

AN ABSTRACT OF THE THESIS OF

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The structure of bird communities in riparian forest successional seres in east central Kansas was analyzed for density, diversity, and equitability. Species were arranged into four residence classifications, monthly occurrence, four- and six-season occurrences, nesting guild classification, food and foraging guild classifications, and foraging height percentages. Three categories of succession were recognized: a pioneer cottonwood-silver maple sere, an intermediate boxelder-mixed sere, and a climax bur oak sere. Bird densities, equitability, and diversity generally increased with forest succession with a decline at the climax forest stage. Physiognomic diversity and habitat heterogeneity associated with ecological succession were considered the major underlying controlling factors in riparian forest avian community organization.

AVIAN COMMUNITY STRUCTURE IN KANSAS RIPARIAN FORESTS

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INTRODUCTION

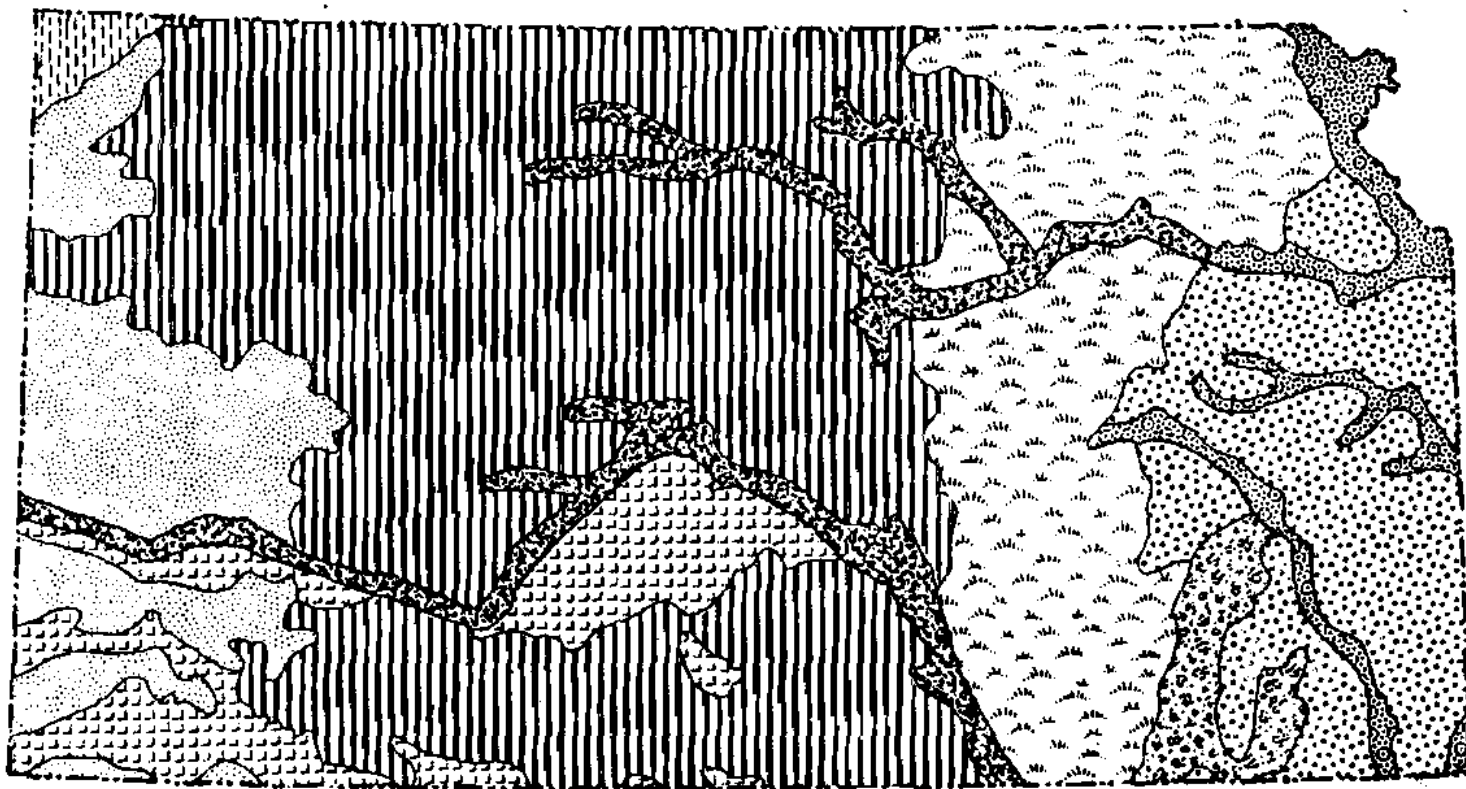
Bird communities consist of individual species that select a definable area because of the presence of requirements necessary for survival and reproduction. The actual process of habitat selection is complex, but can be viewed as a system designed to provide the species with food, water, shelter, and the correct physiognomy (Hilden 1965). The factors that serve as initial attractants may be irrelevant to the bird per se but serve as reliable indicators of the species' probability of success because the area is suitable for breeding (Balda 1975). Avian community studies, therefore, have become a problem of trying to identify what structural features of the habitat are selected by specific species.


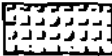







In Kansas, a significant ecological distribution is seen when bird species are analyzed according to habitat preferences. Approximately 58 percent of the resident species are classified as woodland or forest species (Johnston 1964). The presence of these woodland species, in a state predominantly vegetated by prairie grasses, is due to the existence and abundance of riparian habitat (Rising 1974; Tubbs 1980).

Riparian habitat has been described as the water-land interface which is part of the transition region between upland and aquatic ecosystems (Henderson and Shields 1985). Broadly defined, this ecological zone includes all vegetation adjacent to water, however, the riparian areas identified as important to bird species in Kansas are the wooded zones along riverine floodplain and streambank ecosystems.

Kuchler (1974) described the eastern riparian ecosystems of Kansas as a diversity of medium to tall broadleaf trees with dense undergrowth (Figure 1). He called these forests a mosaic of bluestem prairie and

Figure 1. Vegetation map of Kansas. (Map taken from Kuchler, 1969).



- | | | | | | |
|---|---|---|------------------------|---|---------------------------------|
|  | Oak-hickory forest |  | Sandsage-bluestem |  | Grama-buffalograss |
|  | Mosaic of bluestem prairie and oak-hickory forest |  | Bluestem-grama prairie |  | Wheatgrass-bluestem-needlegrass |
|  | Cross timbers |  | Bluestem prairie | | |
|  | Northern floodplain forest | | | | |

oak-hickory trees. As riparian forests progress westward they become narrower, lower, and often less dense. In western Kansas riparian forests are dominated by few tree species and have been described as the Northern Floodplain forests (Kuchler 1964). A gradual transition that links the eastern and western riparian forest types is located within the bluestem prairie.

Riparian ecosystems have been found to be among the most productive and valuable wildlife habitats wherever they occur (Hubbard 1977; Sands and Howe 1977; Fritzgerald 1978). The stream-riparian and riparian-upland interfaces provide habitat typically higher in wildlife use than equal areas of monotypic habitat due to the "edge effect" (Karr 1968; Henderson and Shields 1985). The riparian zone provides a diversity of habitat types that is desirable from an ecological standpoint (Brinson et al. 1981; Atchison 1984). The structure of avian communities depends largely on the diversity of woody, herbaceous, and grassy vegetation (plant physiognomy) provided by the riparian forest. This physiognomic diversity of forest stands tends to increase with ecological succession (DesGrange 1980; McCracken et al. 1981). If the plant profile changes, the predictability of bird composition will change accordingly (Bennett and Hendrickson 1939; MacArthur et al. 1962; Shugart and James 1973; Branan and Burdick 1981). Therefore, land modification or succession of a riparian area which alters one type of habitat while creating another, will cause more tolerant species to replace rapidly growing intolerant species (Karr 1971; Dickson 1978). A general theory which prevails is that avian species and density will increase through progressive successional communities (Kendeigh 1948; Karr 1968) followed by a subsequent decline in diversity in the last successional stages (Odum 1950; Margalef 1958).

This is due to the successional progression of numerous habitat parameters associated with bird communities, such as the number of vertical foliage layers (MacArthur and MacArthur 1961), total foliage volume (Willson 1974), foliage density near ground (Dickson 1978), and habitat heterogeneity (Roth 1976). A decline in diversity at climax stages has not been uniformly noted in winter bird populations (Shugart et al. 1978). The result, regardless of seasonal aspects, is that succession leads to more complex physiognomy and heterogeneity, which results in greater stability and diversification of feeding niches. Unhindered, succession will continue until the species composition best suited to the regional climate and site is established (Drury and Nisbet 1973). Riparian zones, however, are always in a state of flux. Due to human disturbance and the physical nature of a stream or river, most floodplains contain several successional stages and exhibit a diverse configuration of avian species. Most avian community studies to date in the Midwest have not measured components of riparian plant succession and compared these to their associated bird communities (Beidleman 1954; Johnson and Jones 1977; Ports 1978; Schulenberg and Schulenberg 1985).

The intention of this study was to compare avian community structure in three successional riparian ecosystems in Kansas. The objectives of the study were twofold. First, to make comparisons of avian seasonal population shifts among the three riparian habitats. Second, each riparian habitat was compared in relation to avian ecological guild structure.

Identification and common and scientific names used in this study were taken from the following sources: trees (Stephens 1969);

herbaceous plants (Bare 1979); birds (AOU Checklist 1982). A summary of vegetation surveyed in each area is listed in Appendix 1.

Scientific names of birds surveyed during the study are listed in Appendix 2.

METHODS AND MATERIALS

Study areas

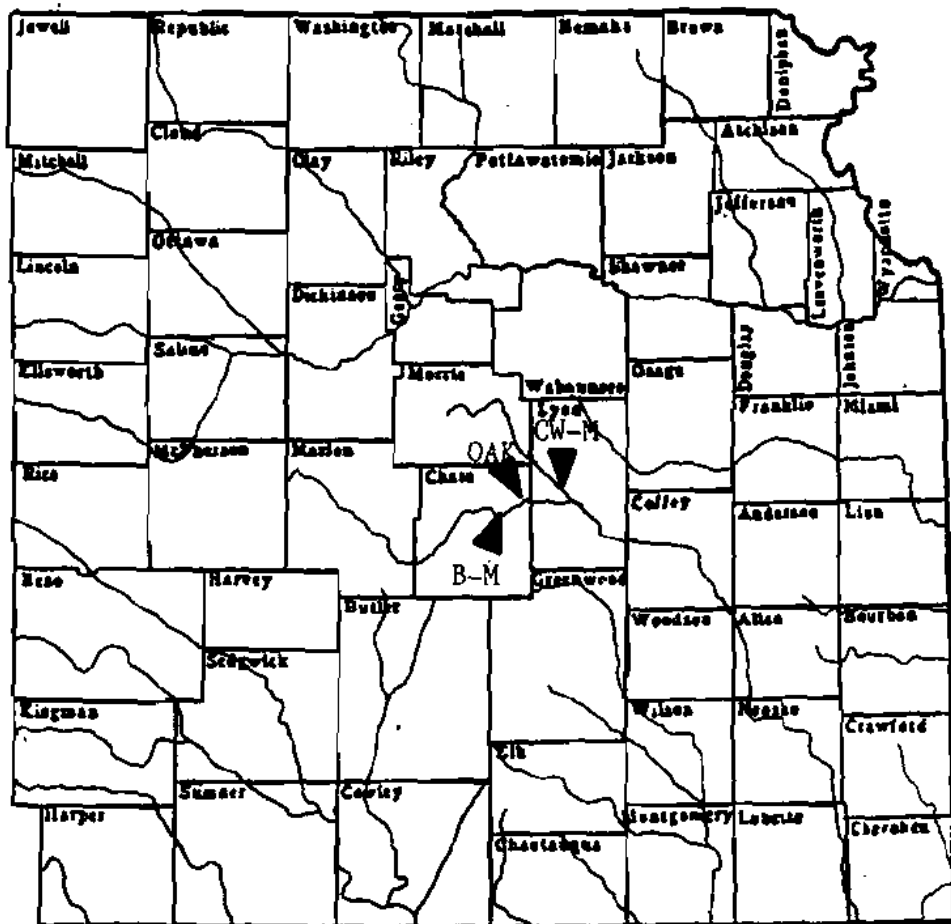
Three wooded areas were selected from riparian forests in east central Kansas. Each area represented a seral stage in the strategy of floodplain succession described by Teskey and Hinckley (1978) for transitional zones linking the eastern and western forest types. These areas included: a pioneer stage of cottonwood-silver maple, an intermediate stage of boxelder-mixed with a diversity of other tree species, and a climax or subclimax stage of bur oak trees (Figure 2).

