages also are ordered largely along structural rather than compositional gradients (Fig. 3b). Because structure did not differ between native and introduced grasslands, structural gradients may be attributed to land management practices (e.g., disturbances such as grazing, haying) and interactions among climate, season of year, and disturbance intensity.

Herbivory appears to be a major factor influencing horizontal structure of vegetation and therefore bird assemblages in these grasslands. For example, sites receiving long-term rest from grazing were associated positively with greater horizontal patchiness, whereas hay fields, most CRP fields, and heavily grazed pastures were more homogeneous in horizontal structure (Fig. 3a, Table 1). Establishment success of seeded introduced grasses also appears to influence horizontal heterogeneity, and therefore, the bird assemblage (Bollinger 1995, Millenbah et al. 1996). For example, site I4, a CRP field, and site I8, an ungrazed pasture, were the most patchy and had the lowest cover of grass and the lowest cover among introduced grasslands of the seeded grass species (e.g., Old World bluestem; data not shown) (Fig. 3a). Those 2 sites were correlated with abundance of birds that require horizontal patchiness (e.g., northern bobwhite). Horizontal patchiness of those and similar ungrazed sites can result from widely spaced seedings, as in newly established or young CRP fields, or older plantings that are not well established (Millenbah et al. 1996).

Species, such as grasshopper sparrow and western meadowlark, that require uniform, often short to mid stature, herbaceous vegetation with high grass cover and moderate litter cover (Lanyon 1994, Vickery 1996) were associated with hay fields and other CRP fields of our study that contained generally uniform stands of Old World bluestem with homogenous horizontal structure. Heavy grazing, such as on sites I1 and I3, contributes to homogeneity of horizontal structure because forage utilization is more uniform with increasing grazing use whereas grazing at low to moderate stocking rates results in patches of lightly grazed and heavily grazed vegetation (Holechek et al. 1998). Bird assemblages within moderately grazed grasslands varied considerably along the gradient of horizontal patchiness (Fig. 3a, Table 1). This may suggest that bird species on our grassland sites are less sensitive to moderate grazing use than to grazing use at either end of the extreme (e.g., either heavy or nil).

By altering vertical structure, amount and spatial pattern of herbivory also appears to influence the bird assemblage in these grasslands. Native grasslands receiving a long-term rest from grazing (e.g., site N8) had high levels of vertical structure. In contrast, a hay field (I5), a uniform CRP field (I6), and the 2 heavily grazed sites (I1 and I5) had low levels of vertical structure (Fig. 3a, Table 1). Low levels of vertical structure achieved with heavy grazing use results from uniform, close utilization of forage (Holechek et al. 1998). Bird assemblages among moderately grazed grassland sites in our study varied in arrangement along the gradients of structure of vegetation (VOB and CVGRASS). Again, this may suggest that bird species in our study grasslands are less sensitive to intermediate levels of herbivory. Indeed, the amount of vertical structure retained by light to moderate grazing does not reduce the capacity of grasslands to provide sufficient amounts of vertical structure for many species of grassland birds (Dale 1984, Klute et al. 1997). Dickcissels and eastern meadowlarks were correlated positively with greater plant species richness and greater visual obstruction (Fig. 3b). Dickcissels and eastern meadowlarks prefer open areas of structurally heterogeneous habitat with tall herbaceous vegetation and higher percentages of forb cover (Zimmerman 1971, 1982; Lanyon 1995).

Woody vegetation, primarily sand sagebrush and sand plum, also increased height of structure of vegetation on native grasslands of the this study. This explains the positive correlation of bird species associated with woody vegetation with increasing visual obstruction (e.g., northern mockingbirds and brown-headed cowbirds; Fig. 3b). The negative correlation of field sparrows to visual obstruction in this study is not typical of the species. Field sparrows breed in brushy pastures and succesional scrub habitats (Carey et al. 1994). Field sparrows were abundant on 1 native site with high visual obstruction, but field sparrows also were present in low abundance on other native and introduced sites with low visual obstruction. This resulted in placement of field sparrows coincident with low visual obstruction. Birds species associated with shrub and woodland habitat are expected to increase in abundance and richness due to encroachment of eastern redcedar (*Juniperus virginiana*) onto grasslands of southern mixed prairie (Chapman 2000).

MANAGEMENT IMPLICATIONS

We found no clear benefit of native grasslands over introduced grassland in terms of habitat attributes, avifaunal assemblages, or abundance of individual bird species. This suggests that management programs and policies to establish perennial grassland from cropland could legitimately favor introduced grasslands given the establishment, production, and socioeconomic advantages of introduced plant species for revegetation (Whisenant 1999). In fact, conservation easement programs that allow introduced species, like the CRP, provide important habitat for grassland birds in areas of intensive agriculture (Johnson and Schwartz 1993*b*, Berthelsen and Smith 1995, King and Savidge 1995, Best et al. 1997, Koford 1999) and may contribute to recovery of declining species of grassland birds (Johnson and Schwartz 1993a, Reynolds et al. 1994, Johnson and Igl 1995, Herkert 1997).

