

Bird Community Relationships to Succession in Green Ash (*Fraxinus pennsylvanica*) Woodlands

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ABSTRACT. - We studied the relationship between breeding birds and seral stages of green ash (*Fraxinus pennsylvanica*) woodlands in central South Dakota between 1990 and 1992. Stands of early seral green ash undergoing primary succession had few small trees with western snowberry (*Symphoricarpos occidentalis*) in the understory. Some early seral green ash stands resulted from retrogression and had large trees with grass understory. Late seral green ash stands were represented by greater overstory cover consisting of green ash and chokecherry (*Prunus virginiana*) shrubs and small trees in the understory. Sixty-five of 81 bird species that were observed in these woodlands required woodland vegetation as part of their habitat. Tree- and shrub-nesting birds were the most common and were associated with late seral stages. Ground-nesting birds had mixed relationships between early and late seral stages. Cavity-nesting birds used snags and dead tree branches which occurred in all seral stages. Correlations of birds with vegetation measurements suggested habitat features birds may have selected for in these woodlands.

INTRODUCTION

Prairie woodlands are riparian-like habitats (Boldt *et al.*, 1978; Uresk and Boldt, 1986) and occupy about 1% of the semiarid northern Great Plains (Girard *et al.*, 1989). However, the importance of prairie woodlands to natural resources is disproportionate to the area they occupy on the Great Plains. The increased vegetation structure in prairie woodlands supports a richer bird community than grasslands (Faanes, 1984; Sieg, 1991a, b; Knopf and Samson, 1994). Prairie woodlands are also used extensively by livestock (Uresk, 1982; Bjugstad and Girard, 1984) and for human recreation and woodcutting (Bjugstad and Sorg, 1985).

Managing lands as ecosystems requires that land managers understand the relationships between ecological processes in plant communities and the associated wildlife communities. However, knowledge linking succession in plant communities to wildlife communities in prairie woodlands is lacking. Some populations of woodland birds that occupy prairie woodlands have declined over the past several decades (Peterjohn *et al.*, 1995; Rodenhouse *et al.*, 1995). Yet, current state of knowledge of wildlife relationships in green ash woodlands is that open-canopy woodlands support different bird communities than do closed-canopy green ash woodlands (Hodorff *et al.*, 1988). We initiated this study to investigate the habitat relationships of nongame birds to the successional patterns in green ash woodlands.

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STUDY AREA AND METHODS

Green ash woodlands are narrow (often <30 m wide) bands or small patches of trees that occur when topographic conditions promote increased soil moisture, soil development and availability of nutrients for trees in a prairie landscape (Mack, 1981; Girard *et al.*, 1989). Many occur in first- or second- order watersheds of the prairie (Bjugstad and Sorg, 1985). Vegetation of green ash woodlands is described by Hansen *et al.* (1984), Hansen and Hoffman (1988) and Girard *et al.* (1989). Although green ash is the dominant species, other common tree species include box elder (*Acer negundo*), American elm (*Ulmus americana*) and plains cottonwood (*Populus deltoides*). Common shrub species in green ash woodlands include chokecherry (*Prunus virginiana*), Saskatoon serviceberry (*Amelanchier alnifolia*), American plum (*Prunus americana*) and western snowberry (*Symphoricarpos occidentalis*).

Site selection.- We selected 40 sites representing the range of seral stages, from early to late succession, in green ash/chokecherry woodlands along or near the Missouri River between Fort Thompson and Mobridge, South Dakota. We classified sites as early, early-intermediate, late-intermediate or late seral stages before selecting them using quantitative coefficients for basal area of green ash, percent ground-canopy cover of chokecherry <2 m tall and percent ground-cover of western snowberry (D. Uresk, undated report). This classification was based on quantitative methodology that included multivariate cluster analysis and discriminant function analysis to identify indicator variables, develop classification coefficients and to estimate classification error rates (Uresk, 1990). Data for classifying sites were collected from a temporary macroplot (Daubenmire, 1952) before the site was selected. The plot size varied depending on the width of the woodland and was 20- X 40-m, 15- X 40-m, or 10- X 40-m. Our initial design called for 10 sites in each of the four seral stages, but availability of sites resulted in fewer sites in the late-intermediate and late seral stages. Six sites were in the late seral stage, 7 were in the late-intermediate seral stage, 14 were in the early-intermediate seral stage and 13 were early seral stage.

