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Breeding bird communities in regenerating and mature broadleaf forests in the USA Lake States

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ABSTRACT

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When Lake States aspen tree canopy is removed by clearcut harvest, bird species turnover is almost complete. Bird species richness and total populations were highest in mature stands with well-developed understories and in regenerating stands about 4 years after clearcutting. However, species composition in regenerating stands was different to that in mature stands. Most bird species that are of regional concern were restricted to more mature stands. The lack of a direct relationship between species richness and increasing stand age was related to compensatory trends in species populations among five foraging groups of birds.

INTRODUCTION

Several studies have examined how patterns of avian density, diversity, and species composition change with stand age during forest regeneration. Initially, researchers studied bird communities in old-field secondary succession (e.g. Odum, 1950; Johnston and Odum, 1956; MacArthur and MacArthur, 1961; Kricher, 1973; Shugart and James, 1973). More recently, researchers have documented the effects of timber harvest on breeding birds (e.g. Ahle'n, 1975; Franzreb, 1977; Webb et al., 1977; Titterington et al., 1979; DeByle, 1981; Crawford et al., 1981; Szaro and Balda, 1982; Scott and Gottfried, 1983; Steffen, 1984; Niemi and Hanowski, 1984). Only a few studies have included a representative range of seral stages between harvested stands and mature forest (Conner and Adkisson, 1975; Probst, 1979; Dickson and Segelquist, 1979; Conner et al., 1979).

These studies of bird communities and secondary succession have shown

overlapping replacement of bird species along stand-age gradients. Avian diversity and total populations tend to be directly related, and both increase with greater structural complexity of vegetation. Many studies have related avian species diversity to habitat complexity, especially vertical foliage stratification (MacArthur and MacArthur, 1961; Karr, 1968; Karr and Roth, 1971; Willson, 1974; Probst, 1976). Because habitat complexity usually increases with secondary plant succession, avian density and diversity also increase along the same gradient. However, mid-aged forest stages can have a simple vegetation structure, so avian diversity may decline temporarily in the middle period of forest regeneration (Dickson and Segelquist, 1979) or even peak in the earlier stages (Probst, 1976; Faaborg, 1980; Steffen, 1984).

Few studies of avian communities and forest management have examined a variety of stages of forest regeneration with replicates in most or all age classes. Many studies of animal communities have drawn conclusions from single-sample surveys (Wiens, 1981). In this study, we examined avian density, species richness, and species composition with respect to stand age of 20 aspen (*Populus tremuloides*) stand-age samples in Michigan and Minnesota. The data on avian density and species composition were gathered to accomplish two objectives: (1) to provide preliminary estimates of the range of avian population responses to forest harvesting and regeneration for representative stand ages in upland broadleaf forests; and (2) to provide information basic to general large-scale avian population projections in mostly forested areas in the Lake States. The information provided here, although incomplete, is generally applicable to upland broadleaf forests in the eastern USA.

METHODS

Our study plots were located in the Chippewa National Forest and Cloquet Forestry Center in Minnesota and the Ottawa National Forest in Michigan (Table 1). Study plots were between 6.5 and 20.6 ha in size ($\bar{X}=11.2$), and were part of much larger forested tracts. Two mature stands (Cloquet and Wabana) were bordered by more open land on one edge only. The 20 stand samples were separated into five categories based on height and structure (Table 2), as well as an index of similarity for bird species (see below). We studied two stands both before and after tree harvesting. Several regenerating stands were sampled for 2 or more years. Of the five mature stands, one was sampled for 3 years, one for 2 years, and the remaining three stands were sampled once.

Bird census

Bird densities were estimated using a modification of the spot-mapping techniques described by Robbins (1970). Six or seven census visits were made to each study plot between 20 May and 10 July 1977–1984. Prior to census-

TABLE 1

Stand age, stand size, and average height of tree regeneration in 20 stand samples in ten aspen stands