We evaluated bird – habitat associations on native and introduced grasslands in terms of abundance of breeding birds, which is only 1 measure of habitat suitability. Reproductive capacity of birds occupying native and introduced grasslands of similar structure and composition also must be considered when assessing habitat quality (Van Horne 1983, Johnson and Temple 1986, Vickery et al. 1992). No study has reported nesting success on similar grasslands of native and introduced vegetation, which is required before definitive conclusions on differences in habitat suitability between introduced grasslands and native grasslands can be made. Furthermore, the ability of introduced grasslands to provide a sufficient food supply for breeding birds and their broods remains unclear. Old World bluestems typical of introduced grasslands of southern mixed prairie have chaffy seeds, which are not preferred by seed-eating birds (Baumgartner et al. 1952). Forb species, which are largely absent in introduced grasslands, provide an assortment of seed and abundant invertebrate food resources (Blenden et al. 1986, Evans 1988).

Introduced grasslands support bird assemblages with similar abundances as native grasslands, but bird abundance alone does not indicate habitat quality (Van Horne 1983). Although introduced and native grasslands are structurally equivalent, introduced grasslands are inferior to native grasslands in terms of diversity of plant species. Therefore, restoration of grasslands to mimic native grasslands and conservation of existing native grasslands should remain high priority throughout the central grasslands of North America. Our results suggest, however, that disturbance practices applied to grasslands create habitat heterogeneity required by a diverse assemblage of bird species. Programs that establish grasslands, either native or introduced, and do not allow for suitable disturbance regimes will selectively benefit a narrow suite of birds.

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Table 1. Type of management on introduced (I; n = 8) and native (N; n = 8) grasslands within southern mixed prairie of northwestern Oklahoma.

Study site	Type of management
I1	Continuous, heavily grazed – cow/calf
I2	Hay field
I3	Rotational, heavily grazed – stocker cattle, horses
I4	Conservation Reserve Program field
I5	Hay field
I6	Conservation Reserve Program field
I7	Conservation Reserve Program field
I8	Long-term rest from grazing
N1	Continuous lightly grazed – cow/calf
N2	Continuous moderately grazed – cow/calf
N3	Continuous moderately grazed – cow/calf
N4	Continuous moderately grazed – cow/calf
N5	Continuous moderately grazed – cow/calf
N6	Continuous moderately grazed – cow/calf
N7	Continuous moderately grazed – cow/calf
N8	Long-term rest from grazing

Table 2. Mean ($\bar{x}$) and standard error (SE) of habitat attributes in native (n = 8) versus introduced (n = 8) grasslands within southern mixed prairie of northwestern Oklahoma.

		Introduced		Native		
Habitat attribute	Abbreviation	$\bar{x}$	SE	$\bar{x}$	SE	P-value[2]
Visual obstruction (cm)	VOB	39.6	6.4	48.7	4.5	0.16
CV of % grass cover	CVGRASS	35.2	3.6	48.0	6.4	0.08
Composition of vegetation (%)[1]	COMP	0.2	0.1	2.8	0.1	0.001

[1]importance value derived from axis-1 site scores (n = 16) from a partial detrended correspondence analysis (pDCA) of plant species coverage

[2]from a Wilcoxon 2-sample signed-rank test

Table 3. Results from a partial canonical correspondence analysis (pCCA; $F = 1.74$, $P = 0.01$) of relative abundance of breeding birds and habitat attributes on introduced ($n = 8$) and native ($n = 8$) grasslands within southern mixed prairie. And comparison of site scores (mean [$\bar{x}$], ± standard error [SE]) from pCCA axes to detect differences in bird assemblages on introduced and native grasslands along defined gradients.

	Results of ordination (pCCA)			Effect of grassland type				
				Introduced		Native		
pCCA axis	Gradient Defined[1]	Eigenvalue	Variance Explained (%)[2]	$\bar{x}$	SE	$\bar{x}$	SE	*P*-value[3]
axis 1	CVGRASS (0.90)	0.15	56	-0.3	0.5	0.0	0.3	0.32
axis 2	VOB (0.84)	0.07	26	-0.2	0.4	0.2	0.4	0.57
axis 3	COMP (-0.98)	0.05	18	1.0	0.3	-0.8	0.4	0.003

[1]identified by inter-set correlations. *r*-value in parentheses

[2]between bird relative abundance and habitat attributes

[3]from a Wilcoxon 2-sample signed-rank test

Table 4. Relative abundance (mean [$\bar{x}$] individuals/40 ha, ±standard error [SE]) of bird species occupying habitat patches of introduced (n = 8) and native vegetation (n = 8), and P-value from a Wilcoxon 2-sample test, within the southern mixed prairie.

