Restoring Savanna Using Fire: Impact on the Breeding Bird Community

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Abstract

Restoration of many terrestrial plant communities involves the reintroduction of fire. However, there have been few studies of the effects of fire on the avifauna during the restoration process. To study the effects of oak savanna restoration on avian communities, breeding birds were censused and the vegetation structure documented in seven experimental burn units (8–18 ha) that had experienced different frequencies of controlled burns during the past 31 years (0–26 burns). Data were analyzed with both direct and indirect gradient analyses using multivariate techniques. The results showed that, as savanna restoration proceeded, there was a general decline in predominantly insectivorous species, particularly those that feed in the upper canopy region (leaves and air space), and a general increase in omnivorous species, particularly those that feed on the ground and in the lower canopy. Insectivorous bark gleaners (woodpeckers) also increased during restoration and were correlated with the increase in standing dead trees resulting from the fires. Overall, savanna restoration resulted in increases in the abundance of many open country bird species, including many species that have been declining in central and eastern North America, including red-headed woodpecker, Baltimore oriole, eastern kingbird, vesper sparrow, field sparrow, lark sparrow, brown thrasher, American goldfinch, and brown-headed cowbird. The shifts in species and guilds were correlated with changes in burn frequency and the macro vegetation structure—tree and shrub density, leaf area index, and relative proportion of standing dead trees. The findings show that savanna restoration can increase bird diversity and provide important habitat for uncommon or declining bird species. These birds are most likely attracted to one or more of the distinctive habitat features of the restored savanna environments, including scattered mature trees, standing dead trees and snags, and presence of both shrubby and grassland vegetation. The findings also suggest that restoration ecologists and wildlife biologists will need to work together to achieve desired goals, since different types of savanna restoration efforts may produce different effects on the breeding bird community.

Key words: savanna, oaks, fire, bird communities, bird foraging guilds, restoration ecology.

Introduction

Efforts to restore endangered or threatened North American ecosystems normally focus on vegetation, despite the fact that restored ecosystems are becoming increasingly important habitats for many animal species (Morrison 1995). Although some recent efforts have included animals in restoration goals (Leach & Ross 1995), data needed to implement these recovery efforts are usually lacking or insufficient. For example, although the restoration of many terrestrial plant communities involves the reintroduction of fire, there have been few studies of the effects of fire on the resident bird communities (Lowe et al. 1975; Whelan 1995).

In central and eastern North America, many bird species that typically inhabit open country environments (e.g., grassland, orchard, savanna, and successional scrub) have declined during the last 35 years (DeGraaf & Rudis 1986; Askins 1993; Herkert 1994; Peterjohn & Sauer 1994). Declines in such open country species as vesper sparrow, lark sparrrow, Baltimore oriole, eastern kingbird, and red-headed woodpecker are believed to be caused by habitat destruction and by the change in vegetation structure in savanna and successional-scrub environments, many of which have been converted into forested habitats because of natural succession (Askins 1993; Peterjohn & Sauer 1994). Most of the

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open country species that are declining inhabit midwestern oak savannas (Robinson 1994; Sample & Mossman 1994). Unfortunately, although oak savannas were once common in midwestern North America, few of these environments remain, the rest having been destroyed through land clearing for agriculture and housing or converted to woodland and forest through succession in the absence of fire (Nuzzo 1986).

Recently, midwestern oak savannas have been the focus of restoration efforts (Leach & Ross 1995). Restoring oak savannas from converted oak woodland and forest usually involves the reintroduction of fire (Irving 1970; Faber-Langendoen & Davis 1995; Leach & Ross 1995). Although some preliminary observations have been made regarding the bird communities in managed and unmanaged oak savanna and woodland communities in this region (Mossman & Sample 1994; Robinson 1994; Sample & Mossman 1994), the effects of fire on avian communities in midwestern oak savannas and forests are poorly understood (Brawn 1994; Robinson 1994). In particular, there have been few reports on the impact of oak savanna restoration on bird species that have been declining in numbers in central and eastern North America.

The goals of this study were to determine if there is a change in the composition of the breeding bird community during savanna restoration by fire, to describe these changes if they exist, to determine what changes in the vegetation structure were likely responsible for any observed changes in the avifauna, and to determine whether savanna restoration can provide suitable habitat for some of the bird species currently in decline in central and eastern North America.

This study is organized around the concept of a "restoration gradient" defined as "a more or less continuous and predictable change in some biological or physical component of the site(s) being restored." Examples of possible restoration gradients include: change in tree density, change in disturbance frequency, and change in the composition of the bird or small mammal community. The concept of a restoration gradient is similar to the ecological concept of a "succession gradient" (Begon et al. 1996), but is distinguished by the fact that the gradient is produced by human manipulation of the environment. Like succession gradients, one restoration gradient (e.g., change in fire frequency) can influence another gradient (e.g., vegetation structure), which in turn can influence another (e.g., animal community).