Plot name	Stand (years)	Ave. height (m)	% Shrub cover	Census area (ha)	Year censused	Location
0–1.8 m						
Ottawa #1	1	0.8	16.9	8.98	1980	Ottawa NF, MI
Cloquet	1.5	1.2	19.5	9.87	1980	Cloquet Forestry Center, MN
Ottawa #2	2	0.9	16.2	13.88	1978	Ottawa NF, MI
Ottawa #1	2	1.4	38.1	8.98	1981	Ottawa NF, MI
Ottawa #1	3	1.7	48.3	8.98	1982	Ottawa NF, MI
1.9–4.0 m						
Murphy Lake	4	2.4	43.6	10.40	1977	Chippewa NH, MN
Ottawa #2	4	2.0	52.7	18.45	1980	Ottawa NF, MI
Ottawa #2	5	2.3	51.6	18.45	1981	Ottawa NF, MI
Ottawa #2	6	2.8	42.3	18.45	1982	Ottawa NF, MI
Murphy Lake	6	3.1	28.8	9.75	1979	Chippewa NF, MN
Jessie Lake	8	1.9	96.0	10.50	1978	Chippewa NF, MN
4.1–8.0 m						
Murphy Lake	8	5.2	48.6	10.64	1981	Chippewa NF, MN
Bowstring	9	6.4	78.0	6.35	1979	Chippewa NF,MN
Jessie Lake	12	6.2	23.3	10.52	1982	Chippewa NF, MN
8.1–14.0 m						
Norway Aspen	19	9.6	70.5	7.08	1979	Chippewa NF, MN
> 14.1 m						
Birch Lake	Mature	15.1	17.3	8.09	1981	Chippewa NF, MN
Ottawa #1	Mature	17.0	23.4	8.98	1978	Ottawa NF, MI
Pike Bay	Mature	20.6	–	17.00	1977	Chippewa NF, MN
		–	32.4	13.84	1979	
		–	–	13.84	1981	
Cloquet	Mature	15.5	–	20.48	1977	Cloquet Forestry Center, MN
		–	72.0	14.00	1978	
Wabana	Mature	19.1	54.4	8.70	1978	Chippewa NF, MN

ing, a 6 ha subplot of homogeneous habitat was selected within each stand to standardize the areas for bird species richness comparisons. The numbers of species in the subplots and whole stands were determined by including partial territories, but non-breeding visitors were omitted from the subplot species counts (Table 2). The number of singing males of each species was based on the total number heard or seen each trip (non-territorial species) or the number of discrete locations where a species was found (territorial species). Mapping of individual birds was facilitated by flagging a 50 m × 50 m grid on each study plot. The number of males of non-singing species was estimated by assuming an even sex ratio and halving the average number of individuals counted each trip. Species' populations that foraged within the study areas

TABLE 2

Average number of bird species, total abundance, and total consuming biomass of birds in five stand height categories (ranges are in parentheses)

Stand category	No. species (all stand samples)	No. species (whole plot)	No. species (6 ha subplot)	Density all species (No. males per 40 ha)	Consuming biomass (g per 40 ha)[1]
0–1.8 m (N=5)	30	10.8 (5–21)	10.6 (5–19)	93.6 (33–190)	1947 (776–4368)
1.9–4.0 m (N=6)	32	18.5 (14–24)	17.3 (13–20)	177.8 (80–359)	2632 (1550–5339)
4.1–8.0 m (N=3)	20	13.3 (11–17)	12.3 (11–15)	115.7 (108–131)	2155 (1921–2472)
8.1–14.0 m (N=1)	8	8.0	8.0	113.0	1730
>14.1 m (N=5)	37	13.7 (9–18)	11.5 (5–17)	165.8 (97–324)	2707 (1440–5268)

[1]Consuming biomass = $W^{0.75}$ to correct for metabolic difference per unit weight of different sizes of birds.

but nested elsewhere were estimated by averaging the number of individuals seen on each census trip. The estimated density for each singing, territorial species was calculated by summing the number of territories in the plot plus the estimated fractions of territories not completely contained within each census plot. Breeding bird densities were expressed as the number of males per 40 ha.

Most censuses were done by a single observer (Rakstad), thus reducing observer variability. The 1977 censuses were conducted by Probst and Deanna Dawson. The 1978 censuses were done by Probst, Rakstad, and Connie Cooper. Bird censuses from 1979 through 1984 were conducted by Rakstad (supplemented with a single visit to each by Probst).