Bird counts.- Near the center of each macroplot for classifying seral stages, we marked a point from which to count birds. On each visit to a site, we recorded birds seen or heard and the estimated distance recorded during a 5-min interval beginning immediately upon arrival at the count point. We also recorded whether the birds were within the green ash woodland vegetation or in the surrounding grassland vegetation. Birds flushed from near the count point while approaching it were included in our counts, but birds observed flying over during counts were not included. One sample session constituted three consecutive days of bird counts. We completed one sample session between 25 June and 3 July 1990 and three sample sessions between 28 May and 2 July 1991 and 19 May 1992. The timing of bird counts was scheduled to maximize recording of breeding birds (Robbins *et al.*, 1989). All counts began at sunrise and were completed before 1100. Access to sites spread >320 km on both sides of the Missouri River was very restricted. We used five observers to count birds. All observers were experienced, practiced in audio and visual identification of birds and in estimating distances (Verner and Milne, 1989) before and during the bird counts. To maximize the number of species counted and to minimize bias associated with time that birds were counted, we changed the order that sites were visited within each sample session to spread counts of individual plots throughout the morning activity period of birds (Verner and Milne, 1989). We did not count birds when wind speeds exceeded 10 km/h or during rainfall (Manuwal and Carey, 1991).

Vegetation measurements.- To characterize the vegetation at each site, we located a macroplot (Daubenmire, 1952) that was centered over the bird count point. On most sites we established a 20- X 40-m plot with the long axis oriented to correspond with the drainage

in which the woodland occurred. Some sites were too narrow to establish a plot 20 m wide without including the woodland/prairie ecotone, so we established 15- X40-m plots on three sites and 10- X40-m plots on five sites. In these plots, we recorded diameter at breast height (DBH) and species of all live trees (>2.5 cm DBH) and calculated average DBH, tree density, and tree basal area. We also tallied all dead trees (snags) >13 cm DBH in each plot.

We established two, parallel 30-m transects, 10 m apart (in 10 m X 20 m macroplots, transects were 5 m apart) along the long axis of the macroplot. Percent canopy cover in six cover classes (0 to 5%, >5 to 25%, >25 to 50%, >50 to 75%, >75 to 95% and >95 to 100%; Daubenmire, 1959) was estimated for total understory vegetation (<1 m tall), grasses, forbs and shrubs in a 0.10 m² quadrat at 1-m intervals. We estimated overstory canopy cover with a spherical densiometer (Griffing, 1985) at both ends and at the midpoint of each transect. Foliage-height density was tabulated as the number of vegetation contacts on a vertical pole in 0 to 0.50 m, >0.5 to 1.0 m and >1 to 2 m height-intervals (Noon, 1981) at 2-m intervals along each transect. We calculated coefficients of variation for overstory canopy cover and each interval of foliage-height density as measures of patchiness (Rotenberry and Wiens, 1980).

Analyses.--We averaged vegetation measurements for each transect and then the transects for site averages. Minor or trivial variables can produce spurious results (Everitt, 1977; Uresk, 1990), so we excluded variables for which percent understory cover averaged $<1\%$ or the frequency of occurrence among sites was less than 5. Initial analyses of bird abundance among the four seral stages showed few differences because sample sizes were too low. Therefore, we combined vegetation and bird abundance data for the early and early-intermediate seral stages (hereafter referred to as early seral stages) and the late-intermediate and late seral stages (hereafter referred to as late seral stages). Mann-Whitney U-tests were used to compare vegetation characteristics between early and late seral stages.