Study Site

The study was conducted at Cedar Creek Natural History Area (CCNHA), a protected scientific and study area located in east central Minnesota (45°25′N, 93°10′W). CCNHA is situated on the Anoka Sandplain, a glacial outwash area that is characterized by coarse textured soils low in nitrogen (Grigal et al. 1974). This area is located in the transition zone between the central grasslands and the mixed deciduous and coniferous forest of eastern North America. Prior to settlement by Europeans, oak savanna and barrens were among the dominant vegetation types at CCHNA, with *Quercus macrocarpa* Michx. (bur oak) and *Quercus ellipsoidalis* E. J. Hill (northern pin oak) being the two dominant tree species (Grigal et al. 1974; Wovcha et al. 1995). Important shrubs and woody ground cover in the oak savanna/woodland at CCNHA include *Corylus americana* (American hazel), *Rhus glabra* (smooth sumac), *Prunus virginiana* (chokecherry), *Parthenocissus* spp. (Virginia creeper) and *Toxicodendron radicans* (poison ivy), and dominant grasses/sedges are *Andropogon gerardii*, *Schizachyrium scoparius*, *Sorghastrum nutans*, *Poa pratensis*, and *Carex pensylvanica.*

In 1964 a prescribed burning program was initiated at CCNHA to restore and maintain oak savanna and woodland vegetation and to test the effects of different burn frequencies on vegetation structure (Irving 1970). An area of 210 ha was divided into 14 burn management units. Management units were assigned to one of seven burn frequencies, ranging from nearly every year to complete fire exclusion. This study was conducted in seven of these burn units, ranging in size from 8.1 to 18.2 ha. From 1964 to 1995, the respective burn units experienced 0 to 26 fires. All burns were conducted in the spring, except two late summer fires in unit 107 (see Rimmel 1979 for more information regarding the burns). Although no vegetation data were collected prior to the start of the controlled burning program in 1964, several subsequent studies have documented fire-induced changes in the vegetation structure (e.g., tree and shrub density and cover) in the burn units (Irving & Aksamit 1983; White 1983; Tester 1989; Peterson 1998; Fig. 1).

Methods

The controlled burning program began in 1964, and all burn units were the same age, 31 years. However, the units differed in the intensity of the restoration effort (number of burns). Since the focus of the study was the effects on the bird community of changes in the vegetation produced during restoration, it was important to be able to exclude other factors that are known to affect the structure of bird communities, such as size of the site (Harris 1984; Blake & Karr 1987), location of the site in the landscape (Temple et al. 1979; Wiens 1996), and regional effects (i.e., the presence or absence of particular bird species at the larger, regional scale; Temple 1998).

The 32-year controlled burning experiment at CCNHA provided a unique opportunity to study the impact of savanna restoration on bird communities because these other variables could be excluded as possible factors af-

Figure 1. Burn unit 104 (burned 26 times in 32 years). Frequently burned units (restored oak savanna habitat) are characterized by scattered mature trees, mostly *Quercus macrocarpa* (bur oak), some standing dead trees and snags, and varying degrees of shrubby cover, consisting either of true shrubs (e.g., *Corylus americana* [American hazel]), or patches of resprouting oaks, particularly *Quercus ellipsoidalis* (pin oak). Unburned units, representing oak woodland, are characterized by higher densities of trees, including many in the sapling stage, the presence of more fire intolerant canopy and subcanopy tree species (e.g., *Prunus serotina* [black cherry], *Acer rubrum* [red maple], *Prunus virginiana* [chokecherry], and *Amelanchier* spp. [serviceberry]), a prominent shrub layer, particulary American hazel, and proportionately fewer standing dead trees. Restored oak savanna environments, such as the one shown, provide new habitat for many open country bird species that have been declining in eastern and central North America. The birds are most likely attracted to one or more of the distinctive habitat features of the restored savanna environments, including scattered mature trees, standing dead trees and snags, and presence of both shrubby and grassland vegetation.

fecting the results. All burn units were approximately the same size (8–18 ha) and all were located within an area less than 300 ha. Thus, all units were located in the same region and were surrounded by the same landscape matrix of woodlands, old fields, wetlands, agricultural land, and low-density rural housing, thereby ruling out possible effects of landscape location. As a result, if differences in bird communities were observed among the burn units, the differences would most likely be due to differences in vegetation among burn units. Owing to the close proximity of the burn units to one another, and to the mobility of birds, it is possible that the avian composition of particular burn units could be influenced by the vegetation structure of nearby units. If true, the results should be affected in a conservative way since such effects, if they existed, would tend to reduce differences among units. Thus, any observed differences in the avian composition among burn units can be viewed as minimum differences produced by the different fire regimes.

Vegetation Sampling

In 1995 vegetation was sampled in permanent plots (50 × 75 m, 0.375 ha) that had been established in 1984 (one plot per burn unit). The number of live tree stems in the plot with diameter at breast height (dbh) greater than 5 cm was recorded. Tree stems that forked less than 0.5 m from the ground were counted as separate stems. Since many birds use standing dead trees for nesting, foraging, and/or perching, and since controlled burns in oak woodlands kill some trees (Irving & Aksamit 1983), standing dead stems with dbh greater than 10 cm were also counted. Shrub vegetation was sampled by counting stems in circular (1-m radius) subplots, 24 per plot. In addition to stem counts, measurements of leaf area index (LAI) (trees and shrubs combined) were made in burn units using a Licor LAI2000 positioned 50 cm above the ground. The LAI values obtained using the LAI2000 were compared with LAI estimates made from litter fall traps in the same burn units. Tree and shrub densities were converted to density per ha, and the importance of large standing dead trees in a burn unit was calculated as the ratio of dead to live trees counted in the plots.