Common name, scientific name	Code	Introduced		Native		P-value[1]
		$\bar{x}$	SE	$\bar{x}$	SE	
Killdeer, *Charadrius vociferus*	KILL	4.5	2.6	1.9	0.7	0.86
Upland sandpiper, *Bartramia longicauda*	UPSA	0.4	0.4	0.0	0.0	0.38
Wild turkey, *Meleagris gallopavo*	WITU	0.0	0.0	0.9	0.9	0.38
Ring-necked pheasant, *Phasianus colchicus*	RNPH	0.2	0.2	0.2	0.2	1.00
Northern bobwhite, *Colinus virginianus*	NOBO	0.9	0.6	0.4	0.3	0.84
Mourning dove, *Zenaida macroura*	MODO	4.0	1.9	9.1	6.8	1.00
Yellow-billed cuckoo, *Coccyzus americanus*	YBCU	0.2	0.2	0.0	0.0	0.38
Red-headed woodpecker, *Melanerpes erythrocephalus*	RHWO	0.0	0.0	0.9	0.9	0.38
Northern flicker, *Colaptes auratus*	NOFL	0.0	0.0	0.4	0.4	0.38
Scissor-tailed flycatcher, *Muscivora forficata*	STFL	0.9	0.6	3.8	1.7	0.20
Eastern kingbird, *Tyrannus tyrannus*	EAKI	0.2	0.2	0.9	0.5	0.27
Western kingbird, *Tyrannus verticalis*	WEKI	0.2	0.2	0.0	0.0	0.40
Great-crested flycatcher, *Myiarchus crinitus*	GCFL	0.2	0.2	1.3	1.3	1.00
Blue jay, *Cyanocitta cristata*	BLJA	0.2	0.2	1.3	1.3	1.00
Northern mockingbird, *Mimus polyglottos*	NOMO	0.0	0.0	1.1	0.6	0.08
American robin, *Turdus migratorius*	AMRO	0.0	0.0	0.2	0.2	0.38
Red-winged blackbird, *Agelaius phoeniceus*	RWBL	0.4	0.4	2.1	1.0	0.13
Brown-headed cowbird, *Molothrus ater*	BHCO	3.0	2.1	4.5	2.4	0.78
Common grackle, *Quiscalus quiscula*	COGR	0.6	0.4	0.0	0.0	0.17
Great-tailed grackle, *Quiscalus mexicanus*	GTGR	0.0	0.0	0.9	0.6	0.19
Eastern meadowlark, *Sturnella magna*	EAME	10.0	4.5	11.5	4.3	0.53
Western meadowlark, *Sturnella neglecta*	WEME	14.7	9.0	14.0	6.3	0.92
Northern oriole, *Icterus galbula*	NOOR	0.2	0.2	0.9	0.9	1.00

Table 4. Continued.

Common name, scientific name	Code	Introduced		Native		*P*-value[1]
		$\bar{x}$	SE	$\bar{x}$	SE	
Dickcissel, *Spiza americana*	DICK	6.0	2.9	15.5	11.1	0.63
Northern cardinal, *Cardinalis cardinalis*	NOCA	0.0	0.0	0.9	0.9	0.38
Indigo bunting, *Passerina cyanea*	INBU	0.0	0.0	0.2	0.2	0.38
Painted bunting, *Passerina ciris*	PABU	0.2	0.2	0.2	0.2	1.00
Field sparrow, *Spizella pusilla*	FISP	0.6	0.4	2.8	1.6	0.44
Lark sparrow, *Chondestes grammacus*	LASP	3.0	1.6	8.3	2.8	0.09
Grasshopper sparrow, *Ammodrammus savannarum*	GRSP	36.7	13.3	37.4	8.0	0.37
Total bird abundance		87.3	20.1	121.7	14.8	0.11
Species richness		7.5	1.0	10.1	0.9	0.14