The cottonwood-silver maple woods was located east of Emporia, Lyon County, Kansas (Sec. 8, T-19-S, R-12-E) (Figure 2). The area was approximately 3.4 ha in size, bounded by the Neosho River on the northeast and surrounded by agricultural land. Soils were considered poorly drained with periodic flooding occurring throughout the summer months. A small number of shrubs grew in the area and the ground strata remained partially bare during the growing season.

The intermediate successional stage, approximately 3.0 ha in size, was located southeast of Saffordville, Chase County, Kansas (Sec. 14, T-19-S, R-9-E) (Figure 2). The area bordered Bull Creek which flowed southeast to the Cottonwood River. Soils were considered moderately well-drained with a small percentage of the area being flooded during the summer months. Dominant vegetation consisted of boxelder, but a mixture of other species were relatively frequent.

The bur oak woods was located east of Saffordville, Chase County, Kansas (Sec. 13, T-19-S, R-9-E) (Figure 2). The area was 4.0 ha in size and paralleled Buckeye Creek which also flowed southeast to the Cottonwood River. Soils were considered moderately well drained and flooding did not occur during the study. Bur oak was the dominant

Figure 2. Study area locations on the Cottonwood and Neosho Rivers. (CW-M= cottonwood-silver maple, B-M= boxelder-mixed, OAK= bur oak complex).



species. There were large numbers of shrub species and the ground strata contained various herbaceous species.

Vegetation

Habitat analysis consisted of vegetation surveys in tree, shrub, and ground strata. Surveys were conducted in July and August, 1982. Survey techniques included the areal tenth-acre (0.04 ha) circular method (Lindsey et al. 1958; James and Shugart 1970) and the step-point method (Evens and Love 1957).

The areal method was used to survey tree and shrub strata. Five 0.04 ha circles were randomly selected in each study area. Circles were sampled by recording species and breast-height diameters (DBH) of all trees within the 11.28 m radius. Woody plants with DBH's of 7.6 cm or greater were defined as tree strata vegetation. Dead trees (snags) also were counted and measured. Two transects were run in each circle to survey shrubs. Transects crossed at right angles at the circle's center-point. Woody stems of less than 7.6 cm in diameter which were intercepted 0.61 m on either side of the transect were counted.

Canopy cover was measured by taking 20 vertical sightings through an ocular tube with a 3.8 cm diameter. Readings were taken by recording the presence or absence of tree foliage. The step-point method was used to survey ground strata. Herbaceous vegetation was surveyed along four 10 m long transects radiating at 90 degree angles from the center point of each areal circle. A single pin was lowered at a 30 degree angle to the ground at one m intervals. A total of 200 step-points (40 per circle) were established in each study area. If the needle hit a plant or below the foliage of a plant, it was recorded as a hit. If the needle hit bare ground, it was recorded as a miss and

the nearest plant was recorded. In both cases, plant species were recorded and heights measured.

Vegetation analysis

Tree species were ordered by relative dominance; those with the greatest percentage of total dominance were considered as "common trees." Diversity and equitability were determined for each area according to methods outlined by Pielou (1966). Tree density and basal area were calculated per 0.4 ha based on methods by James and Shugart (1970). Relative density of shrubs was estimated from total stems counted in all transects for each study area. Percent tree canopy cover was based on positive and negative sightings recorded in the field. Ground strata composition and canopy cover were converted into percent grasses and forbs as described by Ports (1978).

Avian census

Avian censuses were conducted from June 1981 to October 1982 using a fixed-width strip transect technique outlined by Conner and Dickson (1980). A series of three parallel transects were established in each area. The initial transect was located 35 m from the boundaries to reduce surveying ecotones. Strip transects averaged one km in length, combined, and were 20 m wide on either side. Transect censusing was conducted between 0600 hours and 1530 hours during the spring, summer, and fall to allow adequate community sampling (Shields 1977; Dawson 1981). Winter censusing depended more on weather conditions than on time of day (Grubb 1978). Transect lines were marked with survey flags. An attempt was made to alleviate erroneously high density estimates by moving along the transects at a moderately fast, constant pace (Franzreb 1981). All birds seen or heard in the strip transect were counted. This included birds that flew out of, or landed within

the strip width, but not those flying more than 20 m overhead. A total of 52 surveys per area was made during the study. There were 12 surveys in the spring, 16 in the summer, 9 in the winter, and 15 in the fall.

Avian analysis

Community composition and seasonal population changes in each of the three riparian stands sampled were analyzed for density, diversity, and equitability. Densities were determined for each bird species per survey and a mean density was calculated according to each species' resident status. Diversity and equitability (MacArthur and MacArthur 1961; Tramer 1969) were determined for each bird community using the same resident classifications. Species were classified as permanent, summer, winter, migrant, and occasional residents (Appendix 3). Permanent residents were observed all months of the year. Summer residents included species that arrived in the spring, nested or were presumed to have nested during June, July or August, then left the woods. Winter residents included those species that occupied the woods during December, January, and February, but left during the spring to nest elsewhere. Migrants were observed only during species-specific migration dates taken from Johnston (1965). Occasional visitors were species which occurred sporadically during times other than migration.

Three approaches were used to test for seasonal effects (Edwards et al. 1981). Mean densities were arranged into monthly, four-season, and six-season categories. Four-season categories included: fall (September, October, November), winter (December, January, February), spring (March, April, May), and summer (June, July, August). The modified six-season arrangement included: fall (September, October),

winter (November, December, January, February), early spring (March, April), late spring (May), early summer (June), and late summer (July, August). The six seasons were based on changes in bird activity.

To compare avian community structure, mean densities were calculated from behavioral data per census taken on the basis of three coexistence mechanisms defined by Cody (1974) as food preferences, foraging patterns, and foraging heights. Nest selection also was analyzed. Species guild determinations were based on field observations and information taken from Pearson (1936), Bent (1961 a,b, 1963, 1964 a,b,c,d, 1965, 1968), and Terres (1980).

Two nesting guilds were analyzed: non-ground Cup nesters and Cavity nesters. Six feeding guilds were selected based on food items which made up more than 50 percent of the birds' diets during various seasons. Feeding guilds included: Insectivores, which fed on small invertebrates; Granivores, which utilized seeds and nuts; Carnivores, which ate flesh or preyed on vertebrates; Omnivores, which ate a variety of plant and animal matter; Frugivores, which fed on fruit and berries; and Nectarivores, that consumed nectar or plant sap. Six foraging patterns resulted: Hawking birds, were birds that searched for food in flight and then trapped prey on the ground or on a perch; Sally-gleaners, were birds which sallied from a perch to capture prey and returned to the perch to feed; Timber-foliage searchers, were birds which obtained food among leaves and on branches of trees and shrubs; Timber-gleaners, included birds that searched bark surfaces for prey; Timber-drillers, were birds that pecked or hacked into wood of trees in search of prey; and Ground/Slash birds, which were birds that scratched or pecked on the ground substrate for food. Community subdivisions by height strata included heights of 0.61, 1.22, 3.1, 6.1, 10.7, 15.2, and

18.3 m. The cumulative percentages of individual birds, regardless of species, were developed from Anderson et al. (1979). Species guild classifications for all birds surveyed are included in Appendix 3.

Densities within guilds, months, and seasons were analyzed for statistical significance among the three study areas. Densities were first transformed using the square root transformation (Sokal and Rohlf 1981) in order to make the variances independent of the means. Since many of the guilds contained density counts of zero, 1.0 was added to each density before finding the square root to correct for this (Snedecor and Cochran 1980). Because each analysis compared densities for groups of five or six guilds, 12 months, four seasons or six seasons in three different areas, the transformed densities were subjected to factorial analysis of variance (Sokal and Rohlf 1981). The Linear Statistical Model (General Linear Model) (Sokal and Rohlf 1981) used in the analysis of variance contained the main effects of guild, month, four-season, or six-season, area, and the interaction of the two. The arithmetic density means were converted by this model to least square means (Snedecor and Cochran 1980) to adjust ANOVA and means for unequal subclasses.

Differences between least square means were ascertained using Fisher's Least Significant Difference method (Snedecor and Cochran 1980). This mean separation analysis assigns statistical significance to means with the least significant difference.

Analyses were performed on the mainframe computer at the University of Missouri, Columbia, Missouri. Programs were run on Statistical Analysis Systems (SAS) (1982) and executed by Dr. Mark Eilersieck, Research Analyst, Food Science and Nutrition, University of Missouri, Columbia.

RESULTS

Vegetation

Areal circular surveys showed that each riparian area selected was composed of dissimilar tree complexes. Relative dominance of tree species surveyed is shown in Table 1. Other quantitative aspects of vegetational development are summarized in Table 2.

Seven species of trees, including dead trees as a single species, were surveyed in the cottonwood-silver maple complex (Table 1). Eastern cottonwood and silver maple trees accounted for 70 percent of the ground area covered. Boxelder and dead trees were the least dense. Tree species diversity, equitability, canopy cover, and total basal area were comparatively low in this area, but tree density was the highest of the areas studied (Table 2). Shrub strata density and ground strata cover were low when compared to the other two areas. Ground strata composition was dominated by relatively small forb species.

Fourteen species of trees were surveyed in the boxelder-mixed complex (Table 1). Boxelder trees accounted for 39 percent of the ground area covered, with black willow, green ash, silver maple, and dead trees relatively dense. Tree species diversity was highest in this study area. Equitability was similar to the bur oak area but higher than the cottonwood-silver maple complex (Table 2). Tree density was lower in this area than in the cottonwood-silver maple area, but total basal area was actually greater when compared to density. Tree and ground strata canopy cover were greatest in this area but shrub cover was less dense than in the bur oak study area. Forbs dominated the ground strata with the average forb and grass height greater than in the cottonwood-silver maple study area.

Table 1. Relative dominance of the common tree species surveyed in the study areas in 1982¹.

Species	Study areas		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
Black Willow	14	13	
Eastern Cottonwood	44	3	
Black Walnut		0.5	
Bur Oak		0.5	78
American Elm		0.5	1
Red Elm		1	4
Hackberry		6	8
Red Mulberry		6	1
American Sycamore	6	5	
Kentucky Coffee Tree		0.5	2
Boxelder	1	39	
Silver Maple	26	9	
Western Buckeye			1
Green Ash	6	9	2
Dead Tree ²	3	7	3

¹ Figures represent percent basal area.

