Habitat selection by birds of riparian communities:

Evaluating the effects of habitat alteration

by

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ABSTRACT

Avifauna of riparian communities were studied in Guthrie County, Iowa during late spring and early summer. Birds were censused by the spot map method on 28 study plots representing a habitat gradient from hayfields to closed-canopy woodlands. Plant species composition and vegetation structure were used to characterize habitats. An index of nesting niche breadth was determined for 22 open-nesting bird species on the basis of vegetation life form(s) utilized for nesting and for 12 cavity-nesting species based upon nest cavity support types(s). The index was used to estimate tolerance to nesting substrate alterations. Cavity-nesters preferred soft snags as nest sites. Floodplain woodlands supported higher densities of breeding birds than herbaceous or upland woodland habitats. Bird species richness increased significantly with the width of wooded riparian habitats; 16 species restricted breeding to relatively wide plots. Wooded habitats supported a maximum of 32 species; herbaceous habitats seven. Observation frequencies of 52 bird species in six general habitat types were used to calculate indices of tolerance to habitat alteration. Microhabitat characteristics selected by each species were determined by comparing bird observation frequencies with 38 vegetation variables, using stepwise multiple regression. The potential effects on the 52 species of six alterations to wooded riparian habitats are predicted.

INTRODUCTION

Efforts to determine habitat requirements in game birds and to apply the results to species management schemes have been extensive (Hooper and Crawford 1969). Nongame birds are also a wildlife resource enjoyed by a substantial portion of the public (Hickey and Henney 1975), but to date, little comprehensive, quantitative research effort has been devoted to the management of these species. Most research concerning nongame bird management is local in nature or concerned with endangered species (Robbins and Erskine 1975). Avian community structure and composition have been studied extensively (Kendeigh 1946, 1948, Johnston and Odum 1956, Bond 1957, Beals 1960, Wiens 1969, Shugart and James 1973, Anderson and Shugart 1974, Zimmerman and Tatschl 1975), and some workers have related avifaunal composition to land-use practices (Dambach 1944, Warbach 1958, Graber and Graber 1963). Minimal intensive work, however, has been done to delineate habitat characteristics critical for individual species comprising a community, and then to apply this information to the management of nongame birds (Schemnitz 1976). Participants in a symposium on habitat management for nongame birds (Smith 1975) stressed the need to integrate quantitative data on habitat selection by birds and habitat management.

Riparian habitats are critical to wildlife (Russell 1967, Allen 1969, Holder 1969, Carothers and Johnson 1975), especially in regions with intensive agriculture. Major concerns about the effects of stream alteration have centered mainly upon the aquatic environment. Recently, however, attention has been focused on the effects of stream channelization on both game and nongame terrestrial wildlife (Allen 1969, Barstow 1971, Choate 1972, Dodge et al. 1976, Ferguson et al. 1976), although the most intensive studies have been restricted to only a few stream segments (Dodge et al. 1976, Ferguson et al. 1976). Reliable assessments of the impact of riparian habitat alterations on the associated wildlife require more research, and the present study is an attempt to partially satisfy that need.

The objectives of this study were to quantify factors critical in nest site and habitat selection by breeding birds of riparian communities over a wide range of habitat types, and then to use the results to evaluate potential effects of habitat perturbations. Such information is of primary importance to habitat managers (Lennartz and Bjugstad 1975). These results are applicable to both riparian and upland habitats of the Central Plains, and with caution could be used in other geographical areas as well.

METHODS

Study Sites and Field Methods

Guthrie County, Iowa was selected as the study area by inspecting aerial photographs; availability of a variety of riparian habitats was the major criterion for selection. In March 1976, 28 stream segments on Brushy Creek, Beaver Creek, and the Middle and South Raccoon Rivers in the southeastern portion of the county were chosen for study and permission was secured from landowners to establish study plots (Fig. 1). The plots represented a gradient of riparian habitats from hayfields to closed-canopy woodland; five segments were on channelized streams.

The plots consisted of transects paralleling the stream channel, with the first transect 25m from the stream edge and successive transects 50m apart. Flagged markers were placed at 25m intervals along each transect. Maximum transect length was 500m and the maximum number of transects per plot was five; the length and number of transects were determined by the extent of relatively homogeneous habitat. Grid maps were drawn for all plots which ranged in size from 0.2 to 12.25ha.

At each grid point, saplings (DBH<5cm) and trees (DBH>5cm) were measured using the point quarter method and the ground slope was recorded. All plant species occurring in and(or) above a $1m^2$ square quadrat, positioned three paces from each grid point at a 45° angle from the transect line, were recorded

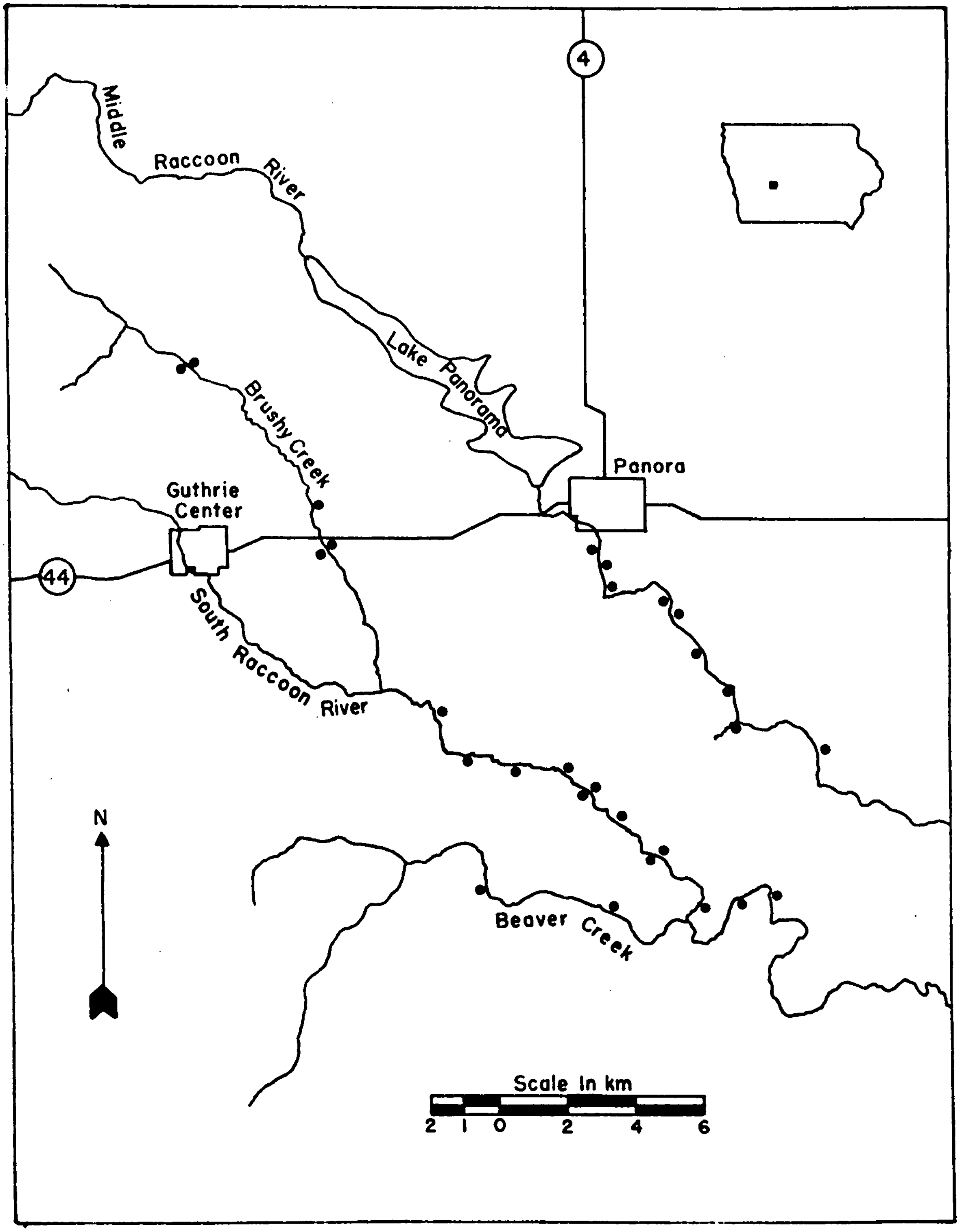

Figure 1. Locations (dots) of the 28 study plots in Guthrie County, Iowa.

and assigned a life form (forb, grass-like, shrub, deciduous tree, evergreen tree, vine). Vegetation measurements were made June through August 1976; methods are detailed by Vogler (1978).

Habitat structure was measured in April 1977. The presence of live vegetation in each of ten height classes (0.0-0.5m, 0.51-1.5m, 1.51-3m, 3.1-5m, 5.1-7m, 7.1-9m, 9.1-12m, 12.1-17.5m, 17.6-22.5,m 22.6m+) was recorded at every grid point. Location, height class, and DBH were recorded for every snag within 15m on either side of each transect line. Snag hardness was classified based upon the percentage of the original limbs still present (soft = 0-33% limbs, intermediate = 34-66% limbs, hard = 67%+ limbs).

Breeding birds were censused on all plots using the spot-map method (Kendeigh 1944). During a census, which began 15 to 30 minutes before sunrise, transect lines were followed until the plot had been completely traversed. On larger plots (two or more transects) successive censuses were begun at opposite sides of the plot to insure that all sections of the plot were covered in the early morning. Observations and behavior of resident birds 25m on either side of the transects were recorded on grid maps of the plots; occurrence of transients and migrants also was noted (see Appendix B). Morning censuses were not conducted on days with rain or strong wind, but if conditions permitted, compensatory evening censuses were made on plots with only one transect. Plots were censused on a rotational schedule until each had been covered 12 times. In 1976, 16 plots were censused from 18 April through 16 July, and in 1977, 12 plots were censused from 19 April through 13 July. Composite maps were constructed of the observations for all species on each plot and used to estimate breeding bird densities. No density estimate was made for species assumed breeding but lacking clumped observations (see Erskine 1974). The number of observations of each species in 25 X 50m subplots (N = 1349), centered at each grid point, also was compiled from census results for comparison with the vegetation and structure data recorded at each grid point. A total of 16,070 observations for 52 resident species was compiled.