[1]from a Wilcoxon 2-sample signed-rank test

Fig. 1

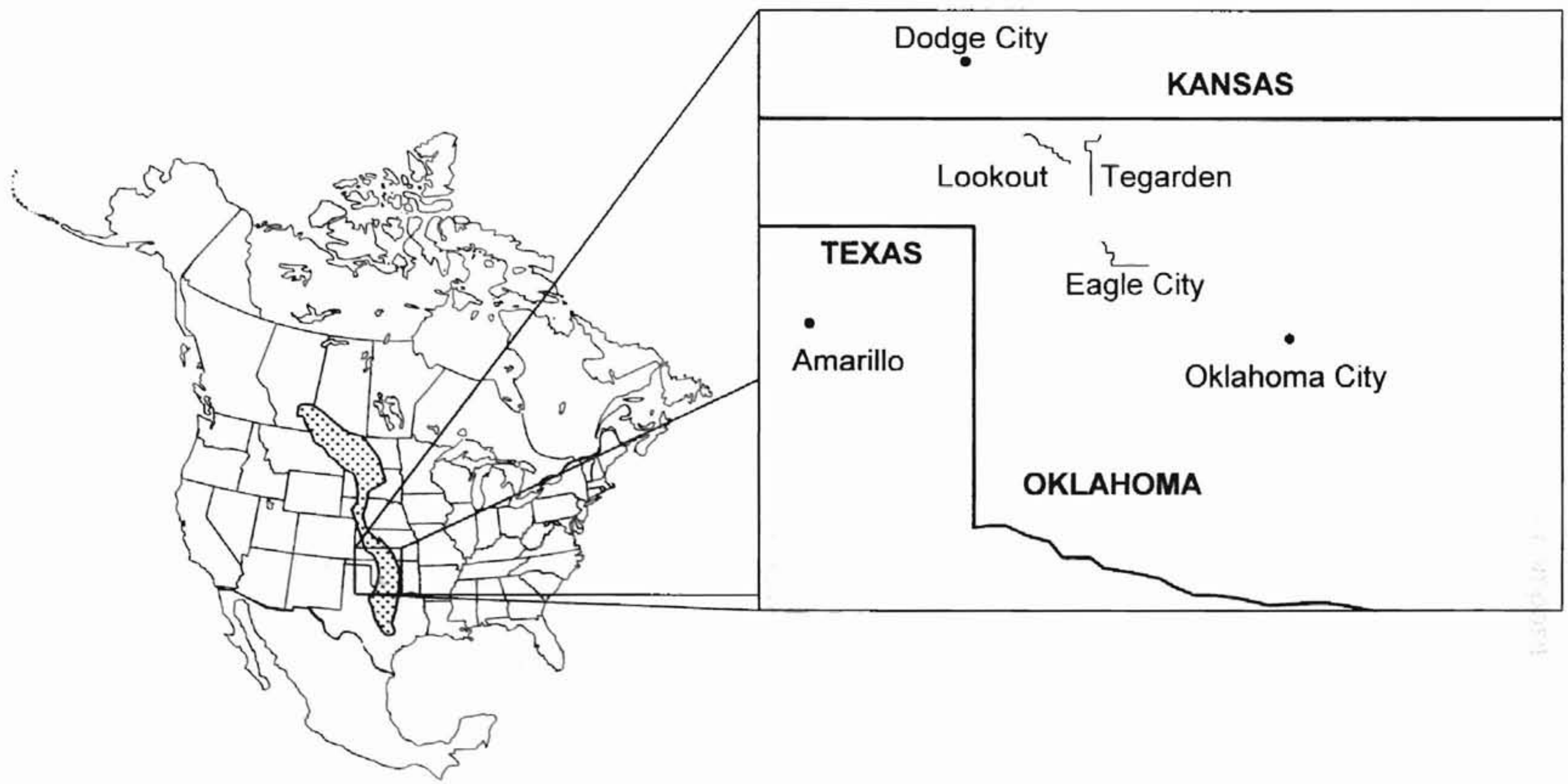
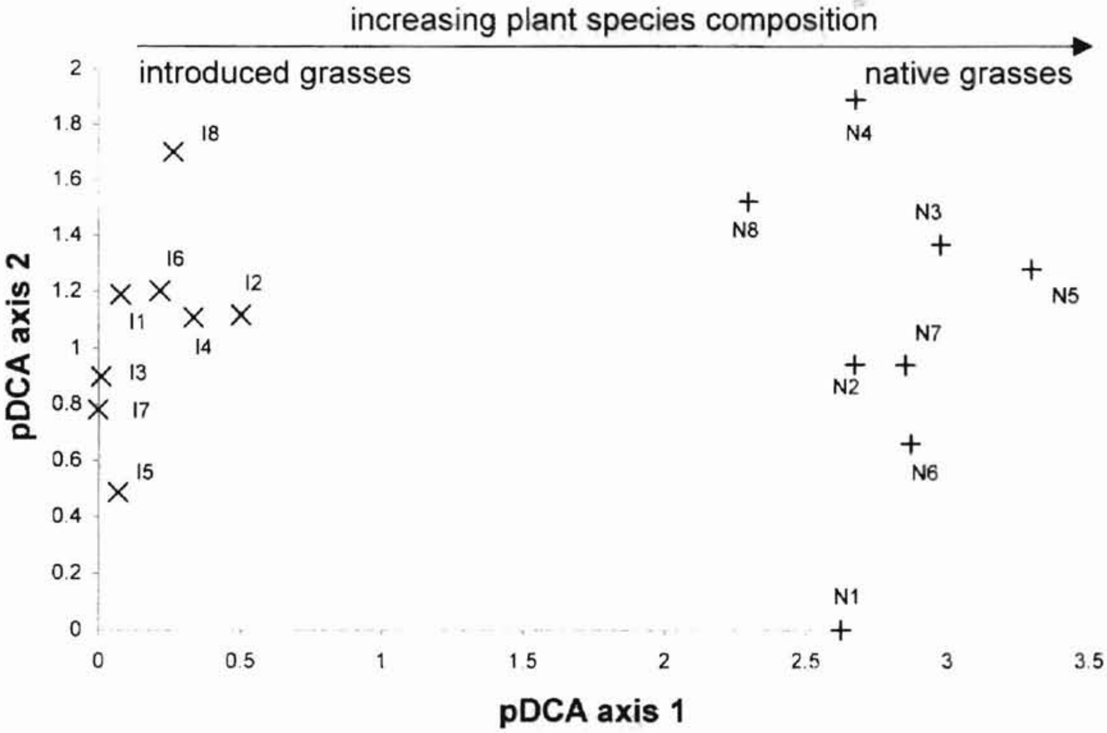

Dodge City
KANSAS
Lookout
Tegarden
TEXAS
Eagle City
Amarillo
Oklahoma City
OKLAHOMA