Bird Censusing

Birds were censused in four of the burn units in June 1995, which included two units that had been burned frequently, units 104 and 106, and two that had not been burned, units 109 and 309. The four units were censused ten times, with the order of censusing rotating so that all units were censused both early and late between the hours of 0600 and 1000. Most migrant species have passed through CCNHA by the first of June and June is the peak nesting season for most breeding birds at CCNHA. Birds were censused along a 200-m transect in each unit in 1995, using the spot-mapping method (Emlen 1971). At 50-meter intervals along the transect, observers recorded birds detected visually or by call during a three minute detection period. Birds flying over more than 10 m above the canopy or estimated to be more than 100 m away were not included in the census.

In June 1996 seven burn units were censused (the four sampled in 1995 plus three others), each visited once per week for four weeks. The 1995 data had shown that four visits were sufficient to identify most of the breeding species in a burn unit. In 1996 birds were censused using a plot method developed by Holmes and Sturges (1975). The census method was changed in 1996 to provide a more direct measure of bird density. Using multiple observers with synchronized watches, this method yields actual counts of birds per plot. Given the size of the burn units, birds were censused in a square 4-ha plot (rather than the rectangular 10-ha plots used by Holmes and Sturges) established near the center of each burn unit. Larger census plots would have exceeded the boundaries of some of the units, and/or included small wetlands in the plot. In both years, some species breeding in adjacent wetlands (e.g., red-winged blackbirds) were occasionally observed in the study plots but were not included in the census. Since our goal was to compare the composition of the bird communities among the different burn units, we did not try to map or count individual bird territories.

In order to determine if restoration affected not only species composition, but also the composition of bird functional groups, or guilds (Root 1967), we used the foraging guild classification for North American birds developed by DeGraaf et al. (1985). In this scheme, birds are assigned to a foraging guild based on three aspects of foraging: food type, substrate where the food is found (e.g., bark, air, ground, upper canopy), and foraging technique (e.g., sallier, gleaner). Each bird is assigned a three-part code to represent its foraging guild. For species that forage differently during the breeding and nonbreeding season, DeGraaf et al. provided foraging guilds for both time periods. The breeding foraging guilds used in this study are shown in Appendix I. Several omnivorous species obtain their food by feeding frequently both on the ground and in the low canopy, that is, they feed commonly on two different substrates. In order to assign these species to a single guild, a combined guild was created: omnivorous, lower canopy/ground, foragers (OLCGF) (Appendix I).

Data Analysis

In order to assess the extent of variation in the composition of the avian community in the burn units between 1995 and 1996, we compared the data collected in the four burn units during both years using the percent similarity index, I_{PS} (Smith 1992). Although different census procedures were used in the two years, the same general approach was used (censusing via visual and auditory detection of individual birds), and comparable areas were censused (approximately 4 ha in each burn unit) in both years. Since the between year comparisons of the data were of a general nature, it is unlikely they would be substantially affected by the change in the censusing procedures.

More comprehensive analyses on the relationship between fire frequency, vegetation structure, and the avian communities in the different burn units were conducted on the 1996 data. We used the summed counts from the four visits in each plot, broken down by species, guilds, and guild components in these analyses. We used summed counts to avoid fractional bird counts. Essential results of the analyses would not have changed had we used birds per plot, summed count divided by four, or birds per hectare, summed count divided by 16. Species in which only a single individual was observed throughout all seven burn units during 1996 were excluded from these analyses.

In order to examine the distribution of species and guilds along the fire gradient, 1996 data were analyzed with both direct and indirect gradient analyses using multivariate techniques. Data were first analyzed using an indirect gradient analysis method, Correspondence Analysis (CA). CA, sometimes referred to as Reciprocal Averaging (McCune & Mefford 1997), is a graphical ordination technique that displays rows and columns of a data matrix (in this study, sites and species, and sites and guilds) as points in a low-dimension vector space (Greenacre & Underhill 1982). Relative distances between sites and species (or guilds) in this vector space indicate the strength of the association between the two. It is generally acknowledged that CA gives reasonable representations of only one axis and that subsequent axes introduce an arch into the first axis (Palmer 1993; McCune & Mefford 1997). Thus, only first axis CA results are reported. The nature of the distributions of the species, guilds, and guild components along the five possible environmental gradients recorded in this study (fire frequency, tree density, shrub density, LAI, and the importance of dead trees) was then examined by correlating the respective CA first axis coordinates of the sites with the measurements of these variables at the respective sites. Strong correlations between the axis and one or more environmental variables would provide an ecological context in which to interpret the graphical display.

An advantage of indirect gradient analysis is that the ordination is not dependent on the investigator knowing the key environmental variables ahead of time, a requirement of direct gradient analysis. However, if one does know the key environmental variables associated with the sites and species, direct gradient analysis, sometimes referred to as constrained ordination (Okland 1996), is an effective method of ordinating both sites and species that is optimized with respect to the specified set of environmental variables (ter Braak & Prentice 1988). The method of direct gradient analysis used in this study was Canonical Correlation Analysis (CCA) (Palmer 1993; Okland 1996). Environmental variables that were found to be correlated ($p < 0.1$) with the first CA ordination axis were included in the CCA of the species and guild data.

An advantage of CCA is that the strength and direction of the environmental variables can be plotted in the same vector space along with sites and species. The value of such a graph in this study is that the three different restoration gradients—sites, birds, and environmental variables—can all be shown with respect to one another. A second advantage is that CCA is not seriously affected by the arch effect (Palmer 1993), which permits the use of more than one ordination axis. To determine if any particular species or guilds were significantly correlated with either of the first two CCA axes, a correlation analysis was performed (number of individuals of a species or guild in each of the seven burn units versus the CCA axis 1 and 2 scores for the respective units).