Most nests were located by observing breeding behavior and searching suitable vegetation immediately after morning censuses and during early evening. Additional nests were found during censuses. The life form of the plant providing nest support was recorded. Ground nests were assigned the life form of the plant affording cover and nests positioned in vines (12 nests) were assigned the life form most similar to the structure of the vine. The nest sample is biased because a disproportionate number of nests was found in the more open plots where birds were followed more easily.

Analysis Methods

Vogler (1978) identified 46 habitat types on the study plots by reciprocal averaging ordination (Hill 1973) of the plant species frequencies on each plot. Data from both quadrat and point quarter sampling were used. For this study, the 46 habitat types were consolidated into 24 (representing six general habitat categories; Appendix A), based upon similarities in vegetation composition and physiognomy. The total area of each general habitat type was determined using a compensating polar planimeter. The number of times each bird species was observed in the general habitat types was determined from the census observations.

The reciprocal of Simpson's (1949) Index ($1/\Sigma p_i^2$, where p_i = the proportion of the total sample in the i^{th} group) was used as an expression of niche breadth across the resource states being analyzed (Whittaker and Levin 1975:169). Index values were calculated for habitat selection of 52 species based upon their densities in the six general habitat types, and for nest site selection of 22 open-nesting species based upon vegetation life form(s) utilized for nesting and 12 cavity-nesting species based upon nest cavity support type(s). Habitat and nest site indices were not calculated unless data for at least 10 habitat observations or four nests were available, respectively. Species with broader niches (higher index values) were assumed to be more tolerant of habitat alterations. Hereafter, the index will be referred to as the tolerance index. Where sample sizes are small the indices should be interpreted with caution because a small shift in observation distribution can radically alter the index value.

The following variables were derived from vegetation and habitat structure measurements made at each of the subplots and then compared with the total bird counts in the subplots (see Table 6). Point quarter data were used to estimate species richness, mean DBH, mean density, horizontal patchiness (calculated as the coefficient of variation [CV] of distance to trees/saplings from the grid points, see Roth 1976), and vertical patchiness (CV of sapling/tree DBH) for saplings and trees. Plant species richness in each of six life forms, overall plant species richness, and life form richness were estimated from the vegetation quadrat measurements. The degree of vegetation stratification within the shrub (0-3m), understory (3-9m), and canopy (9m+) layers was calculated as the percentage of height classes with vegetation within each layer. An index of overall stratification also was calculated using the percentage of all 10 height classes with vegetation. The following snag measurements were used as variables: total number, number in each hardness class, number in each of the three strata previously mentioned, mean DBH, and number in DBH classes <25cm, 25-50cm, 51-75cm, and >75cm. Slope was also included as a variable. The numbers of each bird species observed in the subplots approximated a Poisson distribution and therefore were transformed using square roots (Sokal and Rohlf 1969:384). The transformed species counts were then regressed on the independent variables using stepwise multiple regression (F to enter = 6.63, $P \leq 0.01$) to determine relationships between bird densities and the independent variables. A significant relationship between bird density and a measured variable was assumed to indicate either preference for or avoidance of that variable.

RESULTS AND DISCUSSION

Nest Site Selection

Nest site availability is an important prerequisite in habitat selection by birds (von Haartman 1956, Hilden 1965, Willson 1966, Root 1967, Johnston 1970, Zimmerman 1971, Verner 1975). The nesting period is critical to population survival, and without adequate nest sites, reproductive potential cannot be realized. Thus, nest site availability can limit population size of a species (Johnston 1970, Zimmerman 1971, Holm 1973, Carothers et al. 1974, Savidge 1974, Carothers and Johnson 1975, Thomas et al. 1976). Suitable nest sites also can reduce predation through inaccessibility (Schaefer 1976) or minimize adverse climatic conditions (Collias 1964, Horvath 1964, Calder 1973, Austin 1976).

Alteration of nesting substrates has varied effects on different species. Dambach (1944) reported the loss of numerous nesting birds from a community after shrub depletion caused by grazing, and Johnston (1970) recorded an increase in the number of edge species with an increase in shrub cover resulting from urbanization. Best (1972) reported a reduction in the nesting density of Brewer's sparrows (Spizella breweri) associated with sagebrush control. Removal of the preferred understory nesting sites reduced populations of some species in an upland woodland (Burr and Jones 1968), although American robins (Turdus migratorius) and wood thrushes (Hylocichla mustelina) adjusted by placing nests in the canopy. Preston (1946) and Preston and Norris (1947) also noted a tendency for some birds to adapt to understory disturbance by nesting in higher strata. The importance of adequate density and distribution of snags utilized for foraging and nesting by cavity-nesting species has been recognized; snag depletion has resulted in a decline of nesting populations (Balda 1974, Zeedyk and Evans 1975, Thomas et al. 1976).

Birds appear to select nest sites on the basis of substrate structure rather than plant species composition (Beecher 1942, Nickell 1965, Willson 1966, Burr and Jones 1968, Francis 1971, Holm 1973). Accordingly, the variety of vegetation life forms (representing substrate structure) utilized by a species for nest support should indicate its adaptability to changes in habitat structure. As species become more flexible in choice of nest sites, factors other than suitable nesting substrates probably become more important in habitat selection (Hilden 1965).

The results presented below are most applicable to species nesting in riparian habitats of the Central Plains. Application to other geographical areas or habitats should be made with caution because a species appearing to have inflexible nesting requirements in one area may be more adaptable elsewhere, and nesting requirements may vary in different regions (Verner 1975).

Open-nesting species

Tolerance indices were calculated for 24 species on the basis of the life form(s) used for nest placement (see Methods). The species tolerances of nesting habitat alteration (Table 1) were classified into three categories. The first category (tolerance indices <1.30) represents species specialized in their selection of nesting substrates. Such species would be intolerant of a reduction in their preferred nesting substrate. Species dependent on deciduous trees for nest support were the eastern kingbird (*Tyrannus tyrannus*), eastern wood pewee (*Contopus virens*), and northern oriole (*Icterus galbula*) (see also Tyler 1968, Graber et al. 1974). I found the American robin, blue jay (*Cyanocitta cristata*), and wood thrush also to be dependent on deciduous trees for nest sites, but in other habitats robins and blue jays will nest on man-made structures and in coniferous trees (Brackbill 1950, Headstrom 1970:117, Graber et al. 1971, Knupp et al. 1977). Burr and Jones (1968) reported that wood thrushes nested mainly in deciduous saplings. The common yellowthroat (*Geothlypis trichas*), a specialized grass nester, would be affected adversely by elimination of a well-developed grass layer (see also Stewart 1953).

The second category (tolerance indices 1.50-2.10) represents species demonstrating preference for a particular nesting substrate, but which also utilize alternative nesting sites.

Table 1. Distribution of nests among various support life forms and life form tolerance indices for open-nesting species.

		Percent of nests in each life form						
Species	N	Forb	Grass	Shrub	Deciduous sapling	Deciduous tree	Evergreen tree	Tolerance index
Eastern wood pewee	21					100.0		1.00
American robin	17					100.0		1.00
Northern oriole	13					100.0		1.00
Eastern kingbird	4					100.0		1.00
Blue jay	34					94.1	5.9	1.12
Common yellowthroat	12		91.7	8.3				1.18
Wood thrush	8			12.5		87.5		1.28
Brown thrasher	31			77.4	3.2	16.1	3.2	1.59
Rose-breasted grosbeak	47			21.3	6.4	72.3		1.75
Song sparrow	12	66.7	33.3					1.79
Gray catbird	92			71.7	10.9	14.1	2.2	1.83

Yellow warbler	5			60.0		40.0		1.92
Yellow-billed cuckoo	9			11.1	22.2	66.7		1.98
Field sparrow	9	11.1		66.7			22.2	1.98
American redstart	6			16.7	16.7	66.7		2.00
Mourning dove	58			12.1	10.9	67.2	15.5	2.03
Indigo bunting	41	41.5		39.0	19.5			2.76
American goldfinch	5	40.0			20.0	40.0		2.78
Black-billed cuckoo	5			40.0	20.0	40.0		2.78
Cardinal	76			50.0	19.7	19.7	10.5	2.96
Dickcissel	9	44.4	33.3	11.1	11.1			3.00
Red-winged blackbird	31	19.4	48.4	19.4	9.7	3.2		3.12

These species are capable of persisting in a habitat after alteration of their preferred nesting substrate by shifting to alternative life forms; however, nesting densities may decline. Gray catbirds (Dumatella carolinensis), brown thrashers (Toxostoma rufum), yellow warblers (Dendroica petechia), and field sparrows (Spizella pusilla) would be affected adversely by loss of shrubs (see also Zimmerman 1963, Nickell 1965, 1969, Walkinshaw 1968, Graber et al. 1970). These species could persist in a habitat by nesting in forbs (field sparrow), deciduous saplings and trees (brown thrasher, gray catbird, yellow warbler), or evergreen trees (field sparrow, brown thrasher, gray catbird). Grass is also an important nesting substrate for field sparrows early in the nesting season (Best 1978).

Song sparrows (Melospiza melodia) restricted nesting to the two herbaceous life forms, thus, if herbaceous cover were depleted, this species might fail to nest; however, song sparrows also have been known to use saplings and shrubs (Nolan 1968). The rose-breasted grosbeak (Pheucticus ludovicianus), yellow-billed cuckoo (Coccyzus americanus), American redstart (Setophaga ruticilla), and mourning dove (Zenaida macroura) were dependent primarily upon deciduous trees for nesting substrates (see also Carter 1956, Nolan 1963, Ficken 1964, Bent 1968, Nickell 1969, LaPerriere 1971), but alternatively all can utilize shrubs and saplings. Mourning doves and rose-breasted grosbeaks (Bent 1968) also will nest in evergreen trees. Additionally, Graber and Graber (1963) reported mourning doves nesting on the ground in hayfields. Excepting song sparrows and possibly field sparrows and mourning doves, all species in this second category would be eliminated from the nesting community with the loss of woody vegetation.