² Includes all species.

Table 2. Vegetation analysis of the tree, shrub, and ground strata surveyed in the study areas in 1982.

Foliage strata	Study areas		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
<u>Tree strata</u>			
Diversity	1.45	2.19	1.83
Equitability	0.75	0.83	0.83
Species	7	14	9
Individuals per 0.4 ha	386	298	266
Total basal area - Square feet per 0.4 ha	271	233	290
Percent canopy cover	75	85	75
<u>Shrub strata</u>			
Species	5	6	11
Stems per 0.4 ha	2,000	10,400	16,300
<u>Ground strata</u>			
Species	7	12	14
Percent grass composition	3.5	19.5	33
Percent forb composition	83.5	80.5	67
Percent grass canopy cover	2	19.5	21
Percent forb canopy cover	51	56.5	47.5
Total percent canopy cover	53	76	68.5
Plant height in centimeters	25-50	50-75	50-75

Nine species of trees were surveyed in the bur oak complex (Table 1). Bur oak dominated the area comprising 78 percent of the ground area covered. Species diversity was higher than in the cottonwood-silver maple complex but lower than the boxelder-mixed area (Table 2). Equitability was greater in this area than in the cottonwood-silver maple complex. Density of trees was lower than total basal area measured. Percent canopy cover in this study area was similar to that found in the cottonwood-silver maple complex. Shrub density was highest in this area and percent ground cover was intermediate between the other two areas. Tall forbs also dominated this site and percent grass composition was largest.

Avian residence status

A total of 116 bird species was recorded during the two-year study with 38 species common to all areas surveyed (Appendix 2). A summary of the avian censuses conducted in the three riparian study areas is given in Tables 3 and 4. Data arrangement is according to predicted habitat succession.

Significant differences among bird population densities in the three study areas were analyzed for months, four seasons, and six seasons. Results are shown in Tables 5 and 6. Data are again arranged according to the predicted successional series.

Monthly comparisons of mean densities showed that the cottonwood-silver maple woods contained the lowest bird densities with the boxelder-mixed area significantly higher in seven of 12 months, and in the bur oak area, significantly higher in six of 12 months (Table 5). Only during October (fall migration) were densities significantly higher in the bur oak area compared to the boxelder-mixed woods.

Table 3. Comparison of avian species number, total mean densities per hectare, diversity (H'), and equitability (J') in the study areas based on species' residence status from June 1981 to October 1982.

	Study areas		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
<u>Summer residents</u>			
Total species	19	22	23
Total mean density	3.90	10.74	9.34
H'	2.38	2.58	2.68
J'	0.81	0.84	0.86
<u>Winter residents</u>			
Total species	14	16	18
Total mean density	10.18	13.25	11.13
H'	1.97	2.36	2.40
J'	0.75	0.87	0.82
<u>Occasional visitors</u>			
Total species	14	10	9
Total mean density	2.50	0.59	0.50
H'	1.39	1.84	1.30
J'	0.53	0.80	0.73

Table 4. Comparison of avian species number, total mean densities per hectare, diversity (H'), and equitability (J') in the study areas based on species' migrational occurrence from June 1981 to October 1982.

Migrants	Study areas					
	Cottonwood-Silver Maple		Boxelder-Mixed		Bur Oak Complex	
	<u>Spring</u>	<u>Fall</u>	<u>Spring</u>	<u>Fall</u>	<u>Spring</u>	<u>Fall</u>
Total species	12	20	24	31	30	30
Total mean density	0.96	1.91	3.67	2.40	3.10	3.07
H'	2.19	1.80	2.65	2.94	2.92	2.50
J'	0.88	0.60	0.83	0.86	0.86	0.74

Table 5. Mean avian community densities per hectare (\pm SD) and number of species surveyed for each study area on a monthly basis from June 1981 to October 1982¹.

Months	Density			Number of species		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
September	7.33(3.64) x	12.25(4.08) y	9.73(2.19) xy	25	41	35
October	5.17(3.73) x	11.82(3.40) y	16.00(5.82) z	22	30	35
November	5.90(2.34) x	9.56(1.44) x	7.08(2.16) x	17	20	24
December	4.62(2.70) x	9.69(1.08) x	9.44(0.66) x	14	16	18
January	4.51(2.79) x	9.45(1.37) x	9.45(1.26) x	14	15	17
February	4.05(1.70) x	9.55(0.86) y	9.27(0.87) xy	17	15	17
March	8.73(0.39) x	9.94(0.70) x	10.55(0.52) x	17	15	20
April	5.80(1.60) x	14.49(7.24) y	14.57(7.19) y	14	32	17
May	5.18(1.92) x	9.40(3.61) y	9.18(3.87) y	30	34	54

Table 5. (Continued)

Months	Density			Number of species		
	Cottonwood- Silver Maple	Boxelder- Mixed	Bur Oak Complex	Cottonwood- Silver Maple	Boxelder- Mixed	Bur Oak Complex
June	4.65(2.69) x	11.25(4.08) y	8.55(3.67) y	22	26	27
July	3.11(1.93) x	11.43(1.76) y	10.93(8.08) y	22	22	26
August	6.53(2.77) x	8.93(2.14) xy	11.82(1.63) y	26	34	38

1 Values with different letters were significantly different at $p < 0.05$.

Table 6. Mean avian community densities per hectare (\pm SD) and number of species surveyed for each area on a four- or six-season basis from June 1981 to October 1982¹.

	Density			Number of species		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
<u>Four seasons</u>						
Fall	6.23(3.29) x	11.39(3.32) y	11.11(5.14) y	38	55	54
Winter	4.39(2.12) x	9.56(0.98) y	9.39(0.84) y	17	18	18
Spring	5.93(2.07) x	10.76(4.66) y	10.75(4.81) y	36	48	61
Summer	5.28(2.79) x	10.28(3.19) y	10.26(3.65) y	33	39	40
<u>Six seasons</u>						
Fall	6.35(3.67) x	12.06(3.60) y	12.58(5.17) y	34	52	51
Winter	4.86(2.21) x	9.56(1.08) y	8.68(1.69) y	21	22	25
Early Spring	6.97(1.97) x	12.67(5.71) y	12.96(5.54) y	20	35	24

Table 6. (Continued)

	Density			Number of species		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
Late Spring	5.18(1.92) x	9.40(3.61) y	9.18(3.87) y	30	34	54
Early Summer	4.55(2.69) x	11.25(4.08) y	8.55(3.67) y	22	26	27
Late Summer	5.77(2.92) x	9.49(2.24) y	11.62(3.21) y	31	35	39

1

Values with different letters are significantly different at $p < 0.05$.

Significantly lower densities and lower species numbers existed in the cottonwood-silver maple area for both the four-season and six-season categories when compared to the other study areas (Table 6). No significant differences were detected between the boxelder-mixed and bur oak seasonal classifications, regardless of season.

Avian nesting guilds

Results of nesting activities by birds in the three study areas are shown in Table 7. Both the boxelder-mixed and bur oak areas had significantly more cup and cavity nesters than the pioneering cottonwood-silver maple sere.

Avian food and foraging guilds

Summer food and foraging guilds are shown in Table 8. Results indicated that significantly lower densities of insectivorous, granivorous, and frugivorous birds occurred in the cottonwood-silver maple woods. No significant differences were detected for carnivorous and omnivorous birds among any of the woods. Foraging guilds showed a similar trend. Significantly lower densities of birds that foraged by sally-gleaner, timber-foliage searcher, and ground/slash techniques were found in the cottonwood-silver maple area. Sally-gleaners were significantly more abundant in the bur oak area than in the boxelder-mixed woods. No significant differences were detected among the three study areas for winter food and foraging guilds (Table 9).

Significant differences in avian densities among the study areas occurred during the spring and fall migration periods (Tables 10 and 11). Insectivore densities were significantly higher in the boxelder-mixed woods than in the cottonwood-silver maple area during the spring, and significantly higher than both the cottonwood-silver maple and bur oak areas during the fall (Table 10). Granivorous birds were more

Table 7. Mean avian densities per hectare (+SD) and number of species for each area based on nesting guilds surveyed from 1981 and 1982 Summer seasons¹.

Nesting	Density			Number of species		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
Cup (non-ground)	2.24(1.35) x	4.69(2.12) y	4.78(1.86) y	9	12	11
Cavity	2.69(1.60) x	5.37(2.30) y	5.00(2.05) y	10	10	12

¹

Values with different letters are significantly different at $p < 0.05$.

Table 8. Mean avian densities per hectare (+SD) and number of species for each area based on food and foraging guilds surveyed during the Summer seasons of 1981 and 1982¹.

	Density			Number of species		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
<u>Food guild</u>						
Insectivorous	4.46(2.32) x	9.36(3.66) y	8.23(3.28) y	17	19	19
Granivorous	2.35(1.50) x	3.96(1.76) y	2.90(1.48) xy	8	7	6
Carnivorous	0.0 x	0.03(0.09) x	0.19(0.21) x	0	1	2
Omnivorous	0.48(0.41) x	0.81(0.84) x	1.23(0.79) x	2	1	2
Frugivorous	2.00(1.40) x	3.17(1.72) y	2.81(1.64) xy	5	4	5
<u>Foraging guild</u>						
Hawking	0.0 x	0.03(0.08) x	0.17(0.33) x	0	1	2
Sally-gleaner	0.33(0.22) x	0.64(0.38) x	1.01(0.72) y	2	2	4

Table 8. (Continued)

	Density			Number of species		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
Timber-foliage searcher	1.86(1.17) x	4.64(2.18) y	4.39(1.52) y	6	8	8
Timber-gleaner	0.16(0.24) x	0.34(1.40) x	0.52(0.38) x	1	1	1
Timber-driller	0.82(0.73) x	1.15(0.76) x	0.89(0.65) x	3	3	3
Ground/Slash	1.91(1.36) x	3.15(1.54) y	2.55(1.80) xy	7	7	5

1

Values with different letters are significantly different at $p < 0.05$.

Table 9. Mean avian densities per hectare (\pm SD) and number of species for each area based on food and foraging guilds surveyed during the Winter seasons of 1981 and 1982¹.

	Density			Number of species		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
<u>Food guilds</u>						
Insectivorous	7.62(1.37) x	7.95(1.99) x	8.20(1.49) x	12	12	14
Granivorous	5.38(1.01) x	5.96(3.01) x	5.80(2.63) x	9	10	9
Carnivorous	0.0 x	0.08(0.14) x	0.08(0.14) x	0	1	2
Omnivorous	0.08(0.14) x	0.33(0.38) x	0.33(0.29) x	1	1	1
Frugivorous	1.49(0.66) x	1.99(1.32) x	1.32(0.29) x	4	3	4
<u>Foraging guild</u>						
Hawking	0.0 x	0.08(0.14) x	0.08(0.14) x	0	1	2
Sally-gleaner	0.0 x	0.0 x	0.0 x	0	0	0

Table 9. (Continued)

	Density			Number of species		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
Timber- searcher	3.64(1.00) x	4.80(3.31) x	3.64(2.08) x	4	5	5
Timber-gleaner	1.00(0.86) x	0.50(0.50) x	0.58(0.38) x	2	3	3
Timber-driller	0.91(0.52) x	0.83(0.38) x	0.83(0.62) x	3	2	3
Ground/Slash	2.57(0.94) x	3.15(1.90) x	3.89(4.10) x	5	5	5

1

Values with different letters are significantly different at $p < 0.05$.