Three of the foraging guilds consisted of a single species (granivorous ground gleaner: mourning dove; omnivorous lower canopy forager: indigo bunting; and omnivorous upper canopy gleaner: Baltimore oriole). Since the purpose of the multivariate analyses of guilds was to examine the distribution along the restoration gradient of groups of species with similar foraging strategies, the three guilds composed of a single species were not included in the CA and CCA of guilds.

All multivariate analyses were conducted using PC-ORD (McCune & Mefford 1997). In the CCAs, row and column scores were standardized using the centering and normalizing default option, scaling of ordination scores was performed by optimizing columns (species and guilds), and burn unit scores were graphed as linear combinations of the environmental variables. Correlation analyses were performed using JMP (SAS Institute).

Results

The results of the vegetation surveys are shown in Table 1. The most consistent vegetation change with restoration was the tendency for tree density and leaf area index (LAI) to decline with increasing burn frequency (tree density: $r^2 = 0.80$, $p = 0.0069$; LAI: $r^2 = 0.83$, $p = 0.0046$; Table 1).

Thirty-six bird species were recorded at least once in 1995 in the four burn units (two unburned and two frequently burned), whereas 33 species were recorded at least once in the same four burn units in 1996. Thirty-two species were recorded in both years. The 1996 species list shown in Table 2 (compiled from all seven burn units and including only species recorded at least twice) includes all 33 species recorded in the four burn units during 1996 except for *Buteo jamaicensis* (red-tailed hawk), which was recorded only once in 1996, and two additional species that were recorded in 1996 but not in the four burn units—*Pipilo erythrophthalmus* (eastern towhee) and *Melospiza melodia* (song sparrow). Species recorded in 1995 in the four burn units but not in the same units in 1996 were: *Strix varia* (barred owl), *Melanerpes carolinus* (red-bellied woodpecker), *Colaptes auratus* (northern flicker), and *Quiscalus quiscula* (common grackle). A *Sayornis phoebe* (eastern phoebe) was recorded in the four burn units in 1996 but not 1995. Although the species composition in unburned units differed substantially from that in the frequently burned units in both years ($I_{PS} = 44.1\%$ in 1995; $I_{PS} = 41.9\%$ in 1996), species composition was quite similar from one year to the next within burn treatments ($I_{PS} = 72.9\%$ in frequently burned units; $I_{PS} = 75.9\%$ in unburned units).

In 1995 avian species richness of the unburned units (17 and 23 species) was lower than that of the burned units (30 and 32). As shown in Table 1, this trend was exhibited again in 1996 (unburned units: 16.0 ± 3.0 (SE) species; burned units: 22.4 ± 1.57 species; $t = 2.08$, $p = 0.091$). Table 1 also shows that the burned units exhibited a higher density of detected birds in 1996 (unburned units: 3.82 ± 0.065 birds/ha; burned units: 6.95 ± 1.26 birds/ha; $t = 3.32$, $p = 0.021$).

Thirty-four species of upland birds representing ten foraging guilds were observed at least twice in the seven burn units in 1996 (Table 2). One-dimensional ordination plots of the Correspondence Analyses (points projected onto the first axis) are shown in Figure 2. In

Table 1. Size, burn frequency, and vegetation and 1996 bird data for the seven burn units after 32 years of fire management.

Burn Unit[a]	*Size (ha)*	*Number of Burns*	*Tree Density/ha*[b]	*LAI (Tree & Shrub)*[c]	*Dead:Live Trees*[d]	*Shrub Density stems/ha*	*Bird Species Richness*	*Bird Density/ha*	*CA Axis 1 Score*
105	16.2	15	80	0.44	0.865	15,461	28	8.56	−85
104	18.2	26	74	0.64	0.623	60,403	19	6.94	−80
103	10.9	25	208	0.76	0.551	27,209	20	5.81	−40
106	8.1	20	254	1.35	0.160	18,872	22	7.81	0
108	10.0	12	325	2.36	0.111	162,793	23	5.63	102
309	18.0	0	648	3.78	0.386	94,206	19	3.75	108
109	12.0	0	605	3.38	0.188	94,737	13	3.88	162

[a]Burn units are listed in the order of their axis one scores (right column) from the Correspondence Analysis of bird species.
[b]Tree density is density of live trees 5 cm dbh and greater.
[c]LAI = leaf area index of shrubs and trees.
[d]Dead:Live Trees = the ratio of the number of dead to live trees.
Values listed were obtained using the Licor LAI2000 and were highly correlated with LAI estimates made from litter fall traps in the respective burn units, $r^2 = 0.92$, $p = 0.0006$ (the LAI values listed for 109 and 309, the two unburned units, were about 20% lower than those estimated from the litter fall data).