The third category of open-nesters (tolerance indices >2.70) is composed of species generalized in their selection of nesting substrates and factors other than nest site availability probably determine habitat selection. These species would be relatively tolerant of habitat alterations. Of the six species, only the black-billed cuckoo (*Coccyzus erythropthalmus*) and cardinal (*Cardinalis cardinalis*) restricted their nesting to woody vegetation (see also Nolan 1963, Dow 1969). Any habitat with woody vegetation offers potential nest sites. Red-winged blackbirds (*Agelaius phoeniceus*) and dickcissels (*Spiza americana*) preferred herbaceous life forms but also utilized woody vegetation for nesting (see also Gross 1968, Holcomb and Tweist 1968, Francis 1971, Harmeson 1974).

American goldfinches (*Carduelis tristis*) used both woody and herbaceous life forms, but apparently prefer the former. Holcomb (1969) found 90 of 102 goldfinch nests in woody vegetation, thus, this species may be more restricted to woody nesting substrates than my data indicate. Indigo buntings (*Passerina cyanea*) also nested in both herbaceous and woody substrates, but all nests with woody support were surrounded by dense forb growth (see also Taber and Johnston 1968). Relatively thick herbaceous cover apparently is a prerequisite for nesting in the indigo bunting, and the exact nest support form probably is chosen secondarily after selecting the herbaceous cover (see Habitat Selection). As a result, this species may be more specialized than the index value indicates.

Cavity-nesting species

All cavity-nesting species are specialists in that they nest only in live or dead trees (artificial nest-boxes excepted). Loss of trees and snags would be detrimental to both primary (cavity excavating) and secondary cavity-nesters (Balda 1974, Zeedyk and Evans 1975, Thomas et al. 1976). Potential nest sites can be snags, dead limbs of live trees, or live trees. The tolerance index was calculated for 12 cavity-nesting species on the basis of these three nest sites.

Table 2 presents data on nest sites selected by five primary and seven secondary cavity-nesters. Of the primary cavity-nesters, red-headed (*Melanerpes erythrocephalus*), downy (*Picoides pubescens*), and red-bellied (*M. carolinus*) woodpeckers nested predominately in snags rather than live trees (see also Lawrence 1967, Jackson 1976). Although common flickers (*Colaptes auratus*) also preferred snags, they nested more frequently in live trees than the previously

Table 2. Distribution of nests among various support types and support type tolerance indices for cavity-nesting species.

Species	N	Percent nests in each support type: Snag	Dead limb	Live tree	Tolerance index
Primary cavity-nesters					
Red-headed woodpecker	60	88.4	3.3	8.3	1.27
Downy woodpecker	30	83.3	10.0	6.7	1.41
Red-bellied woodpecker	14	78.6	7.1	14.3	1.56
Hairy woodpecker	4		75.0	25.0	1.60
Common flicker	31	64.5	9.7	25.8	2.03
Secondary cavity-nesters					
Eastern bluebird	4	100.0			1.00
Black-capped chickadee	25	92.0	4.0	4.0	1.17
Northern house wren	82	74.4	23.2	2.4	1.64
European starling	22	68.1	18.2	13.6	1.94
White-breasted nuthatch	9	33.3	11.1	55.6	2.31
House sparrow	13	46.2	23.1	30.8	2.77
Great crested flycatcher	13	38.5	23.1	38.5	2.86

mentioned species. Hairy woodpeckers (P. villosus) did not select snags for nesting, but the sample size was small. Lawrence (1967) reported patterns similar to those I observed in nest site selection by hairy woodpeckers and common flickers. Excepting the hairy woodpecker, removal of snags from wooded habitats would drastically reduce potential nest sites for primary cavity-nesters, although all can use live trees and dead limbs as alternatives.

In general, secondary cavity-nesters are less selective than primary cavity-nesters in choosing nest sites and more frequently use cavities in dead limbs and live trees for nesting. The eastern bluebird (Sialia sialis) appears to be the most selective species, as it nested only in snags, but small sample size makes this conclusion suspect. Graber et al. (1971) reported bluebird nests in natural cavities of live trees, but Pinkowski (1976) found 87 of 98 bluebird nests in dead trees. Black-capped chickadees (Parus atricapillus), northern house wrens (Troglodytes aedon), and European starlings (Sturnus vulgaris) placed a majority of their nests in snags, but also utilized dead limbs and live trees (see also Odum 1941, Headstrom 1970). Kessel (1957) reported that starlings will nest in any available cavity.

White-breasted nuthatches (Sitta carolinensis), house sparrows (Passer domesticus), and great crested flycatchers (Myiarchus crinitus) tended to select dead limbs and live trees rather than snags as nest sites (see also Headstrom 1970, Graber et al. 1974). Of the secondary cavity-nesters, these three species would be affected least by removal of snags from woodlands. In general, the tolerance indices for all cavity-nesting species increased with a decrease in dependence on snags for nest sites. Also, primary cavity-nesters, having more latitude in choice of cavity placement, appear to be more selective in their nest site selection than secondary cavity-nesters, which usually must choose from the cavities already available.

The selection of snags for nesting was dependent on their condition (Table 3). Of the snags on all wooded plots, 49% were soft, 9% were intermediate, and 42% were hard. (The increase of Dutch elm disease by the mid-1960's in Iowa probably accounts for the high proportion of hard snags; R. Q. Landers, Iowa State Univ., pers. comm.) These percentages were compared to the percentage of cavity nests placed in each snag condition class. Except for common flickers, primary cavity-nesters selected soft snags more frequently than intermediate and hard snags. Soft snags are in advanced stages of decay, a condition facilitating cavity excavation (Jackman 1974, McClelland and Frissell 1975, Conner et al. 1976). Secondary cavity-nesters selected soft and sometimes intermediate snags. The distribution of secondary cavity-nests is probably a function of available nest sites abandoned by primary cavity-nesters. Thus, availability of soft snags is of primary importance to cavity-nesting species.

Table 3. Influence of snag condition on nest site selection by cavity-nesting species. Values represent ratios of the percentage of nests in each snag category to the percentage of all sampled snags in that category.

Species	N[a]	Snag condition		
		Soft	Intermediate	Hard
Primary cavity-nesters				
Red-headed woodpecker	32	1.6	0.7	0.3
Downy woodpecker	17	1.4	0.6	0.6
Red-bellied woodpecker	7	2.0	0.0	0.0
Common flicker	13	1.6	1.7	0.2
Secondary cavity-nesters				
Eastern bluebird	4	2.0	0.0	0.0
Black-capped chickadee	15	1.9	0.0	0.2
Northern house wren	36	1.4	1.5	0.4
European starling	12	1.4	2.7	0.2
House sparrow	6	1.4	1.8	0.4
Great crested flycatcher	4	2.0	0.0	0.0

[a]Snag condition was measured only for 1977 nest sites.

Habitat Selection

Suitable breeding habitat is critical for every bird species. A selected habitat must provide food, nesting sites and material, song perches, and protection from predators and weather, which insure reproductive success for the species. Birds primarily respond to proximate factors when selecting habitats, although ultimate factors, such as nest cavities, may also function as proximate stimuli (Hilden 1965, Balda 1975, Verner 1975). Proximate habitat characteristics influencing selection often include vegetation physiognomy (Kendeigh 1948, Brewer 1958, MacArthur 1964, Willson 1966, 1974, Wiens 1969, Zimmerman 1971, Anderson and Shugart 1974, Balda 1975, Roth 1976), physical factors (Bertin 1977) or the size of habitat patches (Beals 1960, Galli et al. 1976, MacClintock et al. 1977).

Most land-use practices do not destroy, but rather alter habitats and the associated avian communities (Zeedyk and Evans 1975). The extent of change in avian community composition depends upon the specificity of each species' habitat requirements. Forests have been converted to cropland and pastures to the detriment of woodland species but the benefit of grassland birds (Graber and Graber 1963). Dodge et al. (1976) found that removal of streamside vegetation benefited swallows and terrestrial foraging species, had no effect on flycatchers, but adversely affected foliage; species richness declined.
In riparian habitats, tree removal substantially reduced bird

numbers (Carothers and Johnson 1975). Partial thinning of upland forests, resulting in four rather than two vegetation strata, was accompanied by an increase in bird species diversity (Adams and Barrett 1976). Whitcomb et al. (1977) found that selective logging increased bird diversity in the short run because of brushy growth, but long-term effects were unknown. Loss of shrubs in woodlands, associated with grazing, reduced bird abundance to one-fourth that found in an ungrazed area (Dambach 1944), and Johnston (1970) noted higher breeding bird numbers in urban areas with a well-developed shrub layer. Habitat manipulations that increase edge area benefit many species (Johnston 1947, Brewer 1958, Warbach 1958) and loss of edge can be detrimental (Graber and Graber 1963).

General results

The mean density of breeding birds on the study plots increased from herbaceous habitats to upland woodlands to floodplain woodlands (Table 4). Similar trends have been noted by Carter (1967), Tramer (1969), and Blem and Blem (1975). Thus, although upland and floodplain woodlands were similar in species richness, the latter supported higher population densities (see also Whitcomb 1977).

Bird species richness increased significantly with the width of wooded riparian habitats (Fig. 2). A similar but nonsignificant trend was evident for herbaceous study plots.

Table 4. Breeding bird densities and species richness in the major habitat types.

Habitat types	Number of plots[a]	Number of species/plot	Pairs/40ha ± 1 s.d.
Herbaceous	4	6-8	153 ± 66
Floodplain woodland	5	23-32	506 ± 103
Upland woodland	9	24-32	339 ± 92

[a]Plots with only one transect are not included because densities were to be overestimated.