Table 10. Mean avian densities per hectare (\pm SD) for each area based on food guilds surveyed during the Spring and Fall seasons of 1981 and 1982¹.

Food guilds	Spring ²			Fall ²		
	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
Insectivorous	0.71(0.96) x	2.80(2.95) y	2.03(1.82) y	0.56(1.01) x	2.45(1.83) y	1.96(2.31) z
Granivorous	0.06(0.22) x	0.35(0.83) x	0.56(0.80) x	0.20(0.44) x	0.38(0.65) x	0.63(0.91) x
Carnivorous	0.10(0.20) x	0.04(0.14) x	0.0 x	0.07(0.18) x	0.05(0.10) x	0.0 x
Omnivorous	0.10(0.23) x	0.17(0.27) x	0.0 x	0.0 x	0.02(0.07) x	0.0 x
Frugivorous	0.25(0.37) x	1.51(1.84) y	0.54(0.92) x	0.07(0.11) x	0.90(0.96) y	0.22(0.35) x
Nectivorous	0.0 x	0.0 x	0.0 x	0.0 x	0.0 x	0.12(0.23) x

¹ Values with different letters are significantly different at $p < 0.05$.

² Values are derived from migrant species only.

Table 11. Mean avian densities per hectare (\pm SD) for each area based on foraging guilds surveyed during the combined migration seasons of 1981 and 1982^{1,2}.

Foraging guild	Cottonwood-Silver Maple	Boxelder-Mixed	Bur Oak Complex
Hawking	0.07(0.15) x	0.07(0.14) x	0.0 x
Sally-gleaner	0.07(0.18) x	0.18(0.39) x	0.18(0.30) x
Timber-foliage searcher	0.39(0.78) x	1.58(1.77) y	1.16(1.82) z
Timber-gleaner	0.06(0.29) x	0.05(0.14) x	0.01(0.05) x
Timber-driller	0.0 x	0.0 x	0.01(0.05) x
Ground/Slash	0.21(0.32) x	0.82(0.70) y	0.86(1.13) y

1

Values with different letters are significantly different at $p < 0.05$.

2

Values are derived from migrant species only.

numerous in the bur oak area during migration but no significant differences were detected. Frugivores were significantly higher in the boxelder-mixed woods during both migrational periods. The only notable significant differences in foraging strategies during migration were the high densities of timber-foliage searchers in the boxelder-mixed woods and low densities of ground/slash birds in the cottonwood-silver maple area (Table 11).

Figures 3, 4, and 5 show seasonal variations of the foraging guilds in the three study areas. The numerical values represent the percentage of individuals in a guild for a specific study area in relation to the total individuals of the community for that area.

The highest percentages of timber-foliage searchers in the three seres were found during spring and fall migration (Figure 5). Ground/slash foragers had the highest percentage of individuals in the cottonwood-silver maple area in the summer, and in the boxelder-mixed and bur oak complexes during the winter, spring, and fall (Figures 3, 4, and 5). No sally-gleaners were observed in the winter in any of the forests (Figure 4). Timber-drillers were greatly reduced during spring and fall in all three seres (Figure 5). The remaining foraging guilds varied slightly among seasons.

Avian foraging heights

Differences in cumulative percentages of individuals (regardless of species) observed by height between the three study areas are shown in Figure 6. The results showed that greater numbers of birds were found at higher strata levels in the boxelder-mixed woods than in the bur oak or cottonwood-silver maple areas.

Figure 3. Percentage of the bird community found in each ecological foraging guild during the Summers of 1981 and 1982 in the three riparian forests. (CW-M= cottonwood-silver maple, B-M= boxelder-mixed, OAK= bur oak complex; H= hawking, S-G= sally-gleaner, T-FS= timber-foliage searcher, T-G= timber-gleaner, T-D= timber-driller, G/S= ground/slash).

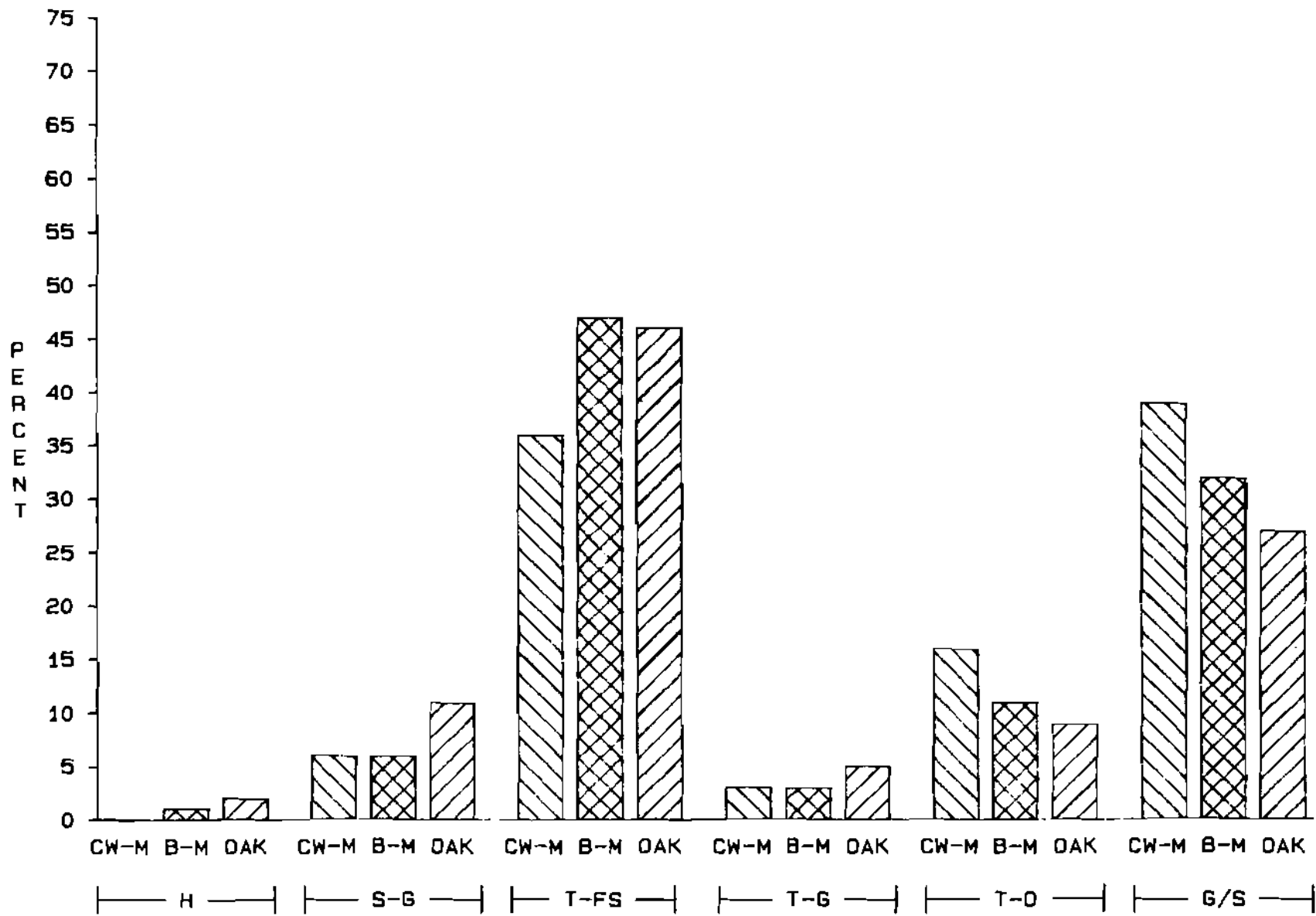


Figure 4. Percentage of the bird community found in each ecological foraging guild during the Winters of 1981 and 1982 in the three riparian forests. (CW-M= cottonwood-silver maple, B-M= boxelder-mixed, OAK= bur oak complex; H= hawking, S-G= sally-gleaner, T-FS= timber-foliage searcher, T-G= timber-gleaner, T-D= timber-driller, G/S= ground/slash).

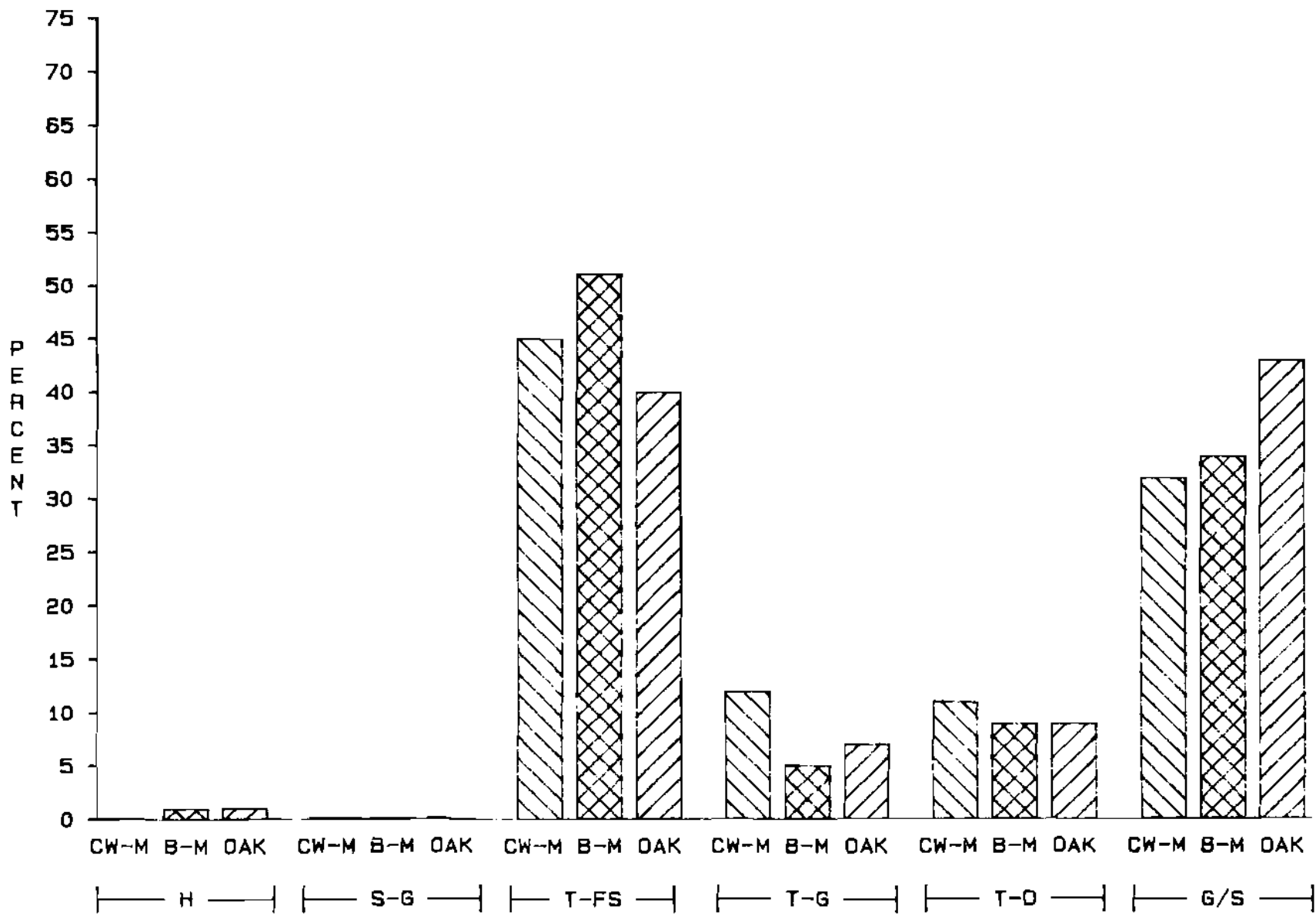


Figure 5. Percentage of the bird community found in each ecological foraging guild during the Spring and Fall migrational periods of 1981 and 1982 in the three riparian forests. (CW-M= cottonwood-silver maple, B-M= boxelder-mixed, OAK= bur oak complex; H= hawking, S-G= sally-gleaner, T-FS= timber-foliage searcher, T-G= timber-gleaner, T-D= timber-driller, G/S= ground/slash).