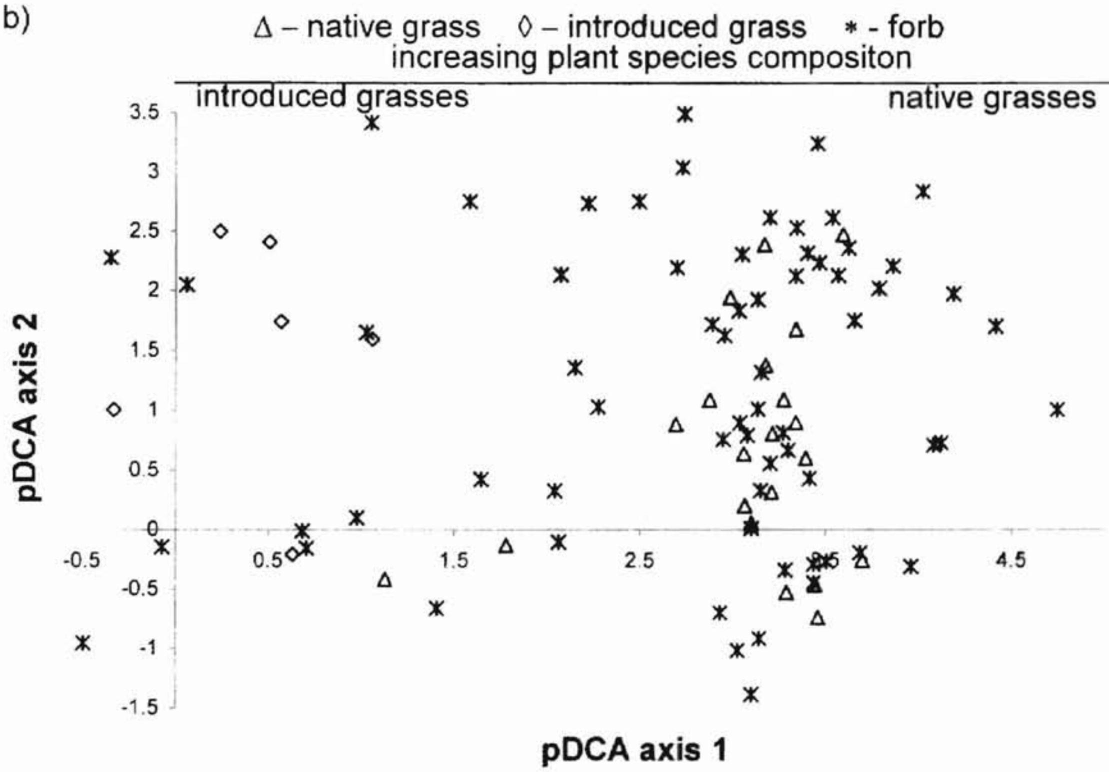
Fig. 2

a)



increasing plant species composition
introduced grasses
native grasses
pDCA axis 2
pDCA axis 1
I1
I2
I3
I4
I5
I6
I7
I8
N1
N2
N3
N4
N5
N6
N7
N8
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
0.5
1.5
2.5
3
3.5

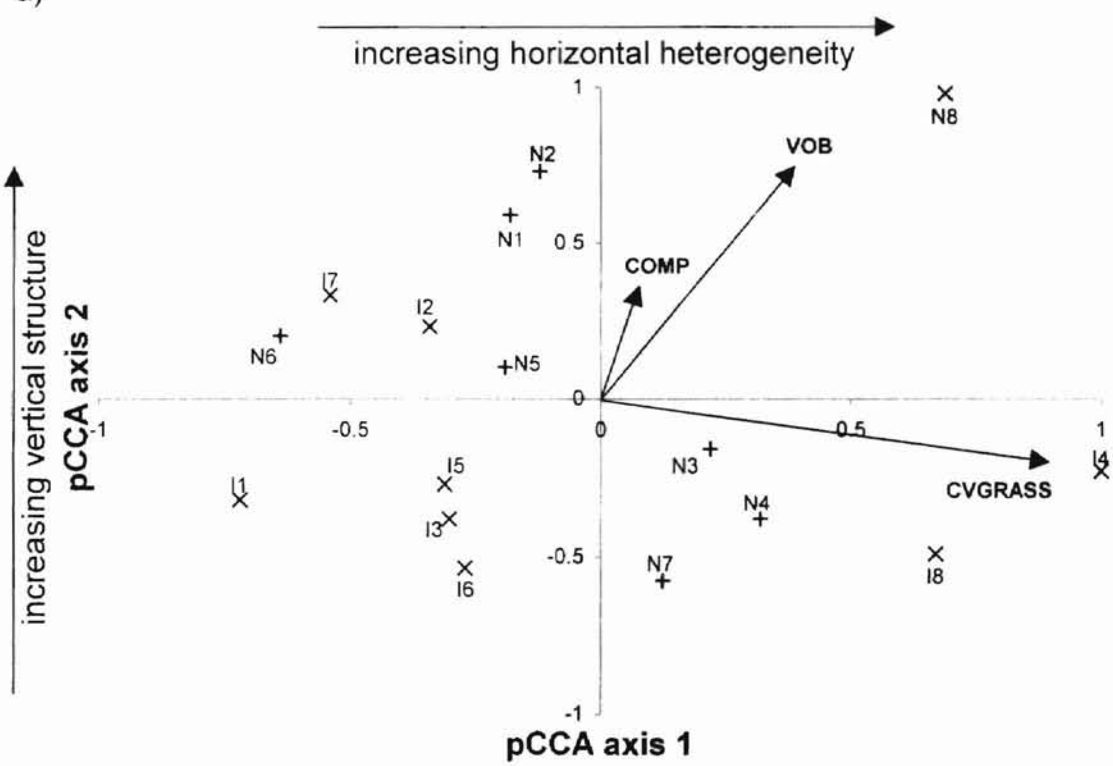
b)