Table 2. List of the 34 bird species recorded at least twice in the burn units in June 1996 and used in the CA and CCA analyses; also listed for each species is the foraging guild (consisting of food type, substrate, and technique) to which each was assigned (DeGraaf et al. 1985).[a,b]

	Guild Components			
Species	*Food*	*Substrate*	*Techniques*	*CA Axis 1 Scores*[c]
Icterus galbula (Baltimore oriole)	O	UC	F	−194
Pooecetes gramineus (vesper sparrow)	O	G	F	−171
Melospiza melodia (song sparrow)	O	G	F	−165
Sialia sialis (eastern bluebird)	I	G	G	−157
Turdus migratorius (American robin)	I	G	G	−139
Chondestes grammacus (lark sparrow)	O	G	F	−138
Bombycilla cedrorum (cedar waxwing)	I	A	S	−134
Cinclocerthia ruficauda (brown thrasher)	O	LCG	F	−132
Carduelis tristis (American goldfinch)	O	LCG	F	−131
Spizella pusilla (field sparrow)	O	G	F	−124
Zenaida macroura (mourning dove)	G	G	G	−104
Melanerpes erythrocephalus (red-headed woodpecker)	I	B	G	−103
Tyrannus tyrannus (eastern kingbird)	I	A	S	−97
Spizella passerina (chipping sparrow)	O	G	F	−88
Picoides villosus (hairy woodpecker)	I	B	G	−75
Poecile atricapillus (black-capped chickadee)	I	LC	G	−58
Sitta carolinensis (white-breasted nuthatch)	I	B	G	−50
Molothrus ater (brown-headed cowbird)	O	G	F	−44
Polioptila caerulea (blue-gray gnatcatcher)	I	UC	G	−36
Picoides pubescens (downy woodpecker)	I	B	G	−18
Sayornis phoebe (eastern phoebe)	I	A	S	26
Passerina cyanea (indigo bunting)	O	LC	F	39
Troglodytes aedon (house wren)	I	LC	G	49
Cyanocitta cristata (blue jay)	O	G	F	50
Contopus virens (eastern wood-pewee)	I	A	S	97
Corvus brachyrhynchos (American crow)	O	G	F	128
Piranga olivacea (scarlet tanager)	I	UC	G	161
Myiarchus tyrannulus (great-crested flycatcher)	I	A	S	174
Dendroica pensylvanica (chestnut-sided warbler)	I	LC	G	214
Empidonax minimus (least flycatcher)	I	A	S	222
Pipilo erythrophthalmus (eastern towhee)	O	G	F	241
Seiurus aurocapillus (ovenbird)	I	G	G	275
Vireo olivaceus (red-eyed vireo)	I	UC	G	283
Dumetella carolinensis (gray catbird)	O	LCG	F	318

[a]Key to guild abbreviations—Food: I, insectivore (including other invertebrates); G, granivore; O, omnivore; Substrate: A, air; B, bark; G, ground; LC, lower canopy; LCG, lower canopy and ground; UC, upper canopy; Technique: F, forager; G, gleaner; S, sallier.
[b]Birds are listed in the order of their CA axis one scores; negative values are associated with a more open savanna habitat, whereas positive values are associated more with a closed woodland habitat (thus, the change in species composition recorded during savanna restoration using fire can be viewed by reading the table from the bottom up; conversely, if fire is absent and the savanna converts to woodland through secondary succession, the expected change in bird species composition can be viewed by reading the table from the top down).
[c]The last column consists of the first axis scores from the Correspondence Analysis.

each of the five analyses (bird species, guild, and the three guild components), the first axis was significantly negatively correlated ($p < 0.1$) with burn frequency and positively correlated with live tree density and LAI. The ratio of dead to live trees was negatively correlated with first axis coordinates in the CAs of species, guilds, and foraging techniques, whereas shrub density was positively correlated with first axis coordinates in the analysis of species.

The correlation analyses show that axis one of the correspondence analyses represents a fire restoration gradient (increased burn frequency accompanied by fewer trees, lower LAI, and increased importance of dead trees). Thus, Figure 2 illustrates several trends in the bird community associated with the fire restoration gradient. As savanna restoration proceeds (right to left in Fig. 2), there is a shift in the dominant food type of the bird community, from predominantly insects to a mixed diet (Fig. 2c). There is a shift in the dominant substrate type for foraging, with upper canopy and air being most closely associated with less frequently burned and unburned units, and bark and ground being most closely associated with frequently