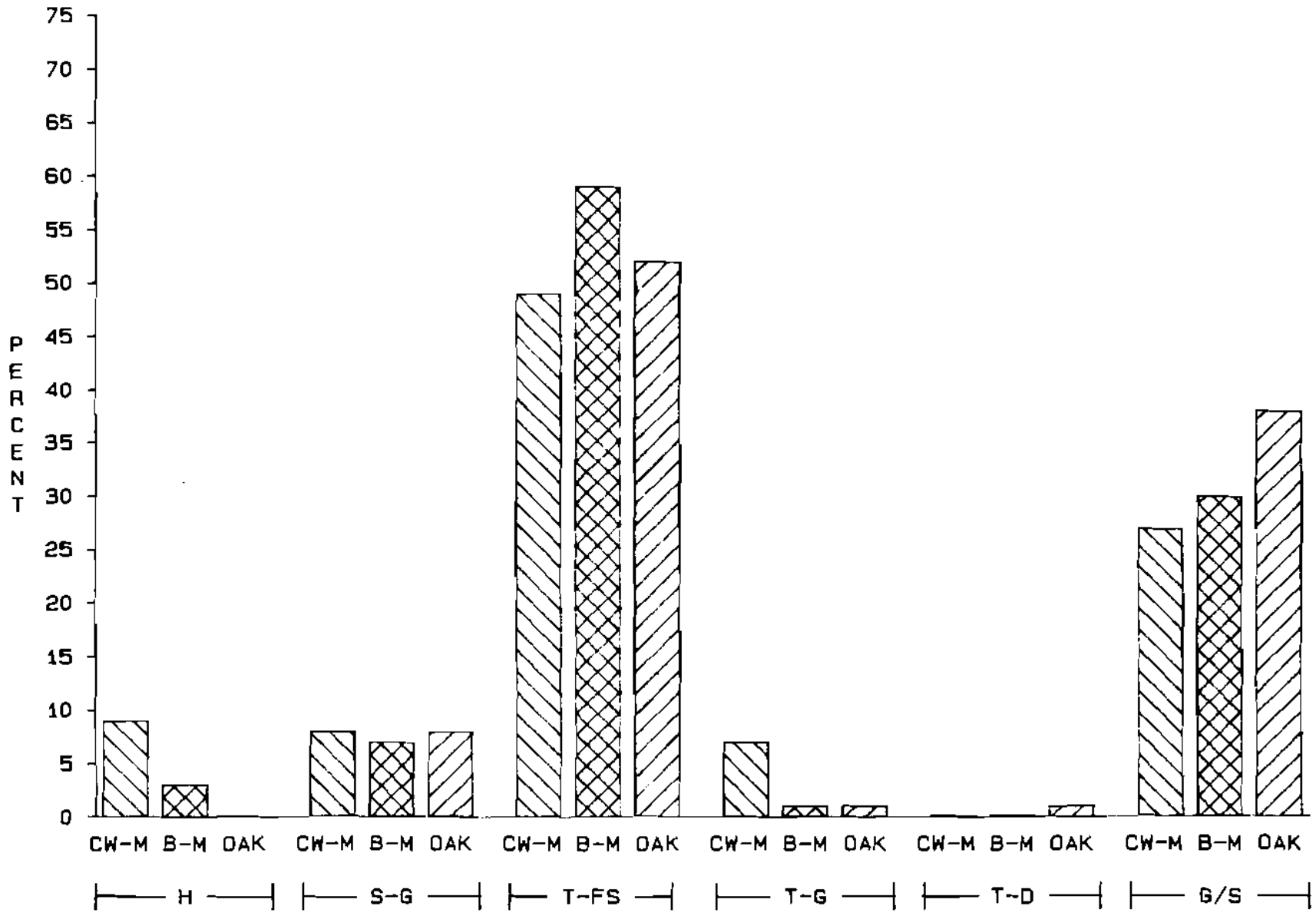
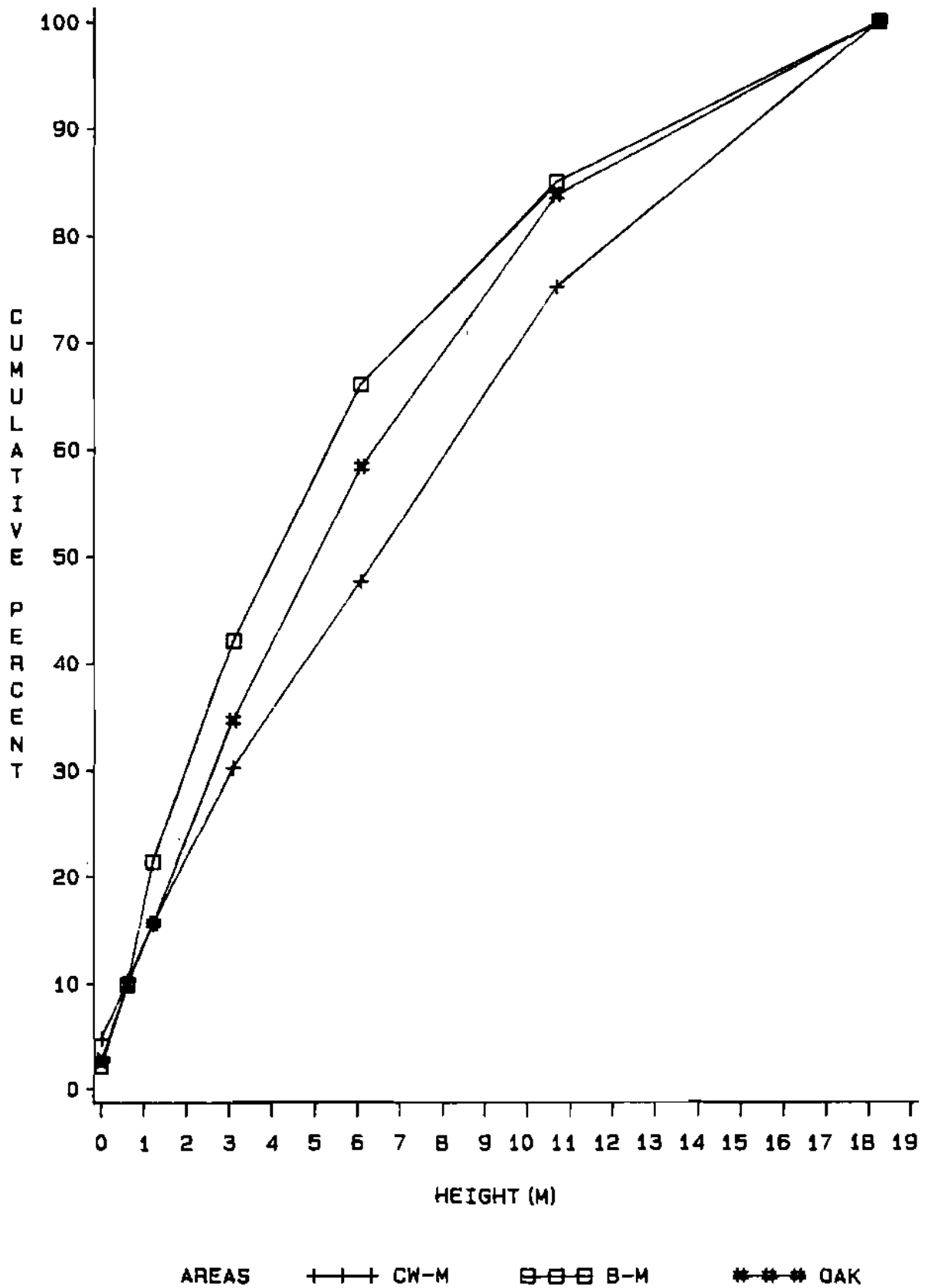


Figure 6. Cumulative percentage of individual birds at observed foraging heights during 1981 and 1982 in the cottonwood-silver maple, boxelder-mixed, and bur oak complexes. (CW-M= cottonwood-silver maple, B-M= boxelder-mixed, OAK= bur oak complex).



DISCUSSION

Vegetation communities

Habitat analyses of the three riparian areas studied indicated a pattern of succession similar to riparian succession described by Teskey and Hinckley (1978) along the Plains Grassland Region of central United States. The pioneer tree community was represented by the cottonwood-silver maple study area. Typical of an early plant successional stage, this community was characterized by high plant densities with small basal areas (Tables 1 and 2). Numerous small trees, combined with few species and one-sided dominance, caused low species diversity and equitability in the tree strata. Also, the phenology of the dominant trees was that of a smaller horizontal canopy coverage. The combination of these factors led to the conclusion that the tree strata was structurally simple. Due to periodic flooding and the longevity of the standing water during the summer season, foliage layers near the ground were reduced or eliminated. The results of these factors indicated that this pioneer successional stage community lacked both horizontal patchiness and vertical stratification.

As soil characteristics change (improved soil texture, increased soil nitrogen and organic matter) an intermediate stage of wetland-mesophytic tree species develops. The boxelder-mixed riparian forest represented this intermediate sere. Tree density was lower than in the pioneer sere, but the overall density more closely approached the total tree basal area (Tables 1 and 2). As soil characteristics improved, conditions were presumably adequate to support larger trees. Competition likely played a role in reducing the number of trees and producing a more evenly spaced forest. A greater variety of tree species was able to utilize the available resources of this more

mesophytic condition. These "rare" tree species created the highest diversity among the successional seres (Table 2). Increased variety led to decreased dominance and a higher equitability. The phenology of the trees present in this sere created a more robust forest with an increased canopy. Though tree canopy increased, greater distance between individual trees facilitated light penetration which enabled shrub and herbaceous vegetation to increase dramatically. Shrub stems increased by 8,400 stems per four-tenths ha and ground strata canopy cover increased to 76 percent compared to the cottonwood-silver maple sere. The average height of ground strata vegetation increased from 50 to 75 cm and grasses became more prevalent in the community. The addition of numerous shrub and herbaceous species to this area, diversified in tree species, greatly increased the vegetative complexity and physiognomic diversity of this sere in contrast to the structurally simplistic pioneer stage of cottonwood-silver maple forests.

Succession of the intermediate zone between eastern and western riparian forests in Kansas advances to a completely mesophytic condition. It is at this stage that the terminal tree community of oaks, elm, and possibly hickory develop (Teskey and Hinckley 1978). This climax sere was represented in the present study by the bur oak riparian forest. This sere was characterized by low numbers of large trees (Table 2). Dominance again became more one-sided as the variety of trees became intolerant to the evolving soil type, and an association of a few tree species succeeded (Table 1). Species diversity also showed a decline which coincides with other reports of lower diversities and densities of organisms at the climax stage

(Gauthreaux 1978). Horizontal spatial complexity was reduced with the addition of more shrubs to this community. A closed shrub canopy reduced habitat patchiness. Light penetration necessary for ground foliage growth also was reduced. With less light, ground strata canopy cover dropped by 7.5 percent from the intermediate sere. Mesophytic conditions of the site were reflected by the increase of grass species in the community. Though a variety of vegetative life forms were present, heterogeneity declined from the intermediate sere, to this terminal tree sere, due to the uniformity of vegetation in each strata.