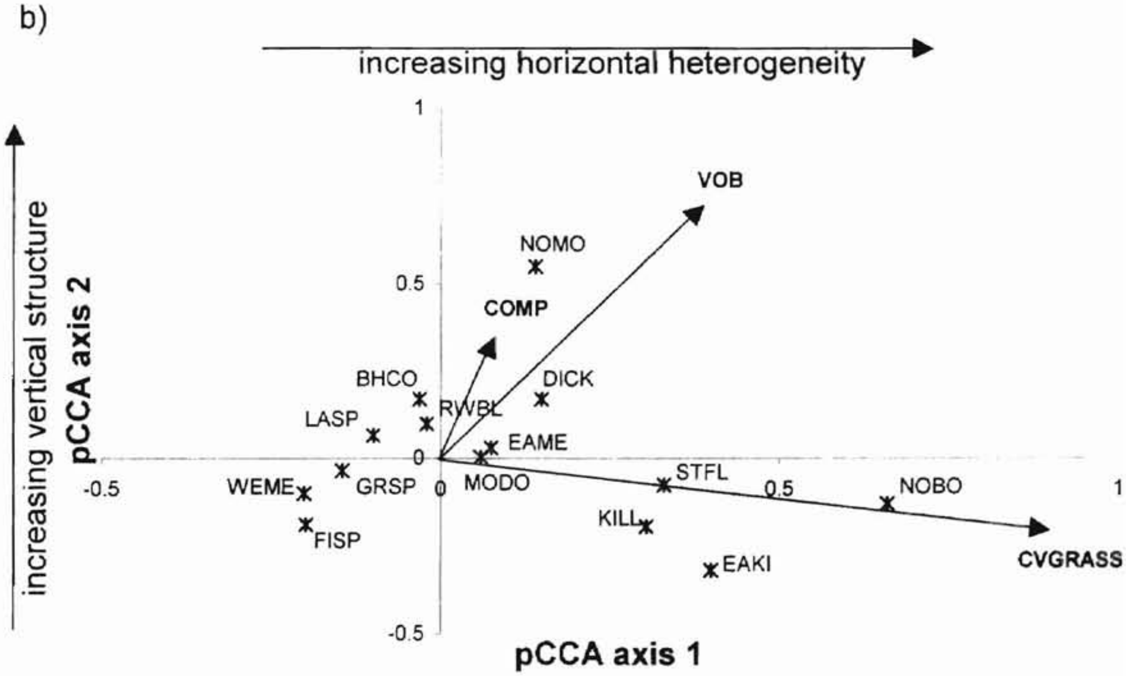
Δ – native grass ◊ – introduced grass * - forb
increasing plant species compositon
introduced grasses
native grasses
pDCA axis 2
pDCA axis 1
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
3
3.5
2.5
4.5

Fig. 3

a)


increasing horizontal heterogeneity
increasing vertical structure
pCCA axis 2
pCCA axis 1
VOB
COMP
CVGRASS
N1
N2
N3
N4
N5
N6
N7
N8
I1
I2
I3
I4
I5
I6
I7
I8
1
0.5
0
-0.5
-1
-1
-0.5
0
0.5
1

b)


increasing horizontal heterogeneity
increasing vertical structure
pCCA axis 2
pCCA axis 1
VOB
COMP
CVGRASS
NOMO
BHCO
RWBL
DICK
LASP
EAME
WEME
GRSP
MODO
STFL
NOBO
KILL
FISP
EAKI
1
0.5
0
-0.5
-0.5
0
0.5
1

APPENDICES

Appendix A. List of plant species by category occurring on study sites within the southern mixed prairie of Oklahoma.

Category Common name	Scientific Name
Native grasses and grass-like plants	
Sand bluestem	*Andropogon hallii*
Annual threeawn	*Aristida oligantha*
Arrowleaf threeawn	*Aristida purpurascens*
Perennial threeawn	*Aristida purpurea*
Sideoats grama	*Bouteloua curtipendula*
Blue grama	*Bouteloua gracilis*
Hairy grama	*Bouteloua hirsuta*
Silver bluestem	*Bothriochloa saccharoides*
Buffalograss	*Buchloe dactyloides*
Sedges	*Carex* spp.
Sandbur	*Cenchrus incertus*
Hooded windmillgrass	*Chloris verticillata*
Western wheatgrass	*Elymus smithii*
Foxtail barley	*Hordeum jubatum*
Little barley	*Hordeum pusillum*
Prairie junegrass	*Koeleria pyramidata*
Fall witchgrass	*Leptoloma cognatum*
Plains Muhly	*Muhlenbergia cuspidata*
Vine-mesquite panicum	*Panicum obtusum*
Scribner panicum	*Panicum scribnerianum*
Switchgrass	*Panicum virgatum*
Sand paspalum	*Paspalum setaceum*
Texas bluegrass	*Poa arachnifera*
Tumblegrass	*Schedonnardus paniculatus*
Little bluestem	*Schizochyrum scoparium*
Indiangrass	*Sorgastrum nutans*
Tall dropseed	*Sporobolus asper*
Sand dropseed	*Sporobolus cryptandrus*
Tridens	*Tridens* spp.
Six weeks fescue	*Vulpia octoflora*
Introduced grasses	
Old World bluestem	*Bothriochloa ischmaeum*
Rescuegrass	*Bromus catharticus*
Japanese brome	*Bromus japonicus*
Downy (cheatgrass) brome	*Bromus tectorum*
Bermudagrass	*Cynodon dactylon*