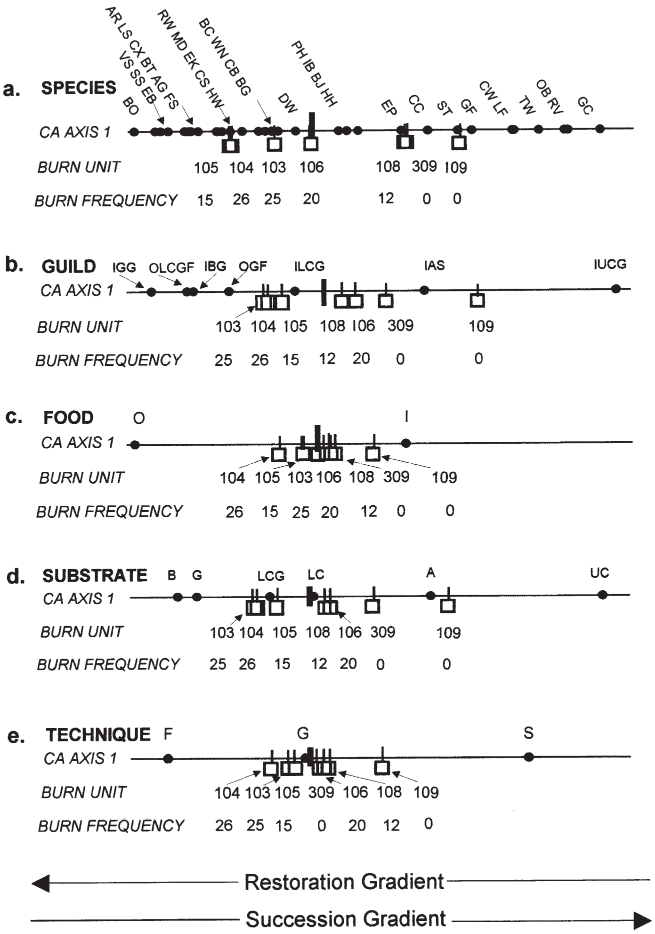

Figure 2. Results of Correspondence Analyses (first axis shown) of (a) species, (b) guilds, and guild components, (c) food type, (d) substrate, and (e) foraging technique (see Appendix I). The location of the burn units on the respective axes is indicated by the squares below the axes. The number of burns experienced by each burn unit is shown below the respective units. In each of the five analyses, the first axis coordinates were significantly correlated with many of the vegetation variables. Thus, the first axis can be viewed as an environmental restoration gradient, with restoration proceeding from right to left. As burn frequency increases and restoration proceeds, tree density and LAI (leaf area index) decrease, whereas the importance of dead trees increases. If fire were supressed, the vegetation variables and bird community would be expected to shift back to the right, part of a succession gradient. Key to Species: AG, American goldfinch; AR, American robin; BC, black-capped chickadee; BG, blue-gray gnatcatcher; BJ, blue jay; BO, Baltimore oriole; BT, brown thrasher; CB, brown-headed cowbird; AC, American crow; CS, chipping sparrow; CW, chestnut-sided warbler; CX, cedar waxwing; DW, downy woodpecker; EB, eastern bluebird; EK, eastern kingbird; EP, eastern wood-pewee; FS, field sparrow; GC, gray catbird; GF, great-crested flycatcher; HH, house wren; HW, hairy woodpecker; IB, indigo bunting; LF, least flycatcher; LS, lark sparrow; MD, mourning dove; OB, ovenbird; PH, eastern phoebe; RV, red-eyed vireo; RW, red-headed woodpecker; SS, song sparrow; ST, scarlet tanager; TW, eastern towhee; VS, vesper sparrow; WN, white-breasted nuthatch. Key to Guilds: IAS, insectivore air sallier; IBG, insectivore bark gleaner; IGG, insectivore ground gleaner; ILCG, insectivore lower canopy gleaner; IUCG, insectivore upper canopy gleaner; OGF, omnivore ground forager; OLCGF, omnivore lower canopy and ground forager.

burned units (Fig. 2d). There is also a shift in the dominant feeding techniques, with sallying being most closely associated with less frequently burned areas and foraging (defined by DeGraaf et al. 1985 as less selective feeding from a substrate) being most closely associated with frequently burned areas (Fig. 2e). Combining food type, substrate type, and feeding technique into foraging guilds (DeGraaf et al. 1985) shows a shift in foraging guilds along the restoration gradient (Fig. 2b). The foraging guilds most closely associated with less frequently burned units were insectivorous upper canopy gleaners and insectivorous air salliers. Guilds most closely associated with frequently burned areas included insectivorous ground gleaners, omnivorous lower canopy/ground foragers, insectivorous bark gleaners, and omnivorous ground foragers.

Figure 2a shows that ten species (gray catbird, red-eyed vireo, ovenbird, rufous-sided towhee, least flycatcher, chestnut-sided warbler, great-crested flycatcher, scarlet tanager, American crow, and eastern wood-pewee) are primarily associated with the less frequently burned and unburned units. Four species (eastern phoebe, indigo bunting, blue jay, and house wren) are clustered together in the middle of the gradient, whereas the remaining 20 species are associated more with frequently burned units. Figure 2b and Table 3 show that the shift in foraging guilds is associated with some taxonomic shifts in the bird communities. For example, three of the five Tyrannid flycatchers (insectivorous air salliers) are associated with the less frequently and unburned units, whereas all five sparrows (omnivorous ground foragers) and all three woodpeckers (insectivorous bark gleaners) are associated with the frequently burned units.

Since all five environmental variables were found to be significantly correlated ($p < 0.1$) with the first axes from the correspondence analyses of species and guilds, all five variables were included in canonical correspondence analyses of species and guilds. A two-dimensional ordination plot of the results of the CCA of guilds is shown in Figure 3. The horizontal direction of four of the environmental variable vectors (tree density, LAI, fire frequency, and importance of dead trees) shows that the first axis can be interpreted as a fire restoration gradient. In the CCA of species, the length and direction of the five environmental vectors were, with only minor differences, the same as shown in the ordination plot for guilds (Fig. 3). Live tree density, LAI (shrubs and trees), fire frequency, and importance of dead trees were significantly positively or

Table 3. List of species and guilds that exhibited a significant ($p < 0.10$) increase or decrease in abundance as restoration proceeded.[a]

	Increased	Decreased
Species	American robin***	gray catbird*
	Baltimore oriole*	great-crested flycatcher*
	brown thrasher**	least flycatcher*
	brown-headed cowbird*	ovenbird**
	cedar waxwing*	red-eyed vireo**
	eastern bluebird*	
	field sparrow*	
	vesper sparrow*	
Guilds	insectivorous bark gleaner*	insectivorous upper canopy gleaner**
	insectivorous ground gleaner**	
	omnivorous ground forager***	
	omnivorous lower canopy and ground forager*	

[a]A positive correlation with axis one of the respective CCA analysis indicated an increase, whereas a negative correlation indicated a decrease in abundance; significant values: * = 0.10, ** = 0.05, *** = 0.01.