Avian communities

Community diversity

Diversity indices as used by ecologists can be thought of as having two components: richness, which is a measure of the number of species in a given community, and equitability, the evenness of numerical abundance of the population in a community (Shugart et al. 1978). Most breeding bird community diversities vary directly with species richness. An increase in species numbers may result in an increase in diversity. The present study confirmed this numerical relationship. Diversity and equitability increased with increasing species numbers (Table 3). The similarity of the values, though, made it difficult to draw many conclusions. Long-term forest patterns in eastern deciduous forests have generally shown that bird diversity is strongly associated with the development of diverse vegetative structure (Karr 1971; Shugart and James 1973). MacArthur and Levins (1967) have suggested that increasing the dimensionality of the resource allows more species to inhabit a community. Karr and Roth (1971) found that the sharpest increase in avian diversity occurred with the addition of the shrub and early tree layers, and that added vegetation beyond that point produced

diminishing returns.

Diversity values found in the three riparian seres showed a similar trend. The pioneering cottonwood-silver maple sere, which had both a paucity of complex tree cover and ground cover (Table 2), contained comparatively lower bird diversity values than the more successional advanced seres (Table 3). The greatest increase in avian diversity occurred as the cottonwood-silver maple sere developed into the intermediate boxelder-mixed woods. It was in that developmental stage that shrub stems increased by 84 percent and ground cover increased to 76 percent (Table 2).

There was a less dramatic increase in avian diversity from the boxelder-mixed to bur oak climax stage (Table 3). The slight increase may have been related to the continued increase in shrubs or to the increased size, approximately 1.0 ha, found at the climax bur oak sere. MacArthur et al. (1966) have shown that as the size of an area decreases there is a decrease in the value of diversity.

Diversity values in the boxelder-mixed and bur oak complex were generally higher during migration than during the other seasons. Interestingly, diversity values during migration in the cottonwood-silver maple woods were lower than during the summer breeding season and similar to winter diversity values of that area (Tables 3 and 4). This seasonal variation may again be linked to the reduced vegetation found in the pioneer sere. Structurally less complex habitats involve harsher environments (Karr 1971). Specifically, competition for food, a primary force shaping avian populations, is greatest during harsh climates (Fretwell 1972). During critical periods (migration and winter) species may avoid habitats lacking complexity due to the

increased competition for food.

Community equitability

Low equitability values occur when the numbers of individuals in a community are unequally divided among the species present. Low equitability, therefore, indicates greater dominance shared between fewer species. The general tendency is for dominance to be shared among more species as the environment becomes more stable (Odum 1971). Equitability values among the three riparian successional stages increased in a similar trend to the diversity values (Tables 3 and 4). The pioneer cottonwood-silver maple sere contained lower equitability values while the boxelder-mixed and bur oak values were more nearly equal. The evolving plant physiognomy found in the cottonwood-silver maple sere may have caused some community instability. Vegetational communities lacking stability attract bird species with generalized niches at the expense of those with specialized niches (DesGrange 1980). This would lead to greater dominance by fewer species. As the riparian seres progressed to the intermediate and climax stages, plant physiognomy may have stabilized due to increased plant diversity. Bird species in both the boxelder-mixed and bur oak complexes may have divided into niches of more equal size. Dominance, therefore, was reduced and equitability values increased in both seres (Tables 3 and 4).

Seasonal densities

Many studies of avian succession have found that the number and density of breeding bird species parallels successional sequence in habitat (Odum 1950; Johnston and Odum 1956; Shugart and James 1973; Shugart et al. 1978). However, Adams (1908), Kendeigh (1948), Margalef (1958), and Gauthreaux (1978) noted declines in bird densities in the

final stage of succession. Monthly comparisons of mean densities in this study also showed a decline towards the climax sere, except for months generally associated with bird migration. Densities were significantly lower in the cottonwood-silver maple woods, and noticeably lower in the bur oak area, than the vegetationally more complex boxelder-mixed woods (Table 5). A comparison of mean densities grouped into four- and six-season classifications followed similar trends (Table 6). The distribution and abundance of birds, therefore, followed the development of the plant strata and depended on the physiognomy of the forest as has been previously reported (DesGrange 1980; McCracken et al. 1981). Gauthreaux (1978) suggested that more productive forest communities have higher numbers and densities of birds. This is due to the increased standing crop and productivity as succession progresses, but productivity frequently falls as the climax sere is reached (Margalef 1969). In comparison to the intermediate sere of boxelder-mixed woods, the bur oak climax sere had lower vegetational densities and diversity. This would indicate that the bur oak sere was less productive than the boxelder-mixed woods. Reduced vegetational productivity, therefore, led to lower bird densities in the climax riparian forest.

During fall, early spring, and late summer, bird densities continued to increase towards climax, with no climactic decline. It was evident that post-fledging, non-migratory, and migratory bird movements increased densities at the climax bur oak sere. The increase in granivorous birds in the bur oak complex was the most noticeable difference during those seasons (Tables 8 and 10).

Avian nesting guilds

Low bird density in the cottonwood-silver maple woods caused significantly lower nesting guild densities when compared to the other riparian forests (Table 7). It is interesting to note that although no significant differences were detected between the boxelder-mixed and bur oak areas, the boxelder-mixed woods had slightly higher densities of cavity nesters and the bur oak area contained higher densities of non-ground cup nesters (Table 7). The increased number of cavity nesters was directly related to the increased dominance of usable snags, dead trees, found in the intermediate sere. The increased number of snags found in the boxelder-mixed woods may have been related to this sere's evolving plant community. It is plausible that the permanence of the climax bur oak forest, as well as the larger tree phenology of that sere, played an important role in determining the increased density of non-ground cup nesters. The canopy of the bur oak complex formed a vegetational screen with trees of similar height and physiognomy. The firmness and greater strength of the bur oak branches probably explains the presence of more tree canopy cup nesting birds.

Avian food and foraging guilds

Guilds are considered subsets of a community in which individuals use a similar class of resources in a similar manner. Analysis of the guild structure of a community helps clarify the functional relationships of species, and thus, interpretation of ecological processes important in coexistence (Landres and MacMahon 1980). In this study, birds were grouped into two guilds likely to be of importance in structuring communities: food and foraging guilds.

Examination of bird densities in relation to five food guilds showed that some trends were evident among the three riparian seres.

Insectivorous birds apparently responded to seasonal changes in temperature and foliage density, and insect density that accompanied those changes (Dickson 1979). Insectivores in the boxelder-mixed and bur oak woods increased in spring as temperatures increased and new foliage grew, and decreased in autumn as leaves hardened, foliage quantity declined, and temperatures decreased (Table 10). Both seres contained low densities during winter. Populations of insectivores in the pioneering cottonwood-silver maple sere followed similar seasonal trends except during winter. Winter populations of insectivorous birds were higher in the pioneer sere than those found in the same sere during summer (Tables 8 and 9). This increase was related to aggregations of chickadees, titmice, and kinglets that consistently utilized the area for short periods of time. The over-all increase in wintering insectivores found in the cottonwood-silver maple woods was only slightly lower than the boxelder-mixed and bur oak woods. Significantly lower insectivores were found in the pioneer cottonwood-silver maple sere during the summer, spring, and fall (Tables 8 and 10). The heavier mass of vegetation found in the boxelder-mixed and bur oak woods, which likely contained larger numbers of insects was probably the primary reason for the higher densities of insectivores in those woods. The high densities of insectivorous birds found in all three riparian forests, when compared to the other food guild categories, was typical of community food guild densities found in other temperate deciduous forests (Karr 1971).

Granivores increased in all three riparian seres from summer to winter, with the highest densities found during the fall (Tables 8, 9, and 10). Dickson (1979) noted that during the fall, much of the energy

of a deciduous forest ecosystem goes into mast production. Mast production in the boxelder-mixed and bur oak complexes was available to birds in the late fall and winter. During those periods large numbers of seed-eating sparrows, nuthatches, and juncos inhabited the forests (Appendix 3). The lack of mast-producing trees in the pioneer cottonwood-silver maple sere reduced the carrying capacity for granivores. Therefore, significantly lower densities were found during the summer and very little influx occurred during the spring and fall. Winter granivore densities in the cottonwood-silver maple woods more nearly equaled densities found in the other riparian woods. The increase in granivores in the cottonwood-silver maple woods during the winter was due to habitat utilization of the area by birds residing in adjoining forests.

Carnivorous bird densities were comparatively lower in all three riparian woods than the other major food guild densities (Tables 8, 9, and 10). Seasonal differences were insignificant. Slight density differences, though, were detected between the three riparian seres. Higher densities were found in the successional older boxelder-mixed and bur oak seres. Only during migration were carnivores noted in the pioneering cottonwood-silver maple sere (Appendix 3). Successful occupation of the riparian seres may have been related to the seres' productivity. Both the boxelder-mixed and bur oak seres were considered more productive than the cottonwood-silver maple woods. Productivity of the cottonwood-silver maple forest possibly increased during spring and fall when migrants appeared in the woods. As more species and increased densities of migrants occurred in the pioneer sere, species of carnivorous hawks and owls extended their ranges to include this sere. When the pioneer sere returned to its normal

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carrying capacity, carnivores reduced their activity in the area.

Low densities of omnivores were detected in the three areas during winter and early spring, however, densities increased in the summer and fall (Tables 8, 9, and 10). Low winter densities were possibly due to shifts in food habits. DesGrange (1980) found that omnivores in coniferous forests were mostly sedentary granivores during winter. Omnivores in the boxelder-mixed and bur oak woods may have shifted to granivorous food habits to utilize available mast produced in those woods. As the mast was depleted, birds returned to omnivorous food habits. During the summer and fall the highest densities of omnivores were found in the climax bur oak sere. DesGrange (1980) also found high numbers of omnivores in climax forests. He determined that the increase in omnivores found at the climax successional stage was related to the permanence of climax forests, as well as the size of the upper stratum.

High densities of frugivorous birds were found in all three riparian woods during spring and fall, however, lower densities were found in the summer and winter (Tables 8, 9, and 10). Fruiting plants were at peak production during spring and fall. Birds were obviously utilizing the abundance of available fruits and berries during those seasons. When available fruits were reduced, competition for food likely increased and frugivorous birds probably were forced to shift their diets to new food sources. The largest number of frugivores were found in the intermediate boxelder-mixed sere. This sere was determined to be more diverse, and therefore, provided more available food sources and more niches. Significantly lower densities of frugivores were found in the vegetationally lacking pioneer cottonwood-

silver maple sere.

Comparison of the foraging guild structures helped clarify the structural patterns between the three riparian forests. Only six species of birds surveyed in the three forests foraged by hawking techniques (Appendix 3). All six species utilized carnivorous food habits and their seasonal and successional trends were similar to the carnivorous food guild patterns. Seasonal trends for the three forests were very similar. Hawking birds represented less than five percent of the total populations found in the boxelder-mixed and bur oak complexes (Figures 3, 4, and 5). A slightly higher percentage, nine percent, was noted in the cottonwood-silver maple forest during spring and fall (Figure 5). Hawking bird densities were generally greater in the older more vegetationally complex riparian seres, with the greatest density during summer found in the climax bur oak sere (Table 8). These results confirm DesGranges' (1980) conclusion that birds foraging by flight generally are found in older forests, which are composed of taller, well-spaced trees sparse enough to provide room for flight.