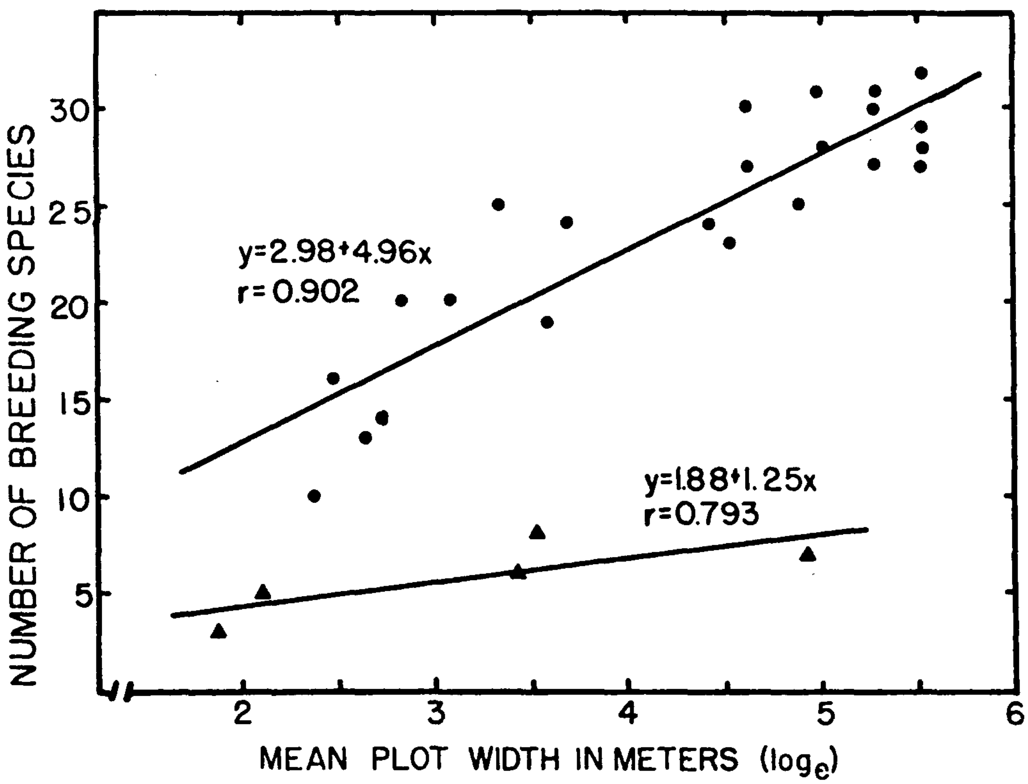

Figure 2. Relationship of species richness to width of wooded (dots) and herbaceous (triangles) streamside habitat. Mean plot width was calculated from 10 measurements, taken at 50m intervals along the stream channel, of the habitat extent from the stream edge to the plot boundary farthest from the stream.

Beals (1960) and Galli et al. (1976) also recorded increased bird species richness as habitat patch size increased. Wooded study plots supported a maximum of 32 species and herbaceous habits 7 (Fig. 2).

Table 5 presents the distribution of breeding bird observations among the six general habitat types. The values can be interpreted as indices representing intensity of habitat use. The habitat receiving the most frequent use by a species was assumed to be preferred by that species, although in some instances the species' abundance in other habitats was similar. Species with low tolerance indices (see Analysis Methods) are restricted to fewer habitats and(or) utilize their selected habitats more inequitably. Such species would be affected more adversely by loss of their preferred habitat than those with higher index values which could utilize alternate habitats. Four general levels of tolerance to habitat alteration were identified: intolerant (tolerance indices <1.90), low tolerance (1.90-2.60), moderate tolerance (2.90-3.60), and tolerant (>3.70).

Microhabitat features selected within the general habitats by each species (Table 6) were determined using the statistical procedures described in the Methods. The following discussion on habitat selection by species derives from Tables 5 and 6 unless otherwise noted.

Table 5. Distribution of bird observations (16,070) among the general habitat types (expressed as the number of observations per hectare per 12 censuses), and the relative tolerance of each species to habitat alteration.[a]

	General habitat type						
	Herbaceous (8.9)[b]	Savannah (5.5)	Scrub (3.8)	Wooded edge (6.8)	Floodplain woodland (28.4)	Upland woodland (88.8)	Tolerance index
Intolerant species							
Bobolink	1.7			0.3			1.34
Grasshopper sparrow	4.3			1.2			1.52
Western meadowlark	6.2			2.4			1.67
Killdeer	0.4	1.4					1.53
Common crow			1.4		0.4	+[c]	1.53
Willow flycatcher				1.8	0.3		1.32
Barred owl					0.5	+	1.00
Blue-gray gnatcatcher					+	0.5	1.00
Rufous-sided towhee					0.1	0.6	1.32
Ovenbird				0.2	0.1	1.5	1.41

Scarlet tanager				0.2	+	0.5	1.69
Wood thrush				0.2	0.3	1.3	1.78
Acadian flycatcher					0.1	0.2	1.80
Low tolerance species							
Eastern bluebird		1.4	1.8	0.4		0.1	2.55
Vesper sparrow	1.1			1.3			1.99
Dickcissel	4.8			5.4	0.8	0.1	2.33
Warbling vireo			0.3	0.2	0.8	+	2.19
Yellow warbler		0.5		0.7	1.6	0.1	2.54
Yellow-throated vireo				0.2	+	0.2	2.00
Field sparrow	0.4			1.4	+	1.8	2.42
Moderate tolerance species							
Red-winged blackbird	14.3	0.4	5.8	5.4	3.1	0.1	3.06
Eastern kingbird	1.1	2.4		1.9	0.2	0.2	3.16
House sparrow	0.3	4.2	0.5	1.6	3.0	0.5	3.42
American robin	0.2	4.9	0.8	2.2	2.2	0.8	3.52
American redstart		0.4	1.8	0.4	0.6	1.1	3.60

[a]Within each tolerance category, species were grouped according to the general habitat type in which they were most dense.

[b]Total area of each habitat type sampled.

[c]Indicates values < 0.05.

Table 5 (continued).

	General habitat type						
	Herbaceous (8.9)[b]	Savannah (5.5)	Scrub (3.8)	Wooded edge (6.8)	Floodplain woodland (28.4)	Upland woodland (88.8)	Tolerance index
Common yellowthroat	4.5		2.1	11.0	7.7	0.7	3.29
Common grackle	0.1		0.3		0.4	0.1	3.00
Rose-breasted grosbeak	0.1	0.2	2.1	3.4	8.2	5.2	3.34
Red-eyed vireo		0.4		0.6	1.2	1.1	3.44
Mourning dove	0.2		1.0	0.9	1.3	3.0	3.27
Tolerant species							
Great crested flycatcher		5.3	5.0	0.9	1.9	3.3	3.93
Red-headed woodpecker	0.6	10.7	4.2	2.5	5.8	5.9	4.26
Red-bellied woodpecker		0.2	1.3	0.4	1.2	1.1	3.88
Tufted titmouse		1.1	1.6	0.2	0.7	1.0	3.99
Black-capped chickadee		2.0	7.6	2.4	7.5	4.6	4.01
Cardinal	0.2	4.9	13.7	6.0	11.2	7.6	4.41
Yellow-billed cuckoo	0.1	0.4	1.3	1.8	1.3	0.2	3.80

American goldfinch	1.8	2.2	4.0	9.8	4.1	1.1	3.83
Song sparrow	6.5	2.4	7.6	10.9	2.2	0.2	3.87
Brown-headed cowbird	3.4	4.9	7.9	10.7	5.7	3.9	5.12
Indigo bunting	3.3	0.7	3.2	8.1	11.8	2.2	3.71
Northern house wren	0.9	5.8	21.0	11.6	34.5	21.3	4.01
Downy woodpecker	0.1	0.9	3.2	5.2	6.0	3.5	4.14
White-breasted nuthatch		1.8	2.6	1.5	4.7	4.1	4.22
Gray catbird	0.3	4.7	8.2	5.9	14.5	7.4	4.32
Northern oriole	0.3	2.0	2.4	1.9	4.2	1.2	4.42
European starling		1.6	1.3	0.9	2.5	1.3	4.44
Hairy woodpecker	0.1	0.7	0.5	0.2	0.9	0.6	4.59
Blue jay	0.3	1.4	0.5	1.8	3.3	4.6	3.73
Eastern wood pewee		3.3	2.9	0.3	3.1	3.8	4.13
Brown thrasher	0.2	0.9	2.1	1.5	0.8	2.1	4.60
Common flicker	0.4	0.7	1.6	1.8	1.7	2.7	4.76

Table 6. Significant ($P \leq 0.01$) positive and negative relationships between bird densities and microhabitat variables.

	Sapling/tree richness[a]	Sapling/tree density[a]	Sapling/tree size[a]	Horizontal patchiness of vegetation[a]	Vertical patchiness of vegetation[a]	Slope
Intolerant species						
Bobolink	$-_{C}$	$+_{T}$				
Grasshopper sparrow		$+_{T}$				
Western meadowlark	$-_{C}$			$-_{T}$		
Killdeer	$-_{C}$	$+_{T}$				
Common crow	$-_{S}$		$+_{S}$	$+_{T}$		
Willow flycatcher				$+_{T}$		

[a]These variables were derived from point quarter data for tree (T), sapling (S), or tree and sapling species combined (C).

[b]Subscripts represent vegetation strata; A = 0-3m, B = 3-9m, C = >9m, T = all strata combined.

[c]S = soft, I = intermediate, H = hard.

[d]Subscripts represent snag height classes (H1 = 0-3m, H2 = 3-9m, H3 > 9m), DBH classes (D1 < 25cm, D2 = 25-50cm, D3 = 51-75cm, D4 > 75cm), or mean DBH (DM).

Plant species richness												
Grass-like	Forb	Shrub	Deciduous tree	Evergreen tree	Vine	All life-forms combined	Life-form richness	Vertical stratification of vegetation[b]	Snag density	Snag hardness[c]	Snag size preference[d]	R^2
+												0.065
+	-				+	+	+	-A				0.154
+	-					+						0.130
+												0.039
									+			0.046
			-									0.015

Table 6 (continued).