Counts that adjust for differing areas sampled and differences in detectability are sufficient for studies of habitat relations in birds (Verner, 1985). Green ash woodlands on the Great Plains are narrow, elongated (following the drainage) and have irregular edges. For our study, it was important to have a high degree of confidence that birds included in analyses occurred in the woodland vegetation. Thirty m is a reasonable distance that skilled observers can estimate distance to $\pm 10\%$ in all seral stages of these woodlands. Accuracy of bird counts declines in plots beyond 30 m (Emlen, 1971; Verner and Ritter, 1988). Our estimates of bird abundance included total observations that occurred in the woodland vegetation ≤ 30 m from the count point. It is impossible to ensure that all birds ≤ 30 m from the count point were recorded, but precise estimates of bird density are not required for studies of habitat relations (Verner, 1985). We did not conduct analyses of abundance for bird species that occurred on ≤ 4 sites, but we included all birds in estimates of abundance in nesting guilds and species richness. Bird species richness was calculated as the average number of species observed per site per sample session. Richness of birds that require woodland vegetation was obtained from (Ehrlich et al., 1988).

We used the Mann-Whitney U-test to examine differences in bird abundances and species richness between early and late seral stages. The richness of woodland species was a subset of total species richness so we used Wilcoxon's signed-rank tests to evaluate whether the richness of woodland birds differed from overall species richness in early and late seral stages.

Exact significance levels for Mann-Whitney U and Wilcoxon's signed-rank tests were calculated using SPSS Exact Tests 7.0 (Mehta and Patel, 1996). To estimate the power of the Mann-Whitney U-test, we conducted rank transformation of abundance in nesting guilds

TABLE 1.—Averages ± SE of vegetative characteristics at 40 sites in early and late seral stages of green ash woodlands in South Dakota

Variables (units) ^{1,2}	Early			Late			Probability ³
	$\bar{x}$	±	SE	$\bar{x}$	±	SE	
Percent canopy cover							
Grass	19.9	1.3		15.5	3.7		0.39
Forbs	9.6	1.3		12.2	4.0		0.68
Shrubs	22.2	2.8		26.9	4.0		0.23
Total understory cover	64.5	4.0		68.4	5.0		0.57
Chokecherry	5.8	1.2		19.0	2.8		<0.01
Western snowberry	1.03	2.7		2.7	1.0		0.03
Chokecherry trees (n/ha)	103.8	37.5		305.1	60.9		<0.01
Green ash trees (n/ha)	400.1	41.7		386.9	50.0		0.85
Total trees (n/ha)	518.5	51.0		692.0	74.5		0.05
Snags > 15 cm DBH (n/ha)	3.6	1.1		6.6	3.0		0.22
Basal area green ash (m ² /ha)	7.3	0.8		14.9	2.3		<0.01
DBH green ash (cm)	9.2	0.8		14.4	1.5		<0.01
Overstory canopy cover (%)	51.2	4.5		72.8	4.6		<0.01
Foliage height-density 0 to 0.5 m	3.4	0.4		3.0	<0.01		0.34
Foliage height-density > 0.5 to 1 m	1.9	0.3		2.6	0.7		0.29
Foliage height-density > 1 to 2 m	1.1	0.2		2.8	0.5		<0.01
Foliage height-density patchiness 0 to 0.5 m	1.1	0.1		1.3	0.1		0.10
Foliage height-density patchiness > 0.5 to 1 m	1.6	0.1		1.5	0.1		0.69
Foliage height-density patchiness > 1 to 2 m	2.3	0.2		1.6	0.2		<0.01
Patchiness in overstory cover	0.6	0.1		0.3	0.1		0.09

¹ Foliage height-density is the number of contacts by vegetation on a pole in the height intervals specified

² Patchiness is calculated as the coefficient of variation for the variable

³ Probability that averages are the same, Mann-Whitney U-test

and used parametric power analyses. Statistical significance was set at $\alpha = 0.10$. At this alpha level, the power of the tests for observed differences in our data ranged from 0.33 for the cavity-nesting guild to 0.90 for the shrub-nesting guild. Scientific names of birds are from AOU (1983) and plant names are from the Great Plains Flora Association (1986).

RESULTS

Vegetation.—Early seral stages of green ash woodlands had lower chokecherry cover in the understory than late seral stages (Table 1). Chokecherry may reach tree (>2.5 cm DBH) status in these woodlands, the density of which was greater in the late seral stages. Greater foliage height-density >1 to 2 m tall and less patchiness in this measure was indicative of greater chokecherry (shrubs and trees) beneath the green ash canopy in the late seral stages than in the early seral stages. Although green ash tree density did not differ between early and late seral stages, green ash basal area and DBH were greater in the late seral stages. Overstory canopy cover was greater and less patchy in the late seral stages, than the early seral stages.