Birds that foraged by sally-gleaning techniques were most numerous during late spring and early summer. As fall approached sally-gleaners declined and eventually departed completely in winter (Figures 3, 4, and 5). Dickson (1979) found similar seasonal trends in Louisiana hardwood forests. He found that air-foraging bird populations increased in the spring with the development and dispersal of adult flying insects, but populations plummeted after August. Successional comparisons showed that sally-gleaner densities were significantly higher in the bur oak climax forest than the boxelder-mixed or cottonwood-silver maple forests (Table 8). Reduced populations of sally-gleaners in the pioneering cottonwood-silver maple were similar to findings by Maurer et al. (1981) in West

Virginia forests. They theorized that the absence of flycatching species from early forest stands was due to a lack of perch sites offered or because the types of insects available in pioneer stands were not acceptable as prey items.

Fifty to 60 percent of the overall community populations found in the three riparian forests during spring and fall migration were timber-
foliage searching birds (Figure 5). During migration members of this foraging guild were dominated by mass influxes of wood warblers and vireos (Appendix 3). Numbers of timber-
foliage searchers were reduced to similar densities during the summer and winter. Densities during spring, summer, and fall were significantly higher in the boxelder-mixed forest, and significantly lower in the cottonwood-silver maple forest (Tables 8 and 11). The greater densities of timber-
foliage searchers in the successional intermediate boxelder-mixed forest was most likely due to this sere's densely numbered and varied shrub and tree foliage layers. The heterogeneity of the boxelder-mixed sere provided a great variety of niches scattered sporadically throughout the forest, therefore supporting a varied number of timber-
foliage searcher bird species.

Densities of birds that foraged by timber-gleaning techniques increased from summer to winter in all three seres with little change occurring during migration (Tables 8, 9, and 11). The most dramatic increase during the winter was found in the pioneering cottonwood-silver maple forest. Members of the timber-gleaner guild increased from three percent in the summer to over 10 percent of the cottonwood-silver maple's winter bird population (Figures 3 and 4). Possibly the phenology of the trees found in this forest offered added foraging advantages to timber-gleaning birds. Most of the branches of the trees in the cottonwood-

silver maple forest were concentrated near the top of the trunks. The lower trunks were usually open and easily exploited by climbing birds. The bur oak forest contained the most stable year-round populations of timber-gleaners. It was interesting to note that similar to the findings of Maurer et al. (1981), Black-and-white Warblers were virtually absent from the climax bur oak forest, but very abundant during migration in the pioneer cottonwood-silver maple sere.

Timber-driller populations showed little seasonal or successional changes among the riparian forest types (Tables 8, 9, and 11). The majority of the species composing this foraging guild were permanent species (Appendix 3). Only one transient, the Yellow-bellied Sapsucker, was noted during the study. The cottonwood-silver maple forest contained one endemic timber-driller, the Pileated Woodpecker. Downy Woodpeckers seemed to be the most abundant species throughout the three forests.

More species of birds composed the ground/slash guild than any other foraging guild (Appendix 3). Ground/slash populations generally accounted for 30 to 40 percent of the foraging guild populations (Figures 3, 4, and 5). The greatest densities were found during early spring, late fall, and winter. Populations dropped during the summer. DesGrange (1980) has shown that greater densities of ground-foraging birds occupied initial successional stages of forests in Quebec, Canada. Annual flooding in the cottonwood-silver maple sere though, reduced foliage layers near the ground and significantly reduced ground/slash foragers during spring, summer, and fall. In the intermediate and climax seres, flooding was reduced or absent. Annual deposits of dead leaves, which turn the ground layer into a rich environment for invertebrates, were increased. This possibly explains why significantly larger concentrations of ground-foraging birds were found in the boxelder-mixed

woods during summer, and relatively higher populations were found in the bur oak complex during the winter (Tables 8 and 9).

Avian foraging height diversity

In an effort to determine what factors accounted for species diversity in selected forest types, MacArthur and MacArthur (1961) published a classic report on the relationship of bird species diversity to vegetation complexity. They showed an extremely strong correlation of bird species diversity with foliage height diversity. To further examine habitat divisions by birds among the three riparian forests, a comparison of the major activity patterns at the observed height was made. The cumulative percentage of individual birds observed by height differed in each of the three riparian forests. The differences in the distributions of the observed vertical activity patterns were attributed to differences in the foliage configurations typical of each of the riparian forest types. The activity patterns were shifted upward in the boxelder-mixed and bur oak complexes, and were shifted downward in the cottonwood-silver maple complex (Figure 6). Slightly more individuals occurred from ground level to 0.61 m in the cottonwood-silver maple forest than in the boxelder-mixed and bur oak forests. As foliage height increased from 0.61 m, carrying capacity of the available habitat increased in the boxelder-mixed forest over the cottonwood-silver maple and bur oak forests. With an increase in foliage height above 1.22 m, the carrying capacity of the available habitat in the bur oak forest increased over that found in the cottonwood-silver maple forest. It was evident from these findings that more birds were found at higher foraging levels in the more vegetationally complex and diverse forests. There seemed to be a direct correlation between vertical stacking of bird numbers and a

—
successionally increasing foliage height diversity. Karr and Roth (1971) and Roth (1976) have found that the height profile of foliage density is in fact, a major component of the floristic community that allows birds to specialize on a particular part of the habitat.

SUMMARY

The intention of this study was to compare avian community structure in three successional riparian ecosystems in east central Kansas. The three seres included a pioneer cottonwood-silver maple stand, an intermediate boxelder-mixed woods, and a climax bur oak complex. The results showed that avian diversity and equitability were strongly associated with the successional development of diverse vegetative structure in the three forest types. The greatest increase in diversity and equitability values occurred with the addition of the shrub and early tree layers to the successional intermediate boxelder-mixed forest stand. The number and density of bird species in the three riparian forests paralleled successional sequences in habitats, except with a decline at the final stage of succession. Mean densities of birds grouped into four- and six-season classifications followed similar trends.

Species were classified into guilds by quantifying nest selection, food use, and foraging behavior, based on investigator-defined resource classes. Densities of cavity nesters were directly related to the increased dominance of usable dead trees found in the intermediate boxelder-mixed forest sere. Tree phenology of the climax bur oak sere played an important role in determining the high density of non-ground cup nesters found in that successional sere. Food guild densities corresponded to seasonal effects on forest productivity. Foraging guild densities were related to the habitat heterogeneity associated with ecological succession of the riparian forest types.

Results showed a strong correlation between foliage height diversity of the three riparian forests and avian forage height utilization. Increased vegetational complexity of the forest stands

increased the number of birds utilizing higher foraging levels.

Based on the results of this study it was determined that the general pattern of avian succession was a manifestation of the habitat preferences and ecological requirements of the bird species as they related to vegetational complexity.

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APPENDIX 1

A summary of vegetation surveyed in each riparian forest.

Cottonwood-Silver Maple Forest

Rye Grass.....	<u>Elymus</u> spp.
Black Willow.....	<u>Salix nigra</u> Marsh.
Eastern Cottonwood.....	<u>Populus deltoides</u> Bartr. ex Marsh.
Canada Wood Nettle.....	<u>Laportea canadensis</u> (L.) Wedd.
Pokeweed.....	<u>Phytolacca americana</u> L.
American Sycamore.....	<u>Platanus occidentalis</u> L.
Cinquefoil.....	<u>Potentilla norvegica</u> L.
Poison Ivy.....	<u>Toxicodendron radicans</u> (L.) Gillis
Boxelder.....	<u>Acer negundo</u> L.
Silver Maple.....	<u>Acer saccharinum</u> L.
Missouri Violet.....	<u>Viola missouriensis</u> Greene
Green Ash.....	<u>Fraxinus pennsylvanica</u> Marsh.
Aster.....	<u>Aster simplex</u> Willd.

Boxelder-Mixed Forest

Rye Grass.....	<u>Elymus</u> spp.
Black Willow.....	<u>Salix nigra</u> Marsh.
Eastern Cottonwood.....	<u>Populus deltoides</u> Bartr. ex Marsh.
Black Walnut.....	<u>Juglans nigra</u> L.
Bur Oak.....	<u>Quercus macrocarpa</u> Michx.
American Elm.....	<u>Ulmus americana</u> L.
Red Elm.....	<u>Ulmus rubra</u> Muhl.
Hackberry.....	<u>Celtis occidentalis</u> L.
Red Mulberry.....	<u>Morus rubra</u> L.
Canada Wood Nettle.....	<u>Laportea canadensis</u> (L.) Wedd.
Tall Nettle.....	<u>Urtica dioica</u> L.
Mild Water-Pepper.....	<u>Polygonum hydropiperoides</u> Michx.
Pokeweed.....	<u>Phytolacca americana</u> L.
American Sycamore.....	<u>Platanus occidentalis</u> L.
Kentucky Coffee Tree.....	<u>Gymnocladus dioica</u> (L.) K. Koch
Poison Ivy.....	<u>Toxicodendron radicans</u> (L.) Gillis
Boxelder.....	<u>Acer negundo</u> L.
Silver Maple.....	<u>Acer saccharinum</u> L.
Riverbank Grape.....	<u>Vitis riparia</u> Michx.
Missouri Violet.....	<u>Viola missouriensis</u> Greene
Green Ash.....	<u>Fraxinus pennsylvanica</u> Marsh.
Morning-Glory.....	<u>Ipomoea pandurata</u> (L.) Mey
American Bellflower.....	<u>Campanula americana</u> L.
Giant Ragweed.....	<u>Ambrosia trifida</u> L.
Beggarticks.....	<u>Bidens</u> spp. L.

Bur Oak Forest

- Rye Grass.....Elymus spp.
- Bristly Greenbrier.....Smilax hispida
- Bur Oak.....Quercus macrocarpa Michx.
- American Elm.....Ulmus americana L.
- Red Elm.....Ulmus rubra Muhl.
- Hackberry.....Celtis occidentalis L.
- Red Mulberry.....Morus rubra L.
- Canada Wood Nettle.....Laportea canadensis (L.) Wedd.
- Mild Water-Pepper.....Polygonum hydropiperoides Michx.
- Maple-Leaved Goosefoot.....Chenopodium gigantospermum Aellen
- Pokeweed.....Phytolacca americana L.
- Pawpaw.....Asimina triloba (L.) Dunal.
- Purple Rocket.....Iodanthus pinnatifidus (Michx.) Steud.
- Kentucky Coffee Tree.....Gymnocladus dioica (L.) K. Kock
- Toothed Spurge.....Euphorbia dentata Michx.
- Poison Ivy.....Toxicodendron radicans (L.) Gillis.
- Western Buckeye.....Aesculus glabra Willd. var. agruta
(Buckl.) Robinson
- Missouri Violet.....Viola missouriensis Greene
- Green Ash.....Fraxinus pennsylvanica Marsh.
- Giant Ragweed.....Ambrosia trifida L.
- Cutleaf Coneflower.....Rudbeckia laciniata L.
- Wingstem.....Verbesina alternifolia (L.) Britt.

APPENDIX 2

Scientific names of birds surveyed during this study.