	Sapling/tree richness[a]	Sapling/tree density[a]	Sapling/tree size[a]	Horizontal patchiness of vegetation[a]	Vertical patchiness of vegetation[a]	Slope
Barred owl			$^{+}_{S}$			
Blue-gray gnatcatcher						
Rufous-sided towhee				$^{+}_{T}$		
Ovenbird	$^{+}_{C}$	$^{+}_{S}$				
Scarlet tanager						
Wood thrush						
Acadian flycatcher						-
Low tolerance species						
Eastern bluebird						
Vesper sparrow	$^{-}_{T}$			$^{-}_{T}$		
Dickcissel	$^{-}_{T}$	$^{-}_{T}$, $^{-}_{S}$	$^{-}_{T}$	$^{-}_{T}$		
Warbling vireo	$^{+}_{T}$					-
Yellow warbler				$^{+}_{T}$		-
Yellow-throated vireo	$^{+}_{C}$					
Field sparrow		$^{-}_{T}$	$^{-}_{T}$	$^{+}_{S}$	$^{+}_{T}$	+
Moderate tolerance species						
Red-winged blackbird	$^{-}_{C}$					
Eastern kingbird		$^{-}_{T}$, $^{+}_{S}$				
House sparrow			$^{+}_{T}$	$^{-}_{S}$	$^{-}_{S}$	

Plant species richness: Grass-like	Forb	Shrub	Deciduous tree	Evergreen tree	Vine	All life-forms combined	Life-form richness	Vertical stratification of vegetation[b]	Snag density	Snag hardness[c]	Snag size preference[d]	R^2
						-						0.017
					+						+D2, +H1	0.028
	-		-		+	+						0.041
	-		+		+						-H3	0.098
			+		+							0.041
-						+		+C				0.052
			+							+H		0.058
+												0.018
												0.028
						-						0.104
						-					-D4, +DM	0.028
			-					+A				0.028
												0.006
+		+		+	-			-T				0.143
+						-	-					0.091
+						-						0.034
								-C		+I	+H1, +D4	0.069

Table 6 (continued).

	Sapling/tree richness[a]	Sapling/tree density[a]	Sapling/tree size[a]	Horizontal patchiness of vegetation[a]	Vertical patchiness of vegetation[a]	Slope
American robin						-
American redstart						-
Common yellowthroat	$^{+}_{S}$		$^{-}_{T}$			-
Common grackle					$^{+}_{T}$	
Rose-breasted grosbeak	$^{+}_{S}$				$^{+}_{T}$	
Red-eyed vireo						
Mourning dove				$^{+}_{T}$, $^{+}_{S}$		
Tolerant species						
Great crested flycatcher	$^{+}_{T}$		$^{+}_{T}$			
Red-headed woodpecker		$^{-}_{T}$	$^{+}_{T}$			
Red-bellied woodpecker	$^{+}_{S}$					
Tufted titmouse	$^{+}_{C}$			$^{-}_{T}$		
Black-capped chickadee	$^{+}_{T}$		$^{+}_{S}$		$^{+}_{S}$	
Cardinal				$^{+}_{T}$	$^{+}_{T}$	
Yellow-billed cuckoo			$^{+}_{T}$			
American goldfinch		$^{-}_{T}$				-
Song sparrow	$^{-}_{T}$	$^{-}_{S}$				
Brown-headed cowbird		$^{-}_{T}$	$^{+}_{S}$			
Indigo bunting	$^{+}_{S}$		$^{+}_{T}$	$^{+}_{T}$		

Plant species richness: Grass-like	Forb	Shrub	Deciduous tree	Evergreen tree	Vine	All-life-forms combined	Life-form richness	Vertical stratification of vegetation[b]	Snag density	Snag hardness[c]	Snag size preference[d]	R^2
+											+D1	0.029
		+								+H		0.064
		-				-	+	+A				0.146
												0.007
						+		+A				0.076
			+					+C				0.030
		+		+				-B, -C		+H		0.147
	+			+							+H3, +D4	0.046
	+							-A	+		+D3	0.113
												0.018
								+C			-H3	0.035
					-					-I	+D1	0.075
+	+										+H2, +DM	0.110
					-			-C, +T		+S		0.030
		-	-					+A				0.054
			-			-			-			0.086
			-			+		+A				0.065
+	+				+	-		+A			+H2	0.163

Table 6 (continued).

	Sapling/tree richness[a]	Sapling/tree density[a]	Sapling/tree size[a]	Horizontal patchiness of vegetation[a]	Vertical patchiness of vegetation[a]	Slope
Northern house wren	$+_S$		$+_T$		$+_T$	
Downy woodpecker	$+_S$		$+_T$		$+_T$	
White-breasted nuthatch	$+_C$		$+_T$			
Gray catbird	$+_S$	$-_T$	$+_T$		$+_T$	-
Northern oriole			$+_S$, $+_T$		$-_S$	-
European starling			$+_S$, $+_T$			
Hairy woodpecker						
Blue jay	$+_T$					+
Eastern wood pewee	$+_T$		$+_T$			
Brown thrasher				$+_T$		
Common flicker	$+_T$					

Plant species richness												
Grass-like	Forb	Shrub	Deciduous tree	Evergreen tree	Vine	All life-forms combined	Life-form richness	Vertical stratification of vegetation[b]	Snag density	Snag hardness[c]	Snag size preference[d]	R^2
									+		−D1, +DM	0.325
										+H		0.061
			+								+DM	0.069
			−		−		+	+A			+D4	0.179
	−											0.064
								−C			+D4, +DM	0.094
										+S		0.008
			+					−A				0.067
											+D3	0.080
		+		+	−	+		−C				0.082
						+			+		+D3	0.053

Habitat selection by species

Intolerant species Bobolinks (*Dolichonyx oryzivorous*), grasshopper sparrows (*Ammodramus savannarum*), and western meadowlarks (*Sturnella neglecta*) were most dense in treeless herbaceous habitats (see also Kendeigh 1948, Beckwith 1954, Graber and Graber 1963, Zimmerman and Tatschl 1975), some of which were adjacent to wooded edge. The three species selected areas with a variety of grasses. High total plant species richness but few forb species also characterized habitats preferred by meadowlarks and grasshopper sparrows. Bobolinks and meadowlarks selected areas with few sapling/tree species and the latter also avoided terrain with patchy tree distribution. Grasshopper sparrows also chose habitats with a poorly-developed shrub layer and many vine species. The positive relationship of bobolinks and grasshopper sparrows to tree density was illogical and difficult to explain.

The savannah habitat supported highest densities of killdeer (*Charadrius vociferus*), which also occurred in areas with only herbaceous cover (see also Graber and Graber 1963). Warbach (1958) reported this species to require areas with exposed ground. Habitats with a variety of grasses and low sapling/tree species richness were typical of this species. The positive relationship with tree density was unexpected and may have resulted from few observations.

Common crows (*Corvus brachyrhynchos*) were most abundant in scrub habitats but also were recorded in floodplain and upland woodlands (see also Kendeigh 1948, Graber and Graber 1963). Johnston (1947) and MacClintock et al. (1977) reported crows as edge species. In my study crows preferred areas with large saplings and patchy tree distribution. Also selected were habitats with low sapling species richness and numerous snags. Crows range over a variety of habitats in their daily activities and probably selected a broader array of habitats than was sampled in this study (see Anderson and Shugart 1974).

Wooded edge and floodplain woodlands were occupied by willow flycatchers (Empidonax traillii), which have been considered edge species (Graber et al. 1974). The flycatchers preferred horizontally patchy habitats with few tree species.

Barred owls (Strix varia) occurred in highest numbers in floodplains but also were observed in upland woodlands (see also Bent 1938, Fawver 1947). The owls appeared to prefer relatively extensive habitat patches (Table 7). Areas low in plant species richness and with large saplings were selected. Nicholls and Warner (1972) reported that barred owls preferred areas with an open understory.

Blue-gray gnatcatchers (Polioptila caerulea), rufous-sided towhees (Pipilo erythrophthalmus), ovenbirds (Seiurus aurocapillus), acadian flycatchers (Empidonax virescens), scarlet tanagers (Piranga olivacea), and wood thrushes were most numerous in upland

Table 7. Minimum mean width of wooded study plots supporting breeding populations of species whose occurrence is apparently restricted by habitat patch size.

	Minimum plot width frequented (m)[a]
Species reported to be restricted by habitat patch size[b]	
Yellow-billed cuckoo	10
Cardinal	11
Downy woodpecker	15
Blue jay	15
Black-capped chickadee	15
White-breasted nuthatch	17
Eastern wood pewee	20
Great crested flycatcher	35
Hairy woodpecker	40
Brown thrasher	40
Red-eyed vireo	40
Yellow-throated vireo	40

[a]The minimum mean width of wooded plots was 10m.

[b]See Johnston (1947), Bond (1957), Galli et al. (1976), Whitcomb et al. (1977).

Table 7 (continued).

	Minimum plot width frequented (m)[a]
Red-bellied woodpecker	90
Wood thrush	145
Blue-gray gnatcatcher	150
Ovenbird	175
Scarlet tanager	200
Acadian flycatcher	215
Other breeding species restricted to wider plots	
Warbling vireo	90
Tufted titmouse	100
Barred owl	145
American redstart	200
Rufous-sided towhee	200

woodlands, and all also were observed in floodplains (see also Kendeigh 1946, 1948, Bond 1957, Shugart and James 1973). Ovenbirds, tanagers, and wood thrushes also occurred in wooded edge. Zimmerman and Tatschl (1975) found acadian flycatchers and scarlet tanagers in floodplain forests and I noticed that acadian flycatchers tended to occur in the more mesic regions of upland habitats (see also Bond 1957). Ovenbirds and wood thrushes also have been reported to prefer mesic forests (Bond 1957, Shugart and James 1973).