Appendix A. Continued

Category Common name	Scientific Name
Introduced grasses	
Weeping lovegrass	*Eragrostis curvula*
Johnsongrass	*Sorghum halepense*
Sorghum	*Sorghum vulgare*
Wheat	*Triticum aestivum*
Forbs	
Common yarrow	*Achillea millefolium*
Garlic	*Allium* spp.
Western ragweed	*Ambrosia psilostachya*
Giant ragweed	*Ambrosia trifida*
Field pussytoes	*Antennaria neglecta*
Pussytoes	*Antennaria* spp.
Lazy daisy	*Aphanostephus skirrhobasis*
Intermediate Pricklypoppy	*Argemone intermedia*
Cudweed sagewort	*Artemisia ludoviciana*
Antelope horns	*Asclepias asperula*
Broad-leaved milkweed	*Asclepias latifolia*
Butterfly milkweed	*Asclepias tuberosa*
Western daisy	*Astranthium integrifolium*
Wine cup	*Callirhoe involucrata*
Shepherds-purse	*Capsella bursa-pastoris*
Queen Ann's thistle	*Carduus nutans*
Yellow paintbrush	*Castilleja citrina*
Chaetopha	*Chaetopha* spp.
Spreading chervil	*Chaerophyllum texanum*
Lambsquarter	*Chenopodium album*
Hairy goldenaster	*Chrysopsis villosa*
Texas thistle	*Cirsium texanum*
Wavyleaf thistle	*Cirsium undulatum*
Erect dayflower	*Commelina erecta*
Field bindweed	*Convolvulus arvensis*
Mares tail	*Conyza canadensis*
Scrambled eggs	*Corydalis micrantha*
Texas croton	*Croton texensis*
Buffalogourd	*Cucurbita foetidissima*
Pinnate tansymustard	*Descurainia pinnata*
Prairie larkspur	*Delphinium virescens*
Poor joe (rough buttonweed)	*Diodia teres*

Appendix A. Continued

Category Common name	Scientific Name
Forbs	
Whitlowgrass	*Draba reptans*
Black samson	*Echinacea angustifolia*
Fleabane daisy	*Erigeron strigosus*
Western wallflower	*Erysimum asperum*
Evax	*Evax* spp.
Wooly evolvulus	*Evolvulus nuttallianus*
Bedstraw	*Galium* spp.
Indian blanket	*Gaillardia pulchella*
Scarlet gaura	*Gaura coccinea*
Common broomweed	*Gutierrezia dracunculoides*
Broom snakeweed	*Gutierrezia sarothrae*
Wax goldenweed	*Haplopappus ciliatus*
Common sunflower	*Helianthus annulus*
Maximillian sunflower	*Helianthus maximilianii*
Rough falsepennyroyal	*Hedeoma hispida*
Camphorweed	*Heterotheca subaxillaris*
Smooth white hymenopappus	*Hymenopappus scabiosaeus*
Stemless hymenoxys	*Hymenoxys acaulis*
Rayless hymenoxys	
Range ratany	*Krameria lanceolata*
Prickly lettuce	*Lactuca serriola*
Peppergrass	*Lepidium* spp.
Bladderpods	*Lesquerella* spp.
Dotted gayfeather	*Liatris punctata*
Blue toadflax	*Linaria canadensis*
Yellow flax	*Linum rigidum*
Grooved flax	*Linum sulcatum*
Narrowleaf puccoon (gromwell)	*Lithospermum incisum*
Stickleaf	*Mentzelia oligosperma*
Tenpetal mentzelia	*Mentzelia decapetala*
Plains horsemint (lemon beebalm)	*Monarda citriodora*
Wild bergamot	*Monarda fistulosa*
Spotted beebalm	*Monarda punctata*
Cutleaf eveningprimrose	*Oenethera laciniata*
Toothleaved eveningprimrose	*Oenethera serrulata*
Common yellow oxalis (woodsorrel)	*Oxalis stricta*
Sheep sour (violet woodsorrel)	*Oxalis violacea*

Appendix A. Continued

Category Common name	Scientific Name
Forbs	
Purple groundcherry	*Physalis lobata*
Wooly plantain	*Plantago patagonica*
Blackseed plantain	*Plantago rugelii*
White milkwort	*Polygala alba*
Annual buckwheat	*Polygonum annulus*
Smartweed	*Polygonum* spp.
Devil's claw	*Proboscidea louisianica*
Heal-all	*Prunella caroliniana*
Plains psilotrophe	*Psilostrophe villosa*
False dandelion	*Pyrrhopappus scaposus*
Prairie coneflower	*Ratibida columnifera*
Black-eyed susan	*Rudbeckia hirta*
Curly dock	*Rumex crispus*
Threadleaf groundsel	*Senecio flaccidus*
Carolina horsenettle	*Solanum carolinense*
Silverleaf nightshade	*Solanum elaeagnifolium*
Buffalobur	*Solanum rostratum*
Goldenrods	*Solidago* spp.
Scarlet globemallow	*Sphaeralcea coccinea*
Common chickweed	*Stellaria media*
Common dandelion	*Taraxacum officinale*
Threadleaf thelesperma	*Thelesperma filifolium*
Rayless thelesperma	*Thelesperma megapotamicum*
Hedge parsley	*Torilis nodosa*
Ohio spiderwort	*Tradescantia ohiensis*
Noseburn	*Tragia ramosa*
Venus looking-glass	*Triodanis perfoliata*
Speedwell	*Veronica* spp.
Cocklebur	*Xanthium strumarium*
Legumes	
Prairie acacia	*Acacia angustissima*
Groundplum milkvetch	*Astragalus crassicarpus*
Wooly loco	*Astragalus mollissimus*
Blue wild indigo	*Baptisia australis*
Golden dalea	*Dalea aurea*
Slender dalea	*Dalea enneandra*
Tick clover	*Desmodium* spp.