Order Ciconiiformes

Family Ardeidae

Great Blue Heron.....Ardea herodiasGreen-backed Heron.....Butorides striatus

Order Falconiformes

Family Accipitridae

Cooper's Hawk.....Accipiter cooperiiRed-tailed Hawk.....Buteo jamaicensis

Family Falconidae

American Kestrel.....Falco sparverius

Order Galliformes

Family Phasianidae

Northern Bobwhite.....Colinus virginianus

Order Charadriiformes

Family Scolopacidae

Spotted Sandpiper.....Actitis maculariaAmerican Woodcock.....Scolopax minor

Order Columbiformes

Family Columbidae

Mourning Dove.....Zenaida macroura

Order Cuculiformes

Family Cuculidae

Yellow-billed Cuckoo.....Coccyzus americanus

Order Strigiformes

Family Strigidae

Great Horned Owl.....Bubo virginianusBarred Owl.....Strix varia

Order Apodiformes

Family Trochilidae

Ruby-throated Hummingbird.....Archilochus colubris

Order Coraciiformes

Family Alcedinidae

Belted Kingfisher.....Ceryle alcyon

Order Piciformes

Family Picidae

Red-headed Woodpecker.....Melanerpes erythrocephalus

Red-bellied Woodpecker.....Melanerpes carolinus

Yellow-bellied Sapsucker.....Sphyrapicus varius

Downy Woodpecker.....Picoides pubescens

Hairy Woodpecker.....Picoides villosus

Northern Flicker.....Colaptes auratus

Pileated Woodpecker.....Dryocopus pileatus

Order Passeriformes

Family Tyrannidae

Olive-sided Flycatcher.....Contopus borealis

Eastern Wood-Pewee.....Contopus virens

Least Flycatcher.....Empidonax minimus

Empidonax Flycatchers.....Empidonax spp.

Eastern Phoebe.....Sayornis phoebe

Great Crested Flycatcher.....Myiarchus crinitus

Western Kingbird.....Tyrannus verticalis

Eastern Kingbird.....Tyrannus tyrannus

Family Corvidae

- Blue Jay.....Cyanocitta cristata
 American Crow.....Corvus brachyrhynchos

Family Paridae

- Black-capped Chickadee.....Parus atricapillus
 Tufted Titmouse.....Parus bicolor

Family Sittidae

- Red-breasted Nuthatch.....Sitta canadensis
 White-breasted Nuthatch.....Sitta carolinensis

Family Certhiidae

- Brown Creeper.....Certhia americana

Family Troglodytidae

- Carolina Wren.....Thryothorus ludovicianus
 House Wren.....Troglodytes aedon

Family Muscicapidae

- Golden-crowned Kinglet.....Regulus satrapa
 Ruby-crowned Kinglet.....Regulus calendula
 Blue-gray Gnatcatcher.....Poliophtila caerulea
 Eastern Bluebird.....Sialia sialis
 Swainson's Thrush.....Catharus ustulatus
 Hermit Thrush.....Catharus guttatus
 Wood Thrush.....Hylocichla mustelina
 American Robin.....Turdus migratorius

Family Mimidae

- Gray Catbird.....Dumetella carolinensis
 Northern Mockingbird.....Mimus polyglottos
 Brown Thrasher.....Toxostoma rufum

Family Bombycillidae

Cedar Waxwing.....Bombycilla cedrorum

Family Sturnidae

European Starling.....Sturnus vulgaris

Family Vireonidae

Bell's Vireo.....Vireo belliiSolitary Vireo.....Vireo solitariusYellow-throated Vireo.....Vireo flavifronsWarbling Vireo.....Vireo gilvusRed-eyed Vireo.....Vireo olivaceus

Family Emberizidae

Tennessee Warbler.....Vermivora peregrinaOrange-crowned Warbler.....Vermivora celataNashville Warbler.....Vermivora ruficapillaNorthern Parula.....Parula americanaYellow Warbler.....Dendroica petechiaChestnut-sided Warbler.....Dendroica pensylvanicaBlack-throated Blue Warbler.....Dendroica caerulescensYellow-rumped Warbler.....Dendroica coronataBlack-throated Green Warbler.....Dendroica virensBlack-and-white Warbler.....Mniotilta variaAmerican Redstart.....Setophaga ruticillaProthonotary Warbler.....Protonotaria citreaOvenbird.....Seiurus aurocapillusKentucky Warbler.....Oporornis formosusConnecticut Warbler.....Oporornis agilis

Mourning Warbler.....	<u>Oporornis philadelphia</u>
Common Yellowthroat.....	<u>Geothlypis trichas</u>
Wilson's Warbler.....	<u>Wilsonia pusilla</u>
Northern Cardinal.....	<u>Cardinalis cardinalis</u>
Rose-breasted Grosbeak.....	<u>Pheucticus ludovicianus</u>
Black-headed Grosbeak.....	<u>Pheucticus melanocephalus</u>
Indigo Bunting.....	<u>Passerina cyanea</u>
Dickcissel.....	<u>Spiza americana</u>
Rufous-sided Towhee.....	<u>Pipilo erythrophthalmus</u>
Chipping Sparrow.....	<u>Spizella passerina</u>
Fox Sparrow.....	<u>Passerella iliaca</u>
Song Sparrow.....	<u>Melospiza melodia</u>
Lincoln's Sparrow.....	<u>Melospiza lincolni</u>
Swamp Sparrow.....	<u>Melospiza georgiana</u>
White-throated Sparrow.....	<u>Zonotrichia albicollis</u>
White-crowned Sparrow.....	<u>Zonotrichia leucophrys</u>
Harris' Sparrow.....	<u>Zonotrichia querula</u>
Dark-eyed Junco.....	<u>Junco hyemalis</u>
Red-winged Blackbird.....	<u>Agelaius phoeniceus</u>
Brewer's Blackbird.....	<u>Euphagus cyanocephalus</u>
Common Grackle.....	<u>Quiscalus quiscula</u>
Brown-headed Cowbird.....	<u>Molothrus ater</u>
Orchard Oriole.....	<u>Icterus spurius</u>
Northern Oriole.....	<u>Icterus galbula</u>

Family Fringillidae

Purple Finch.....	<u>Carpodacus purpureus</u>
Pine Siskin.....	<u>Carduelis pinus</u>
American Goldfinch.....	<u>Carduelis tristis</u>

APPENDIX 3

Species guild classifications for all birds surveyed during this study.

<u>Foraging</u>	<u>Food Types</u> ¹	<u>Nest</u> ²	<u>Residency</u> ³		
			CW-M ⁴	B-M ⁴	OAK ⁴
<u>Timber-foliage searcher</u>					
Ruby-crowned Kinglet	I/G	CU	M	M	M
Blue-gray Gnatcatcher	I	CU		S	S
Cedar Waxwing	F/I	CU		Oc	Oc
Bell's Vireo	I	CU		M	
Solitary Vireo	I	CU	M	M	M
Yellow-throated Vireo	I	CU			M
Warbling Vireo	I	CU	Oc	S	S
Red-eyed Vireo	I	CU	S	S	S
Tennessee Warbler	I/G	GR	M	M	M
Orange-crowned Warbler	I	GR/CU		M	M
Nashville Warbler	I	GR	M	M	M
Northern Parula	I	CU	S	M	M
Yellow Warbler	I	CU		M	M
Chestnut-sided Warbler	I	CU		M	
Black-throated Blue Warbler	I/G	CU		M	
Yellow-rumped Warbler	I	CU	M	M	M
Black-throated Green Warbler	I	CU		M	M
American Redstart	I	CU	M	M	M
Wilson's Warbler	I	GR	M	M	
Rose-breasted Grosbeak	G/I	CU		M	M
Black-headed Grosbeak	G/F/I	CU	M		
Orchard Oriole	I	CU	M	M	M
Northern Oriole	I/F	CU	Oc	S	S
Pine Siskin	G/I	CU		W	W

<u>Foraging</u>	<u>Food Types</u> ¹	<u>Nest</u> ²	<u>Residency</u> ³		
			CW-M ⁴	B-M ⁴	OAK ⁴
<u>Timber-foliage searcher</u>					
American Goldfinch	G	CU	Oc	Oc	Oc
Purple Finch	G	CU	M		
<u>Timber-gleaner</u>					
White-breasted Nuthatch	G/I	CA	P	P	P
Red-breasted Nuthatch	G/I	CA		W	W
Brown Creeper	I	CU	W	W	W
Black-and-white Warbler	I	GR	M	M	M
<u>Timber-driller</u>					
Red-bellied Woodpecker	G/I/F	CA	P	P	P
Yellow-bellied Sapsucker	N/I	CA			M
Downy Woodpecker	I/G/F	CA	P	P	P
Hairy Woodpecker	I	CA	Oc	S	P
Pileated Woodpecker	I/G/F	CA	P		
<u>Ground/slash</u>					
Great Blue Heron	C	CU	Oc		Oc
Green-backed Heron	C	CU		Oc	
Northern Bobwhite	G/I	GR	Oc	Oc	Oc
American Woodcock	I	GR			M
Spotted Sandpiper	I/C	GR	M		Oc
Mourning Dove	G	CU	Oc	P	
Northern Flicker	I/F	CA	P	P	P
American Crow	O	CU	S	Oc	Oc
Carolina Wren	I	CA/CU	M	M	
House Wren	I	CA	M	S	S

<u>Foraging</u>	<u>Food Types</u> ¹	<u>Nest</u> ²	<u>Residency</u> ³		
			CW-M ⁴	B-M ⁴	OAK ⁴
Ground/slash					
Swainson's Thrush	I/F	CU	M	M	M
Hermit Thrush	I/F	GR		M	W
Wood Thrush	I/F	CU	M	M	M
American Robin	I/F	CU	S	M	S
Gray Catbird	I/F	CU		M	M
Northern Mockingbird	I/F	CU		Oc	
Brown Thrasher	I/F	CU	M	M	M
European Starling	I/G	CA	P		
Prothonotary Warbler	I	CA	S		
Ovenbird	I	GR		M	
Kentucky Warbler	I	GR/CU			M
Connecticut Warbler	I	GR			M
Mourning Warbler	I	GR/CU	M	M	M
Common Yellowthroat	I	CU		S	M
Northern Cardinal	I/G/F	CU	P	P	P
Indigo Bunting	I/G	CU	S	S	S
Dickcissel	G/I	CU			M
Rufous-sided Towhee	I/F	GR		M	
Chipping Sparrow	G/I	CU		M	M
Fox Sparrow	G/F	GR			M
Song Sparrow	I/G	GR/CU			M
Lincoln's Sparrow	I/G	GR		M	M
Swamp Sparrow	I/G	CU			M
White-throated Sparrow	G/F/I	GR/CU	M	M	M

<u>Foraging</u>	<u>Food Types</u> ¹	<u>Nest</u> ²	<u>Residency</u> ³		
			CW-M ⁴	B-M ⁴	OAK ⁴
Ground/slash					
White-crowned Sparrow	G/I	GR/CU		M	
Harris' Sparrow	G	GR	W	W	W
Dark-eyed Junco	G/I	GR	W	W	W
Red-winged Blackbird	G	CU	Oc		Oc
Brewer's Blackbird	I/G	CU/GR	M		
Common Grackle	I/G	CU	Oc		Oc
Brown-headed Cowbird	I	CU/GR/CA	Oc	S	Oc

¹Food type: C= Carnivorous, O= Omnivorous, F= Frugivorous, I= Insectivorous, N= Nectarivorous, G= Granivorous

²Nest type: CU= Cup nest (non-ground), CA= Cavity nest, GR= Ground nest

³Residency: S= Summer, W= Winter, M= Migrant, Oc= Occasional, P= Permanent

⁴Study areas: CW-M= Cottonwood-silver maple, B-M= Boxelder-mixed, OAK= Bur Oak