Towhees chose habitats rich in total plant species, but with low forb, deciduous tree, and vine species diversity. Greater horizontal patchiness of trees also was preferred. Although reported to use wooded edge (Warbach 1958), in this study towhees were found breeding only in extensive habitats (Table 7). Towhees typically select shrubby areas (Beckwith 1954, Shugart and James 1973) but Johnston and Odum (1956) reported towhees occurring in several seral stages. Areas with many vine species and with snags 25-50cm DBH and less than 3m high were preferred by blue-gray gnatcatchers. Anderson and Shugart (1974) reported that gnatcatchers require closed-canopy forests with an open understory, although others have considered them to be habitat generalists (Root 1967, James 1971). Ovenbirds, acadian flycatchers, and scarlet tanagers selected habitats with many deciduous tree species, and ovenbirds and tanagers also were associated with many vine species. Additionally, ovenbirds chose areas with few snags over 9m high, few forb species, but dense saplings (see also Bond 1957, Anderson and Shugart 1974). Tanagers reportedly prefer forests with a dense canopy (Anderson and Shugart 1974). Level topography (often indicative of mesic conditions) with many hard snags also characterized acadian flycatcher habitat. Hard snags were often associated with canopy openings which may provide foraging stations. Areas with high total plant species richness but few forb species, and with a well-developed canopy stratum were selected by wood thrushes. Bertin (1977) reported that wood thrushes require trees over 12m tall as song perches. Wood thrushes, ovenbirds, tanagers, and gnatcatchers have been reported to be dependent on large expanses of woodland (Johnston 1947, Bond 1957, Galli et al. 1976, Whitcomb et al. 1977); my study corroborates this (Table 7). Acadian flycatchers also were observed only in the more expansive woodlands.

<u>Low tolerance species</u> Eastern bluebirds were most numerous in scrub and savannah habitats (see also Graber et al. 1971), but also were observed in wooded edge and upland woodlands. Bluebirds are known to prefer open pastures and edge habitats (Kendeigh 1948, Graber et al. 1971, MacClintock et al. 1977). Bluebird occurrence was related significantly only to species richness of grasses.

Wooded edge and herbaceous habitats supported highest densities of vesper sparrows (Pooecetes gramineus) and dickcissels (see also Beckwith 1954, Graber and Graber 1963), although dickcissels also occurred in floodplain and upland woodlands (see also Zimmerman and Tatschl 1975). Low horizontal patchiness and species richness of trees characterized habitats of both species. Additionally, dickcissels avoided areas with many plant species, dense trees and saplings, and large trees. Graber and Graber (1963) reported both species able to adapt to cultivated areas.

Warbling vireos (Vireo gilvus) and yellow warblers appeared to prefer floodplain woodlands (see also Kendeigh 1946, James 1971), although both were observed in upland woodlands and edge habitats. Also, warbling vireos were seen in scrub and yellow warblers in savannah areas. Warbling vireo densities increased with snag DBH, but vireos avoided areas with snags larger than 75cm DBH. In my study, snag DBH was correlated significantly with patchy tree distribution. James (1971) and James (1976) noted that warbling vireos preferred patchy habitats with large trees. Also selected were relatively wide wooded areas (Table 7) with low total plant species richness but high tree species richness. Yellow warblers selected habitats with few tree species, patchily dispersed trees, and a well-developed shrub stratum.

Upland woodlands were preferred by field sparrows (see also

Shugart and James 1973, Holt 1974) and, although I found equal densities in wooded edge and upland woodlands, yellow-throated vireos (Vireo flavifrons) also are reported to prefer upland woodlands (Kendeigh 1948, Bond 1957). Both species occurred in floodplain habitats, and additionally, field sparrows were seen in wooded edge and areas with herbaceous cover. Field sparrows are considered an edge species (Johnston 1947, Whitcomb et al. 1977) and yellow-throated vireos apparently are dependent upon extensive forests (Bond 1957, Whitcomb et al. 1977, Table 7). Yellow-throated vireos were associated only with high sapling/ tree species richness in this study but have been reported to prefer deciduous upland forests with large trees (Kendeigh 1948, Bond 1957, James 1971). Areas with high grass-like, shrub, and evergreen tree species richness, few vine species, and low overall stratification were selected by field sparrows. They also preferred small trees of low density, patchy sapling dispersion, vertically patchy trees, and steeper slopes (which would be more xeric).

Moderate tolerance species Red-winged blackbirds were most numerous in herbaceous habitats, were common in scrub, wooded edge and floodplain areas, and occurred occasionally in savannah and upland woodlands. Graber and Graber (1963) observed red-wings in all habitats but noted a preference for open areas (see also Zimmerman and Tatschl 1975). Red-wings selected habitats with low sapling/tree, total plant species and life form richness, but preferred areas with many grass-like species; indicating usage of open habitats.

The greatest numbers of eastern kingbirds, house sparrows, and American robins were in savannah. Excepting kingbirds in scrub, these species occurred in all other habitats. All three are reportedly edge species (Kendeigh 1948, Johnston and Odum 1956, Galli et al. 1976). Kingbirds selected habitats with dispersed trees but dense saplings and with many grass-like species but low total plant species richness. Level areas rich in grass-like species and having many snags less than 25cm DBH characterized robin habitats. House sparrows chose areas typified by large trees and by evenly dispersed saplings with little vertical patchiness. Also preferred were a poorly-developed canopy stratum and habitats with snags greater than 75cm DBH, less than 3m tall and of intermediate hardness.

American redstarts were most dense in scrub and upland woodlands (see also Kendeigh 1948, Bond 1957). They were also observed in savannah, edge, and floodplains but bred only in extensive wooded habitats (Table 7). Shugart and James (1973) found redstarts only in mesic woods, and I noticed that they preferred mesic areas of upland woodlands. Level areas with many shrub species and hard snags characterized areas chosen by redstarts. Kendeigh (1948) and Bond (1957) associated redstarts with large trees.

A recognized edge species (Johnston 1947, MacClintock et al. 1977), the common yellowthroat, was observed in all habitats except savannah, and was most dense in wooded edge (see also Graber and Graber 1963, Holt 1974, Zimmerman and Tatschl 1975). Yellowthroats selected level areas with many sapling species and small trees. Also preferred were habitats with low shrub and total plant species richness, but represented by many life forms and a well-developed shrub stratum.

Floodplain habitats supported the largest numbers of common grackles (Quiscalus quiscula), rose-breasted grosbeaks and red-eyed vireos (Vireo olivaceous) (see also Bond 1957, Graber and Graber 1963, Zimmerman and Tatschl 1975). Grosbeaks occurred in all other habitats; grackles also were recorded in herbaceous, scrub and upland woodlands; and red-eyed vireos were seen additionally in savannah, edge and upland woodlands. Bond (1957) found grosbeaks essentially limited to xeric woods in Wisconsin. Red-eyed vireos have been reported to be dependent on extensive woodland (Whitcomb et al. 1977, see also Table 7), and grackles have been considered an edge species (Galli et al. 1976). Areas where vertical tree distribution was patchy were preferred by grackles and grosbeaks, and the latter chose habitats with many sapling and total plant species, and a well-developed shrub stratum. Red-eyed vireos selected habitats with a well-developed canopy stratum and many tree species (see also Anderson and Shugart

1974).

Mourning doves preferred upland woodlands but occurred in all other habitats except savannah (see also Beckwith 1954, Graber and Graber 1963, Shugart and James 1973). They have been described as an edge species (Johnston 1947, Whitcomb et al. 1977). Doves selected habitats with many evergreen tree and shrub species, a patchy horizontal distribution of trees and saplings, poorly-developed canopy and sub-canopy strata, and many hard snags.

Tolerant species   Red-headed woodpeckers and great crested flycatchers were most dense in savannah (see also Bond 1957, James 1971, Graber et al. 1974). Excepting crested flycatchers in herbaceous areas, both species were seen in all other habitats. Red-heads have been regarded as edge species and crested flycatchers considered intermediate between edge and forest interior birds (Johnston 1947); both prefer open, wooded habitats (Bond 1957, Graber and Graber 1963, Graber et al. 1974). Crested flycatchers were not found breeding on plots less than 40m wide (Table 7). The two species selected areas with large trees, many forb species, and large snags (snags >75cm DBH and >9m tall, crested flycatcher; 51-75cm DBH, red-head). Crested flycatchers also chose areas with many deciduous tree but few evergreen tree species. Habitats with many snags, dispersed trees, and a poorly stratified shrub layer additionally typified selection by red-heads.

Tufted titmice (*Parus bicolor*), black-capped chickadees, cardinals, and red-bellied woodpeckers were most dense in scrub habitats and also occurred in savannah, wooded edge, and floodplain and upland woodlands (see also Bond 1957, Graber and Graber 1963, James 1971, Shugart and James 1973). Cardinals were also seen in herbaceous habitats. Red-bellied woodpeckers, titmice, and cardinals have been reported to prefer extensive woodlands (Johnston 1947, Bond 1957, Graber and Graber 1963, Whitcomb et al. 1977), although cardinals also have been considered an edge species (Fawver 1947, Johnston 1947). Of the three species, I found only red-bellied woodpeckers restricted by habitat patch width (Table 7). Red-bellied woodpeckers responded significantly only to sapling species richness. Anderson and Shugart (1974) found red-bellied woodpeckers on all their wooded study sites but the birds did not respond to any particular habitat variable. Areas with many sapling/tree species, few snags greater than 9m tall, trees evenly dispersed, and a well-developed canopy stratum typified titmice habitats. Kendeigh (1948) reported that titmice preferred large trees and Anderson and Shugart (1974) noted a positive relationship with open understory. Chickadees selected habitats with many tree species and large saplings that varied in vertical distribution. Few snags of intermediate hardness, many snags less than 25cm DBH, and few vine species also characterized habitats chosen by chickadees. Cardinals preferred habitats with patchy horizontal and vertical tree distribution, many grass-like and forb species, and snags 3-9m tall and large in DBH. James (1971) determined cardinals to be habitat generalists, and Anderson and Shugart (1974) noted a preference for an open-canopy with a dense sub-canopy.

American goldfinches, yellow-billed cuckoos, song sparrows, and brown-headed cowbirds (*Molothrus ater*) occurred in all general habitats but were most dense in wooded edge (see also Beckwith 1954, Bond 1957, Graber and Graber 1963, Shugart and James 1973, Zimmerman and Tatschl 1975). All have been classified as edge species (Johnston 1947, MacClintock et al. 1977), although Galli et al. (1976) reported yellow-billed cuckoos to be dependent on habitat patch size (but see Table 7). Goldfinches selected level areas with few deciduous tree and shrub species, a well-developed shrub stratum, and widely dispersed trees. Few vine species, soft snags, large trees, and a poorly-developed canopy stratum but high overall stratification characterized yellow-billed cuckoo habitat. Song sparrows preferred areas with few snags, low deciduous tree and total plant species richness, and dispersed saplings. Habitats with many plant species but few deciduous tree species, dispersed trees, large saplings, and a well-developed shrub stratum were typical of cowbirds, which are reported to be habitat generalists (James 1971).