Bird abundance in seral stages.—We observed 81 bird species in green ash woodlands; 65 required woodland habitats. Thirty-three species occurred on enough sites to compare abundance between early and late seral stages (Table 2). Most of the birds observed were

TABLE 2.-Abundance of birds and species richness ≤ 30 m of count points in early and late seral stages of green ash woodlands in South Dakota

Guild/species ¹	Early seral stages			Late seral stages			Probability ²
	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE	
<i>Tree-nesting species</i>							
Mourning dove	7.0		1.7	12.2		2.5	0.05
Western kingbird	2.9		1.2	1.8		0.6	0.63
Eastern kingbird	6.7		1.8	8.7		1.4	0.06
Black-billed magpie	0.3		0.2	0.0			0.54
Blue jay	0.9		0.3	1.8		0.8	0.40
American robin	0.5		0.2	0.6		0.2	0.30
Warbling vireo	0.3		0.1	0.8		0.4	0.23
Black-headed grosbeak	2.9		0.6	5.9		1.4	0.07
Common grackle	1.3		0.6	0.2		0.2	0.48
Orchard oriole	1.6		0.5	2.3		0.4	0.08
Northern oriole	1.0		0.3	1.2		0.4	0.50
American goldfinch	1.9		0.5	3.4		0.6	0.01
Tree-nesting guild	29.4		5.5	41.6		5.0	0.03
<i>Shrub-nesting species</i>							
Gray catbird	0.3		0.2	0.7		0.3	0.11
Brown thrasher	3.4		0.6	5.1		0.7	0.09
Bell's vireo	1.0		0.4	2.5		0.6	0.01
Yellow warbler	4.2		1.1	7.5		1.7	0.04
Shrub-nesting guild	14.7		2.4	26.6		3.2	0.01
<i>Ground-nesting species</i>							
Common nighthawk	0.2		0.1	0.1		0.1	0.09
Common yellowthroat	0.4		0.2	0.2		0.2	0.61
Wilson's warbler	0.2		0.1	0.3		0.2	0.79
Rufous-sided towhee	4.7		0.9	9.6		1.8	0.01
Chipping sparrow	0.4		0.2	0.0			0.28
Field sparrow	0.6		0.2	0.1		0.1	0.08
Vesper sparrow	0.4		0.2	0.0			0.14
Lark sparrow	2.0		0.9	0.4		0.2	0.34
Song sparrow	0.8		0.5	0.0			0.28
Ground-nesting guild	9.5		1.5	4.8		0.8	0.06
<i>Cavity-nesting species</i>							
Red-headed woodpecker	0.3		0.1	0.1		0.1	0.36
Downy woodpecker	<0.1		<0.1	0.1		0.1	1.00
Northern flicker	0.9		0.4	1.2		0.6	0.54
Black-capped chickadee	0.6		0.2	0.6		0.4	0.92
House wren	2.8		0.5	5.5		1.6	0.29
Cavity-nesting guild	5.2		0.9	7.5		2.1	0.50
Brown-headed cowbird	6.4		1.3	10.6		1.9	0.04
Total bird abundance	65.4		8.3	91.2		8.6	0.04
Bird species richness	11.1		0.9	12.4		1.1	0.18
Woodland bird richness	7.2		0.4	7.7		0.4	0.33

¹ Categories for guilds include all birds ≤ 30 m of the census point in the green ash woodlands;

² Probability that values for early and late seral stages are the same, Mann-Whitney U-test

tree-nesters and abundance in the tree-nesting guild was greater ($P = 0.03$) in late seral stages. No tree-nesting birds were significantly more abundant in early seral stages than in late seral stages. Tree-nesting species with greater abundance ($P \leq 0.08$) in late seral stages included mourning doves (*Zenaida macoura*), eastern kingbirds (*Tyrannus tyrannus*), black-headed grosbeaks (*Pheucticus melanocephalus*), orchard orioles (*Icterus spurius*) and American goldfinches (*Carduelis tristis*). Abundance of western kingbird (*Tyrannus verticalis*), black-billed magpie (*Pica pica*), blue jay (*Cyanocitta cristata*), American robin (*Turdus migratorius*), warbling vireo (*Vireo gilvus*), common grackle (*Quiscalus quiscula*), and northern oriole (*Icterus spurius*) did not differ between seral stages.