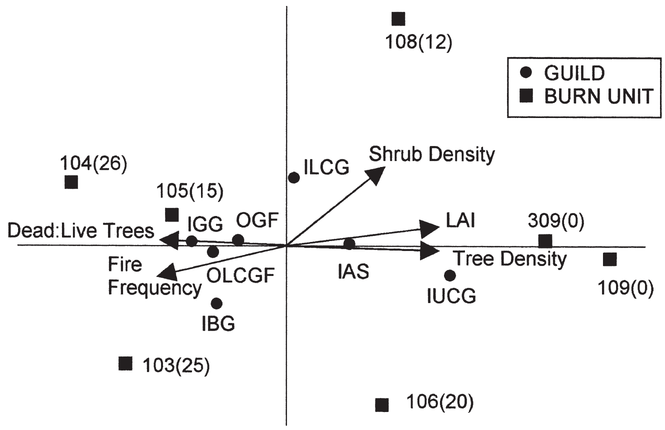

Figure 3. Ordination plot for the canonical correspondence analysis of guilds. The horizontal direction of four of the environmental vectors (live tree density, LAI [leaf area index of shrubs and trees], fire frequency, and the ratio of dead to live trees) indicates that axis one represents a restoration gradient, with restoration proceeding from right to left. Axis two is positively associated with shrub stem density ($p < 0.05$). The number of burns experienced by each of the burn units is shown in parentheses following the burn unit identification number.

negatively correlated ($p < 0.1$) with axis one in both CCAs. In the CCA involving species, shrub density was also positively correlated with axis one. None of the five variables was correlated with axis two in the CCA involving species. Shrub density was significantly positively correlated ($p < 0.05$) with axis two, but not axis one, in the CCA involving guilds (Fig. 3).

The correlation analyses (number of individuals of a species or guild in each of the seven burn units versus the CCA axis 1 and 2 scores for the respective burn units) showed that eight species and four guilds had a significant ($p < 0.1$) positive association with axis one (the restoration gradient; i.e., they increased as restoration proceeded; Table 3). Five species and one guild had a negative association with the restoration gradient, becoming less abundant as restoration continued (Table 3). There was also a significant positive association ($r = 0.836$, $p = 0.019$) between the guild of insectivorous lower canopy gleaners (ILCG: black-capped chickadee, chestnut-sided warbler, and house wren) and axis 2 (Fig. 3), that was significantly correlated with shrub density ($p < 0.05$).

Discussion

Prior to European settlement, fire played an important role in producing and maintaining successional and transitional habitats in central and eastern North America (Abrams 1992). The decline of these habitats as they have been converted to woodlands and forests by successional processes is likely due to fire suppression during the past century (Nuzzo 1986). Our results showed that reintroducing fire into woodland habitat as part of a savanna restoration effort can restore not only a vanishing vegetation type, but also the populations of many bird species. The 20 species associated with frequently burned units were double that associated with infrequently or unburned units (Fig. 2a). Of these 20, nine have been declining in abundance in central and/or eastern North America during the past 35 years (red-headed woodpecker, eastern kingbird, brown thrasher, brown-headed cowbird, Baltimore oriole, American goldfinch, vesper sparrow, field sparrow, and lark sparrow) (Askins 1993; Peterjohn & Sauer 1994). Significantly all nine species inhabit open country environments, and, except for the vesper sparrow which is designated as a grassland species, these species inhabit open country environments containing woody vegetation (e.g., scattered shrubs and/or trees) (DeGraaf & Rudis 1986; Peterjohn & Sauer 1994). Containing both grassland and woody vegetation (scattered shrubs and trees), restored oak savannas can provide important new habitat for these open country bird species.

The value of restored savannas as habitat for uncommon and/or declining species was keenly illustrated when we observed a singing male prairie warbler in burn unit 108 on one census. This observation represented only the eighth sighting of prairie warblers in the state of Minnesota during the past century. The fact that the prairie warbler was observed in unit 108 (with the highest shrub density of the seven burn units) is consistent with this species' reported reliance on shrubby vegetation (Robinson 1994). The increase in cowbirds (brood parasites) as restoration proceeded is not necessarily desirable, however, and our findings support the concern raised by Robinson (1994) that management of woodlands and savannas with fire might exacerbate the cowbird problem.

The decline in woody plant density and cover in frequently burned units is consistent with findings from previous studies at CCNHA (Tester 1989; Faber-Langendoen & Tester 1993; Peterson 1998) and in other fire-managed oak savannas and woodlands (Faber-Langendoen & Davis 1995; Davis et al. 1997). As woody plant cover declined because of fire, there was a general decline in predominantly insectivorous species, particularly those that feed in the upper canopy region (leaves and air space), and a general increase in omnivorous species, particularly those that feed on the ground and in the lower canopy. These findings are consistent with a prediction by Odum (1969) that foraging specialists should be more common later during secondary succession (as woody cover increases) whereas generalists should be more common early in succession (e.g., following a disturbance when woody cover is reduced).