Indigo buntings, northern house wrens, downy woodpeckers, white-breasted nuthatches, gray catbirds, northern orioles, European starlings, and hairy woodpeckers were most dense in floodplain woodlands (see also Kendeigh 1946, Fawver 1947, Bond 1957, Graber and Graber 1963, Zimmerman and Tatschl 1975). Bond (1957), however, found downy woodpeckers most common in xeric forests. Excepting nuthatches and starlings in herbaceous habitats, these species occurred in all other habitats. Catbirds, orioles, buntings, and starlings are regarded as edge species (Galli et al. 1976, MacClintock et al. 1977). Downy and hairy woodpeckers and nuthatches have been reported to be dependent upon extensive woodlands (Johnston 1947, Galli et al. 1976, Whitcomb et al. 1977); however I recorded them breeding in relatively narrow habitat patches (Table 7).

Hairy woodpeckers preferred areas containing many soft snags. Anderson and Shugart (1974) found this species associated with numerous tall trees and high canopy biomass. The other seven species all preferred large trees (see also Kendeigh 1948, James 1971, Anderson and Shugart 1974), and orioles and starlings were also associated with large saplings. Habitats with patchy tree dispersion; many sapling, grass-like, forb, and vine species, but low overall plant species richness; a well-developed shrub stratum; and snags 3-9m tall additionally typified indigo bunting habitats. Fawver (1947) found buntings associated with overstory openings around snags in floodplains. House wrens also chose terrain with many sapling species, patchy vertical tree distribution, numerous, large snags, and few snags less than 25cm DBH. Areas with many tree species, patchy vertical tree distribution, and hard snags additionally were chosen by downy woodpeckers. Anderson and Shugart (1974) reported that downy woodpeckers preferred areas with dense saplings and a high understory biomass. Habitats rich in both tree and sapling species and with large snags also were selected by nuthatches. Anderson and Shugart (1974) noted that nuthatches chose areas with a dense overstory and open understory. Catbirds additionally preferred level terrain with few vine and deciduous tree species but with a variety of life forms, dispersed trees, patchy vertical tree distribution, well-developed shrub stratum, and large snags. Level areas with few forb species and a uniform vertical sapling distribution were also selected by orioles. Starlings additionally selected habitats with a poorly-developed canopy stratum and large snags.

Blue jays, eastern wood pewees, brown thrashers, and common flickers were most abundant in upland woodlands (see also Kendeigh 1948, Bond 1957, Graber and Graber 1963, Shugart and James 1973) and, with the exception of pewees in herbaceous areas, were seen in all habitats. Blue jays, thrashers and flickers are considered edge species (Johnston 1947, Johnston and Odum 1956, Whitcomb et al. 1977), and pewees are regarded intermediate between edge and forest interior birds (Johnston 1947).

Galli et al. (1976), considered blue jays, thrashers, and pewees to be restricted by habitat patch size, but I found them breeding within relatively narrow habitat patches (Table 7). Habitats with many tree species typically were used by blue jays, pewees, and flickers. Blue jays also occupied habitats with steeper slopes and a poorly-developed shrub stratum. Anderson and Shugart (1974) found blue jays on steep slopes with a dense understory and overstory. Pewees also selected habitats with large trees (see also Beals 1960) and snags with 51-75cm DBH. Flickers additionally chose areas with many plant species, numerous snags, and snags 51-75cm DBH. Anderson and Shugart (1974) reported that flickers selected habitats with large trees and a well-developed canopy. Terrain with patchy tree dispersion, a poorly-developed canopy stratum, and high shrub, evergreen tree and total plant species richness but few vine species characterized habitats selected by thrashers. Thrashers reportedly prefer areas with dense shrubs (James 1971, Shugart and James 1973).

Expected Impacts of Habitat Alterations

A knowledge of nest site and habitat requirements can be used to predict the effects of various habitat alterations upon the bird species studied (Table 8). These predictions are based primarily on results from this study, but for species where data were few, the results were supplemented by the cited literature. For any given species, alteration of its preferred habitat (where

Table 8. Predicted effects on breeding bird densities of various habitat alterations of riparian woodlands. E indicates elimination from the community; -, reduction in numbers; blank, no effect; and +, increase in numbers. Predictions are based upon the reported results unless otherwise indicated.

	All woody vegetation removed resulting in pastures or hayfields	Woody vegetation reduced to narrow strips along streams	Woody overstory partly removed	Woody overstory partly removed and shrubs thinned	Shrubs thinned	Snags removed
Intolerant species						
Bobolink	+					
Grasshopper sparrow	+					
Western meadowlark	+					
Killdeer	+					
Common crow	E	-	+	?[a]		
Willow flycatcher	E	+	+	(-)[b]		

Barred owl	E	E	-	-	(+)	
Blue-gray gnatcatcher	E	E	(-)	(-)	(+)	
Rufous-sided towhee	E	-	+	(-)	(-)	
Ovenbird	E	E	(-)	-	-	
Acadian flycatcher	E	E	?	?	(-)	
Scarlet tanager	E	E	(-)	(-)		
Wood thrush	E	E	-	-	(-)	
Low tolerance species						
Eastern bluebird	(+)	-	(+)	(+)		-
Vesper sparrow	+	+				
Dickcissel	+	+				
Warbling vireo	E	-	+	+		
Yellow warbler	E	?	+	-		
Yellow-throated vireo	E	-	?	?		
Field sparrow	E	-	+	-		
Moderate tolerance species						
Red-winged blackbird	+	(+)				
Eastern kingbird	E	?	+	-		
House sparrow	E		+	+		-

[a]? represents insufficient data to make a prediction.

[b]( ) indicates predictions based primarily on literature cited in the text.

Table 8 (continued).

	All woody vegetation removed resulting in pastures or hayfields	Woody vegetation reduced to narrow strips along streams	Woody overstory partly removed	Woody overstory partly removed and shrubs thinned	Shrubs thinned	Snags removed
American robin	E	+	+	+		
American redstart	E	-	?	-	-	
Common yellowthroat	(+)	+	(+)	-		
Common grackle	(-)	(+)	+			
Rose-breasted grosbeak	E	-	+	-	-	
Red-eyed vireo	E	-	-	-		
Mourning dove	-	-	+	-		
Tolerant species						
Great crested flycatcher	E	-	(+)	(+)	(+)	-
Red-headed woodpecker	E	-	+	+	+	-
Red-bellied woodpecker	E	-				-

Tufted titmouse	E	E	-	-	(+)	(-)
Black-capped chickadee	E			(-)	(-)	-
Cardinal	E		+	-	-	
American goldfinch	(+)		+	-		
Yellow-billed cuckoo	E	(+)	+	(-)	(-)	
Song sparrow	+	+	+	-		
Brown-headed cowbird	-	+	+	-	-	
Indigo bunting	-	+	+	-	-	
Northern house wren	E	(+)	+			-
Downy woodpecker	E			(-)	(-)	-
White-breasted nuthatch	E	-	(-)	(-)	(+)	-
Gray catbird	E		+	-	-	
Northern oriole	E	-	(+)			
European starling	(-)		+	(+)	(+)	-
Hairy woodpecker	E	-	(-)	(-)		-
Blue jay	E	-	(-)	(-)	(-)	
Eastern wood pewee	E	-	+	+	+	
Brown thrasher	E	-	+	(-)	-	
Common flicker	E	(-)	(+)	(+)	(+)	-

it is observed in highest numbers) would be more detrimental than perturbations of less desirable habitats. Of the species discussed, American robins, house sparrows, common grackles, and European starlings have adapted well to urban situations and total population numbers would be little affected by alteration of natural habitat (Graber and Graber 1963).

Complete removal of woody vegetation or reduction of woodlands generally results from a desire to increase cultivated land, and is often associated with stream channelization (Allen 1969, Barstow 1971). If all woody vegetation were removed from a riparian community, 36 of the species studied would be eliminated and 5 would decrease in number; the remaining 11 could be benefited (Table 8). Reduction of woody vegetation to narrow strips could provide favorable breeding habitat for 12 species, but densities of 20 species might decrease and 7 species would be eliminated. Woody overstory may be partly removed by selective harvesting of commerical timber (Adams and Barrett 1976) or to provide openings conducive to grass growth for grazing. Shrub and understory stratification may increase after partial overstory removal if there are no additional perturbations (Adams and Barrett 1976). Although 10 species would decrease in abundance if the woody overstory were partly removed, 29 species could benefit. Shrub and understory vegetation also may be removed to stimulate grass growth for grazing although grazing itself may deplete these strata (Dambach 1944). Six species might benefit from shrub removal whereas 15 would be affected detrimentally. If both the shrub and overstory were thinned, only 9 species could benefit while 29 would decrease in numbers. Snags are removed for use as firewood and, in some areas, as a fire protection measure (McClelland and Frissell 1975). This practice would adversely affect 13 cavity-nesting species.

Bird species diversity is correlated with habitat diversity (Willson 1974, Balda 1975, Roth 1976) and it appears that manipulations increasing the structural diversity of the habitat would benefit the greatest number of species. Management for maximum diversity, however, can be detrimental to rare species, which contribute little to overall diversity (Balda 1975). Thus, managers should be cognizant of the specialized requirements of individual species, such as relatively extensive unaltered habitat patches (e.g. woodland species intolerant of habitat alterations) or the presence of snags (e.g. cavity nesters) and plan management schemes accordingly.

GENERAL APPLICATION OF THE METHODS

This study is unique because techniques commonly used to sample vegetation and avian communities were employed (point quarter and quadrat sampling for vegetation, spot map censuses for birds), but the data were analyzed in a manner not previously reported. The utility of this approach is that it does not require special intensive field methods to gain a quantitative description of habitat selection, as have been used by others (James 1971, Anderson and Shugart 1974, Whitmore 1975). The procedures allow extensive sampling in a relatively short period of time.

Tolerance indices provide reasonable estimates of niche breadth for nest sites and habitats selected, and are useful when evaluating effects of habitat perturbations. Such indices, however, appear to be most accurate with large sample sizes. Stepwise multiple regression provides a feasible means of reducing a large field of variables to a subset that best characterizes habitats selected by the individual species composing the community.