Bird abundance in the shrub-nesting guild was greater ($P = 0.01$) in late seral stages than in early seral stages. Gray catbirds (*Dumetella carolinensis*), brown thrashers (*Toxostoma rufum*), Bell's vireos (*Vireo bellii*) and yellow warblers (*Dendroica petechia*) were more abundant ($P \leq 0.09$) in the late seral stages than early seral stages.

Bird abundance in the ground-nesting guild was greater ($P = 0.06$) in early seral stages than in late seral stages. Field sparrows (*Spizella pusilla*) and vesper sparrows (*Poocetes gramineus*) were more abundant ($P = 0.07$) in the early stages than in late stages. However, rufous-sided towhees (*Pipilo erythrophthalmus*) were more abundant in late seral stages of green ash than in early seral stages. Common nighthawk (*Chordeiles minor*), Wilson's warbler (*Wilsonia pusilla*), chipping sparrow (*Spizella passerina*), lark sparrow (*Chondestes grammacus*) and song sparrow (*Melospiza melodia*) were other ground-nesting birds that did not differ between seral stages.

Cavity-nesting birds included red-headed woodpecker (*Melanerpes erthrocephalus*), downy woodpecker (*Picoides pubescens*), northern flicker (*Colaptes auratus*), black-capped chickadee (*Parus atricapillus*) and house wren (*Troglodytes aedon*). None differed between seral stages.

Brown-headed cowbirds (*Molothrus ater*) were the most abundant birds in our study; their abundance was greater ($P = 0.04$) in late seral stages than in early seral stages. Abundance of brown-headed cowbirds was negatively correlated ($P \leq 0.10$) with total abundance of cavity-nesting birds and abundance of northern flickers, black-capped chickadees and house wrens. Brown-headed cowbirds were positively ($P \leq 0.10$) correlated with total bird abundance, abundance in the tree-nesting guild, abundance in the shrub-nesting guild and abundance of several tree or shrub-nesting species.

Total bird abundance was greater ($P = 0.04$) in late seral stages of green ash. Total bird species richness did not differ between early and late seral stages, nor did the richness of woodland dependent birds. Only ca. 63% of the bird species in these woodlands required the woodland vegetation which was significantly ($P \leq 0.01$) less than total species richness in each of the seral stages.

DISCUSSION

Green ash is the most common woodland type in western North and South Dakota (Hansen *et al.*, 1984; Hansen and Hoffman, 1988; Girard *et al.*, 1989). Vegetative patterns among our study sites showed both succession and retrogression in the early seral stages. Livestock grazing or trampling is the primary cause of retrogression, which reduces shrubs and regeneration of green ash (Hansen *et al.*, 1984; Uresk, 1987). The variability in vegetation structure in early seral stages obscured some patterns of bird abundance. Our objective was to find patterns in bird abundance that could be related to seral stages to provide an ecological basis for management of woodlands for some wildlife. Patterns of selection by birds were evident when bird abundances were compared between early and late seral stages.

Green ash woodlands contribute to biological diversity in the semiarid northern Great Plains (Faanes, 1984; Hopkins *et al.*, 1986; Hodorff *et al.*, 1988). In the green ash woodlands, we observed 81 of 96 bird species that occur in prairie woodlands in the northern Great Plains (Hopkins *et al.*, 1986; Sieg, 1991b). More than 60% of these bird species required woodland vegetation (Ehrlich *et al.*, 1988). This was nearly constant between seral stages despite the differing abundances of several species between seral stages. Prairie woodlands, important breeding and migratory habitat for some neotropical migratory birds (Moore *et al.*, 1995; Rodenhouse *et al.*, 1995), contribute to local and regional diversity (Knopf and Samson, 1994).