Insectivorous bark gleaners (woodpeckers) also increased with increasing fire frequency, probably owing to the increased importance of standing dead trees. Taken together, our findings are very similar to those of Lowe et al. (1975) who investigated the effect of fire on the resident bird community in a very different environment—Arizona ponderosa pine forests. Lowe et al. (1975) found that woodpeckers and ground and brush feeding birds generally increased following wildfire in these forests, whereas birds feeding in the tree canopy generally decreased. The fact that both studies documented a similar shift in foraging groups suggests that this foraging shift may be a general phenomenon in the avian community, occurring whenever fire is introduced, or reintroduced, into a forest or woodland environment.

Overall, five of the seven guilds showed a significant positive or negative correlation with the fire restoration gradient (axis 1 in the CCA), whereas only 13 of the 34 species showed a significant positive or negative correlation with the same gradient. These results suggest that it should be easier to predict changes in the avian community during savanna restoration if predictions are based on foraging functional groups (guilds) rather than individual species.

Our findings indicate that reintroduction of fire into oak woodlands produces two important changes in vegetation structure that are likely responsible for most of the changes in the avifauna—decline in tree density (hence, increase in open area) and increase in the relative abundance of standing dead trees. The decline in tree density and concomitant increase in open area is responsible for the decline in canopy feeding and nesting forest birds during restoration and for the increase in ground feeding omnivores, particularly sparrows. The increased importance of standing dead trees is likely responsible for the increase in some of the woodpecker species, particularly red-headed woodpeckers, which nest in holes in the dead trees, and for some species that use the trees for singing perches (e.g., indigo buntings). Robinson (1994) emphasized that certain bird species likely will be dependent on the presence of shrubby vegetation in oak savannas and barrens. Our results confirm Robinson's claim. The insectivorous, lower canopy gleaners (black-capped chickadee, chestnut-sided warbler, and house wren) were positively correlated with axis two of the CCA, which was significantly correlated with shrub density. In addition, several other species associated with the restored savanna units either require or sometimes use shrubby vegetation for nesting (e.g, brown thrasher, vesper sparrow, lark sparrow, field sparrow, American goldfinch) (Baicich & Harrison 1997)

The importance to some bird species of shrubby vegetation or standing dead trees indicates that different savanna restoration goals and techniques will likely have different effects on the avian community. If a woodland is being restored gradually to a savanna using fire, as was the case in this study, then shrubby vegetation and standing dead trees will likely occur along most of the restoration gradient. However, if the goal is to restore a savanna more quickly, then physical removal of trees and shrubs is often part of the restoration effort (Nepstad 1981; Collins et al. 1996). In this case a subset of the potential breeding bird community may be absent during the restoration effort, particularly the insectivorous lower canopy gleaners and shrub nesters. Or, if savanna restoration is taking place in a grassland community, and involves the reintroduction of trees but not shrubs, then the same subset of breeding birds may be absent. The results from our study generally underscore the benefits associated with a more gradual restoration effort, one that results in a more diverse vegetation structure (including some shrubby vegetation and standing dead trees), which in turn results in a more diverse bird community.

The return of particular bird species to a savanna being restored depends on the species being present in the region (Temple 1998). In our case, the mosaic of grassland, old field, and savanna habitat that surrounded the burn units and Cedar Creek had maintained local populations of many bird species that were able to colonize the burn units once they had been sufficiently opened up by fire. Restoration of savanna habitat in a region depauperate in bird diversity (e.g., in a predominantly and intensively farmed district) may not yield the same increase in bird diversity found in this study.

In summary, the results show that restoring savanna using fire produces a change in the avian community that is strongly associated with changes in the macro vegetation structure. The results also show that oak savanna restoration can increase bird diversity and that the restored savanna environments can provide new habitat for many open country bird species that have been declining in eastern and central North America. These birds are most likely attracted to one or more of the distinctive habitat features of the restored savanna environments, including scattered mature trees, standing dead trees and snags, and the presence of both shrubby and grassland vegetation. The findings also indicate that restoration ecologists and wildlife biologists will need to work together in order to achieve desired goals, since different types of savanna restoration efforts will likely produce different effects on the vegetation, which in turn will differentially impact the breeding bird community.

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Appendix 1. List of the guild components and abbreviations used in this study. The explanations are from DeGraaf et al. 1985.

Guild Element and Abbreviation	*Explanation*
Food	Major food items during the breeding season.
Insectivore (I)	Feeds primarily on insects and/or other invertebrates, e.g., earthworms.
Omnivore (O)	Feeds on both animal and plant foods (the less common group makes up at least 10% of the diet).
Granivore (G)	Feeds primarily on seeds and nuts.
Substrate	The place where a food item is found or taken.
Air (A)	Caught in the air.
Bark (B)	On, in, or under the bark of trees.
Ground (G)	On the ground or on very low, weedy vegetation.
Lower Canopy (LC)	On leaves, twigs, and branches of shrubs, saplings, and lower crowns of trees.
Lower Canopy and Ground (LCG)	Feeds both in the lower canopy and on the ground.
Upper Canopy (UC)	On leaves, twigs, and branches of trees in the main substrate.
Technique	Refers to the manner in which food is obtained.
Forager (F)	Takes almost any food items encountered upon the substrate.
Gleaner (G)	Selects particular food items from the substrate.
Sallier (S)	Perches on exposed branch or twig, waits for insect to fly by, and then pursues and catches insect in air.