Appendix A. Continued

Category Common name	Scientific Name
Legumes	
Sericea lespedeza	*Lespedeza cuneata*
Lupine	*Lupinus* spp.
Yellow sweetclover	*Melilotus officinalis*
Catclaw sensitivebrier	*Mimosa quadrivalis*
Loco weed	*Oxytropis lambertii*
Purple prairieclover	*Petalostemon purpureum*
Slimflower scurfpea	*Psoralidium tenuiflora*
Sophora	*Sophora* spp.
Hairy vetch	*Vicia villosa*
Trees and Shrubs	
Sand sagebrush	*Artemesia filifolia*
Hackberry	*Celtis occidentalis*
Roughleaf dogwood	*Cornus drummondii*
Eastern redcedar	*Juniperus virginiana*
Virginia creeper	*Parthernocissus quinquefolia*
Eastern cottonwood	*Populus deltoides*
Sand plum	*Prunus angustifolia*
Shinnery oak	*Quercus havardii*
Blackjack oak	*Quercus marilandica*
Post oak	*Quercus stellata*
Aromatic sumac	*Rhus aromatica*
Winged sumac	*Rhus copallina*
Smooth sumac	*Rhus glabra*
Greenbriers	*Smilax* spp.
Buckbrush	*Symphoricarpos orbiculatus*
Poison-ivy	*Toxicodendron radicans*
American elm	*Ulmus americana*
Plains yucca	*Yucca glauca*
Cactus	
Lace cactus	*Echinocereus reichenbachii*
Prickly pear	*Opuntia* spp.

Appendix B. Biomass (dg) of invertebrate orders within patches of native prairie with encroachment 0f *Juniperus virginiana* (n = 12) of southern mixed prairie.

Juniper cover (%) Order	0.00	0.39	3.42	9.04	9.60	12.80	13.3	14.71	16.16	25.20	25.44	25.92
Acarina	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00
Amblypygi	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Aranea	2.00	0.47	1.68	2.40	0.45	0.38	0.35	0.84	0.50	0.24	1.63	0.89
Coleoptera	2.98	1.17	2.83	3.88	1.44	5.13	4.20	4.28	3.40	1.34	2.67	1.14
Diptera	0.34	0.59	0.43	0.33	3.62	0.42	0.43	0.52	0.09	0.69	1.53	0.26
Hemiptera	0.19	0.19	0.21	0.36	0.27	0.00	0.44	1.23	0.75	1.81	1.00	0.13
Homoptera	3.87	0.68	0.41	2.94	2.37	0.46	6.39	2.77	1.02	0.42	4.52	1.34
Hymenoptera	0.27	0.24	0.91	0.07	3.68	0.50	1.14	0.98	0.16	2.40	1.16	0.21
Lepidoptera	0.41	0.15	0.39	1.25	0.80	0.08	2.58	1.66	0.64	1.90	1.28	1.43
Mantodea	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Neuroptera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00
Odonata	0.24	0.00	0.48	0.23	0.11	0.11	0.32	0.00	0.29	0.07	0.00	0.52
Orthoptera	33.39	3.61	15.76	40.63	30.84	25.50	63.10	82.19	10.45	55.66	35.28	12.95
Phasmatodea	0.00	1.87	1.85	20.62	0.00	0.00	0.00	0.00	0.00	0.00	1.91	2.50
Protura	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Unknown	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.37	0.00	0.00
Total Biomass	43.73	8.97	25.19	72.71	43.58	32.58	78.95	94.47	17.46	64.98	50.99	21.37

Appendix C. Biomass ($\bar{x}$ dg ±SE) of invertebrate orders within introduced (n=8) and native (n = 8) grasslands of southern mixed prairie.

	Introduced		Native		
Order	$\bar{x}$	SE	$\bar{x}$	SE	*P*-value[1]
Acarina	0.01	0.01	0.00	0.00	0.49
Aranea	0.39	0.11	1.06	0.21	0.01
Coleoptera	1.21	0.53	1.68	0.37	0.27
Diptera	0.39	0.06	0.50	0.13	0.79
Hemiptera	0.35	0.12	0.70	0.23	0.17
Homoptera	0.78	0.30	1.56	0.30	0.05
Hymenoptera	0.31	0.17	0.41	0.05	0.07
Lepidoptera	0.39	0.10	0.62	0.14	0.27
Mantodea	0.00	0.00	0.01	0.01	0.38
Neuroptera	0.00	0.00	0.01	0.01	0.38
Odonata	0.02	0.01	0.08	0.03	0.18
Orthoptera	4.17	1.13	13.79	3.47	0.04
Phasmatodea	0.00	0.00	2.93	1.67	0.01
Unknown	0.02	0.02	0.17	0.16	0.85
Total biomass	8.04	1.94	23.50	4.90	0.02

[1]from a Wilcoxon 2-sample signed-rank test

VITA

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