Late seral green ash woodlands supported a greater bird population with more tree- and shrub-nesting birds than early seral stages. None of the tree- or shrub-nesting species was more abundant in early seral stages than late, but black-billed magpies were not observed in late seral stages. Late seral sites had more and larger trees and tall shrubs (e.g., chokecherry and occasionally serviceberry), and small DBH trees were common for nest sites. Early seral sites from retrogression had mature tree canopies, but lacked tall shrubs or small trees for shrub-nesting birds. We applied the seral stage classification to green ash woodland data from Hodorff (1985); early-intermediate green ash woodlands had fewer shrub-nesting species than late-intermediate seral stage (Hodorff *et al.*, 1988). Grazing by livestock reduces vegetation height profiles and the resultant vegetation supports fewer birds that feed and nest in shrubs (Verner, 1984). Heavy browsing by livestock in hardwood forests reduced abundance of shrub-nesting birds (Casey and Hein, 1983), bird species richness and diversity (Medin and Clary, 1990). Livestock grazing in riparian willow (*Salix* spp.) communities in Colorado resulted in a shift in the bird community composition from habitat specialists toward habitat generalists (Knopf *et al.*, 1988).

Ground-nesting birds were generally more abundant in the early seral stages of green ash. Low understory vegetation provided better nest cover for some ground-nesting species than did late seral stages, but this was not consistent for all species. Rufous-sided towhees are ground-nesters that require woodlands (Ehrlich *et al.*, 1988) and were more abundant in late seral stages that had greater tall shrub components. Common yellowthroats and several ground-nesting sparrows also depend on woodlands but abundance was similar in early and late seral stages.

Late seral green ash approaches a mature ecosystem. Snags and dead branches suitable for cavity-nesting species resulted from natural processes associated with older trees in a mature ecosystem. The longevity of green ash trees in this region of the northern Great Plains is often <100 years (Boldt *et al.*, 1978; Sieg, 1991c). Old green ash trees frequently have heart rot (Girard *et al.*, 1989) and few live >50 yr due to environmental stress, disease and cutting (Sieg, 1991c). Early seral woodlands from retrogression also had mature trees and were subject to high rates of tree mortality and disease (Boldt *et al.*, 1978). Lack of snags, but a presence of cavity-nesting birds, suggest that these birds excavated nest cavities in dead branches of diseased or dying trees. Thus, snag density is not a good predictor of cavity-nesting birds in prairie woodlands (Sedgwick and Knopf, 1986). The most common cavity nesting bird, house wrens, are associated with large DBH green ash trees and often nest in dead branches (Sedgwick and Knopf, 1990).

Trees and tall shrubs provide greater foliage volume in late seral stages which increases bird species richness (Dickson *et al.*, 1995). These vegetation features were prominent in late seral stages, but did not affect total species richness or richness of woodland birds. Trees and shrubs apparently were abundant enough for most woodland dependent birds to occur in all seral stages during the breeding season.

The correlation of tree- and shrub-nesting bird abundance to brown-headed cowbirds is

likely related to the abundance of prospective hosts (Rothstein *et al.*, 1986). Because nests of tree- and shrub-nesters are above ground, they are more vulnerable to predation than ground nests (Martin, 1992; Seitz and Zegers, 1993). Birds in forest edges suffer high nest predation or brood parasitism rates (Gates and Gysel, 1978; Brittingham and Temple, 1983; Wilcove *et al.*, 1986). High abundance of cowbirds corresponds with high nest parasitism rates (Donovan *et al.*, 1995). We expect that the song birds in our study were frequently parasitized by cowbirds because of the narrow linear shape of these woodlands and the high abundance of brown-headed cowbirds. Birds in narrow riparian forests of Arizona were also frequently parasited by brown-headed cowbirds (Brown, 1994).

The increased vegetation structure in the green ash woodlands provides habitat that enhances bird diversity in the prairie landscape. Late seral green ash woodlands are uncommon. Benefits of managing for late seral green ash woodlands include increased abundance of tree- and shrub-nesting birds and sustaining these woodlands. Early seral woodlands from retrogression of late seral stages, will eventually disappear (Bold *et al.*, 1978). Loss of these woodlands would dramatically affect the biodiversity of the prairie.

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