Although this study emphasized riparian habitats, sufficient data were obtained on bird utilization of upland habitats to apply the results more generally. More studies such as this are needed in different habitat types and geographical areas to better delineate habitat needs of nongame bird species and to provide information required for their successful management.

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APPENDIX A. CHARACTERISTIC PLANT SPECIES ASSOCIATED WITH EACH HABITAT TYPE

General habitat type	Habitat code	Area sampled (ha)	Characteristic plant species		
			Canopy	Sub-canopy	Herbaceous
Herbaceous	H1	0.5			_Ambrosia trifida_, _Cannabis sativa_, _Elymus canadensis_, _Setaria faberi_
	H2	6.0			_Hordeum jubatum_, _Poa praetensis_, _Taraxacum officinale_, _Trifolium repens_
	H3	2.4			_Bromus inermis_, _Phalaris arundinacea_
Savannah	Sa	5.5	Scattered large, _Fraxinus_ sp.,		_Oxalis stricta_, _Poa praetensis_,

			Juglans nigra, and *Quercus* spp.		*Taraxacum officinale*
Scrub	Sc	3.8	*Crataegus* sp.	*Crataegus* sp.	*Poa praetensis*, *Taraxacum officinale*
Wooded edge[a]	WE1	1.9	Scattered small *Populus deltoides*	*P. deltoides*, *Salix* spp.	*Ambrosia trifida*, *Bromus inermis*, *Phalaris arundinacea*
	WE2	0.4	*Acer saccharinum*	*A. saccharinum*	*Convolvulus* spp., *Phalaris arundinacea*
	WE3	0.7	*Salix* spp., *Ulmus americana*	*U. americana*	*Ambrosia trifida*
	WE4	3.8	*Acer negundo*, *Juglans nigra*, *Ulmus americana*	*U. americana*	*Poa praetensis*, *Taraxacum officinale*, *Trifolium repens*

[a]All edge habitats consisted of narrow bands of trees. WE1 and WE2 were along channelized streams. WE1, 2 and 3 were bordered by row-crops and WE4 by grazed pasture.

General habitat type	Habitat code	Area sampled (ha)	Characteristic plant species		
			Canopy	Sub-canopy	Herbaceous
Floodplain woodland	F1	1.2	*Acer negundo*, *Celtis occidentalis*, *Juglans nigra*		*Ambrosia trifida*, *Chenopodium album*, *Convolvulus* spp., *Elymus canadensis*
	F2	2.0	*Acer saccharinum*, *Salix* spp.	*A. saccharinum*	*Poa praetensis*, *Taraxacum officinale*
	F3	9.6	*Acer negundo*, *A. saccharinum*, *Fraxinus* sp., *Gleditsia triacanthos*, *Ulmus americana*	*A. negundo*, *Fraxinus* sp., *U. americana*	*Ambrosia trifida*, *Cryptotaenia canadensis*, *Leersia virginiana*
	F4	1.5	*Acer negundo*,	*Fraxinus* sp., *U.*	*Cryptotaenia*

			Celtis occidentalis, Juglans nigra, Ulmus americana	americana	canadensis, Laportea canadensis, Symphoricarpos sp.
	F5	5.5	Acer negundo, A. saccharinum	A. negundo, A. saccharinum, Fraxinus sp., Morus alba	Ambrosia trifida, Cryptotaenia canadensis, Elymus canadensis, Laportea canadensis
	F6	8.6	Acer negundo, A. saccharinum, Gleditsia triacanthos, Salix spp., Ulmus americana	A. saccharinum, Fraxinus sp., U. americana	Laportea canadensis, Polygonum spp.
Upland woodland	U1	2.5	Acer negundo, Aesculus glabra, Juglans nigra, Ulmus americana	A. glabra, Celtis occidentalis, Gletsia triacanthos, U. rubra	Ambrosia trifida, Cryptotaenia canadensis, Laportea canadensis, Rudbeckia lanciniata
	U2	7.7	Gleditsia	Ulmus americana	Poa praetensis,

General habitat type	Habitat code	Area sampled (ha)	Characteristic plant species		
			Canopy	Sub-canopy	Herbaceous
			triacanthos, *Juglans nigra*, *Juniperus virginiana*		*Symphoricarpos* sp.
	U3	2.2	*Acer negundo*, *Aesculus glabra*, *Ulmus americana*	*A. glabra*, *Celtis occidentalis*, *Ostrya virginiana*	*Amphicarpa bracteata*, *Symphoricarpos* sp., *Parthenocissus quinquefolia*
	U4	5.1	*Ostrya virginiana*, *Quercus alba*, *Ulmus americana*	*U. americana*	*Amphicarpa bracteata*, *Carex* spp., *Ribes missouriense*, *Symphoricarpos* sp., *Parthenocissus quinquefolia*

U5	6.7	Carya ovata, Crataegus sp., Quercus macrocarpa	Crataegus sp., Xanthoxylum americanum	Muhlenbergia schreberi, Oxalis stricta, Poa praetensis, Taraxacum officinale
U6	2.2	Gleditsia triacanthos, Juniperus virginiana	Ulmus americana	Poa praetensis, Symphoricarpos sp.
U7	12.0	Carya ovata, Juglans nigra	Gleditsia triacanthos, Juniperus virginiana	Carex spp., Symphoricarpos sp., Viola spp.
U8	19.6	Carya ovata, Quercus alba, Q. rubra, Tilia americana	Carya ouata, Juniperus virginiana, Ostrya virginiana	Carex spp., Oxalis stricta, Symphoricarpos sp., Viola spp.
U9	30.8	Ostrya virginiana, Quercus alba, Q. rubra, Tilia americana, Ulmus americana	Celtis occidentalis, Fraxinus sp., O. virginiana	Amphicarpa bracteata, Asarum canadense, Carex spp., Elymus villosus, Eupatorium rugosum, Osmorhiza

General habitat type	Habitat code	Area sampled (ha)	Characteristic plant species		
			Canopy	Sub-canopy	Herbaceous
					claytonia, *Ribes missouriense*, *Symphoricarpos* sp., *Parthenocissus quinquefolia*

APPENDIX B. OCCURRENCE OF MIGRANT AND TRANSIENT BIRD SPECIES IN THE GENERAL HABITAT TYPES

Species	Habitats frequented[a]
Wood duck (*Aix sponsa*)	WE, F
Turkey vulture (*Cathartes aura*)	U
Sharp-shinned hawk (*Accipiter striatus*)	U
Red-tailed hawk (*Buteo jamaicensis*)	F, U
Great blue heron (*Ardea herodius*)	WE, F
Sora (*Porzana carolina*)	H
American woodcock (*Philohela minor*)	U
Common snipe (*Capella gallinago*)	H
Upland sandpiper (*Bartramia longicauda*)	H
Spotted sandpiper (*Actitis macularia*)	H
Solitary sandpiper (*Tringa solitaria*)	H
Eastern phoebe (*Sayornis phoebe*)	WE, U
Alder flycatcher (*Empidonax alnorum*)	WE
Least flycatcher (*E. minimus*)	Sc, WE, F, U
Tree swallow (*Iridoprocne bicolor*)	U
Brown creeper (*Certhia familiaris*)	F
Winter wren (*Troglodytes troglodytes*)	WE
Sedge wren (*Cistothorus platensis*)	H
Hermit thrush (*Catharus guttata*)	F, U
Swainson's thrush (*C. ustulata*)	Sc, WE, F, U
Gray-checked thrush (*C. minima*)	Sc, WE, F, U

[a]H indicates herbaceous habitats; Sa, savannah; Sc, Scrub; WE, wooded edge, F, floodplain woodland; U, upland woodland.

Species	Habitats frequented[a]
Veery (*C. fuscescens*)	F, U
Ruby-crowned kinglet (*Regulus calendula*)	WE, F, U
Solitary vireo (*Vireo solitarius*)	U
White-eyed vireo (*V. griseus*)	U
Bell's vireo (*V. bellii*)	U
Philadelphia vireo (*V. philadelphicus*)	F
Black-and-white warbler (*Mniotilta varia*)	WE, F, U
Golden-winged warbler (*Vermivora chrysoptera*)	U
Blue-winged warbler (*V. pinus*)	U
Tennessee warbler (*V. peregrina*)	Sa, Sc, WE, F, U
Orange-crowned warbler (*V. celata*)	F, U
Nashville warbler (*V. ruficapilla*)	Sa, Sc, WE, F, U
Northern parula (*Parula americana*)	U
Magnolia warbler (*Dendroica magnolia*)	WE, F, U
Yellow-rumped warbler (*D. coronata*)	Sc, WE, F, U
Black-throated green warbler (*D. virens*)	F, U
Blackburnian warbler (*D. fusca*)	F, U
Chestnut-sided warbler (*D. pennsylvanica*)	WE, U
Bay-breasted warbler (*D. castanea*)	U
Blackpoll warbler (*D. striata*)	Sc, WE, F, U
Pine warbler (*D. pinus*)	U
Palm warbler (*D. palmarum*)	F, U
Northern waterthrush (*Seiurus novaboracensis*)	F, U
Louisiana waterthrush (*S. motacilla*)	U
Mourning warbler (*Oporornis philadelphia*)	WE, F, U
Connecticut warbler (*O. agilis*)	U
Wilson's warbler (*Wilsonia pusilla*)	WE, F, U

Species	Habitats frequented[a]
Canada warbler (W. canadensis)	U
Purple finch (Carpodacus purpureus)	WE, U
Savannah sparrow (Passerculus sandwinchensis)	H
Tree sparrow (Spizella arborea)	WE
Clay-colored sparrow (S. pallida)	Sc
Harris' sparrow (Zonotrichia querula)	Sc, WE, F, U
White-crowned sparrow (Z. leucophrys)	WE, F, U
White-throated sparrow (Z. albicollis)	Sa, Sc, WE, F, U
Fox sparrow (Passerella iliaca)	F
Lincoln's sparrow (Melospiza lincolnii)	WE, F, U
Swamp sparrow (M. georgiana)	WE, F