Vegetation

The vegetation of the study plots was measured by line transects. To ensure that recurring spatial patterns in the vegetation were not over or undersampled, two transects were joined into 30.5 m L-shaped units (Lindsey, 1955), spaced at a density of two per hectare. Measurements of lower height, percent cover, and upper height of foliage were recorded for all plants which intersected the line. Shrub, sapling, and tree cover values were obtained by estimating the percentage of a 30.5 m line intercepted by the foliage of a given

species in a layer. All low, woody plants were classified as shrubs if they branched below the arbitrary level of 1.4 m or had a diameter at breast height (dbh) of less than 2.5 cm. Saplings were defined as having a dbh from 2.5 to 6.4 cm or a height of less than 7.6 m. All other stems greater than 6.4 cm dbh were classified as trees. Vegetation on all recently disturbed clearcut plots was measured in July or August of the same year the plots were censused for birds. A few of the mature plots were measured 1 year after bird censusing.

Analysis of data

The vegetation variables selected for analysis–dominant vegetation height, percent shrub cover, percent sapling cover, and shrub/sapling equitability–were chosen for predicting bird populations with few or no field measurements, because that is how land managers commonly evaluate habitat. Understory vegetation was represented by a variable combining independent measurement of percent shrub cover plus percent sapling cover. Thus, the understory variable ranged between 0 and 200%. Shrub/sapling equitability (as relative amounts of sapling and shrub cover) was defined as follows to avoid division by zero: letting PSh be the proportion of sapling cover relative to understory (shrub plus sapling) cover, then equitability equals $2 \times \text{PSh}$ for $\text{PSh} < 0.5$ or $2 \times (1 - \text{PSh})$ for $\text{PSh} > 0.5$. Equitability will be 0 when shrub cover represents all or none of the understory cover, and reaches a maximum of 1 when shrub cover and sapling cover are equal. An index of similarity was used to cluster bird communities using the Pearson Correlation Coefficient Average Linkage Method as a guide for establishing category boundaries. Bird densities in mature stands censused for more than 1 year were averaged for each species, since annual variation within mature stands was less than that between stands.

Forest birds were classified into one or more of five foraging groups for examining stand-age trends in avian species composition. The birds in each group were hypothesized to show a common response to changes in vegetation structure and life form. A few species (e.g. blue jay (*Cyanocitta cristata*)) did not fit into any of the categories and were classified as generalists. Non-forest birds (e.g. killdeer (*Charadrius vociferus*), common snipe (*Capella gallinago*)) were excluded from the species composition comparisons.

The first group was composed of bark foragers, such as nuthatches and woodpeckers; they are not common until stands have larger trees (>15 cm dbh), including some dead and dying trees. The second group was composed of birds that do most of their foraging on the ground, such as sparrows and thrushes. Foliage gleaners that forage in the tree canopy (e.g. red-eyed vireo (*Vireo olivaceous*)) made up the third group, while foliage gleaners that forage in the shrub/sapling understory (e.g. mourning warbler (*Oporornis philadelphia*)) made up the fourth. The fifth group was composed of birds that

find favorable conditions in more open habitat or openings in mature forest canopies. This group included 'pursuers' like flycatchers that hawk or sally after aerial prey, but also the larger, less active gleaners (e.g. tanagers, cuckoos) that use a slower 'sight and pursuit' strategy to capture non-aerial prey.

Because the number of replicate stands was small for some stand height classes, most analyses involved modeling relationships between continuous variables and bird population trends using multiple linear regression and nonlinear regression. Single-species models were developed after converting population density to a logarithmic scale. A description of models including estimates of model parameters and their standard errors, *t*-values, and *P*-values are available by request from Probst.

RESULTS

Avian diversity and population density

Number of avian species

Each 6 ha subplot contained from 5 to 20 bird species (Table 2). The highest number of species occurred in the 1.9–4.0 m regeneration category, while the lowest number occured in recent clearcuts and in the 8.1–14.0 m regeneration category (Fig. 1). The number of species increased again in mature stands (>14.1 m), but did not reach the level observed in the 1.9–4.0 m

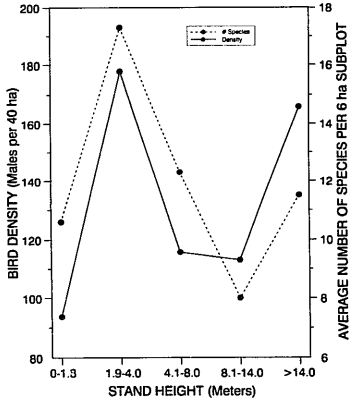

Fig. 1. Total bird density (whole stand) and average number of species (6 ha subplot) in each of five stand height categories.

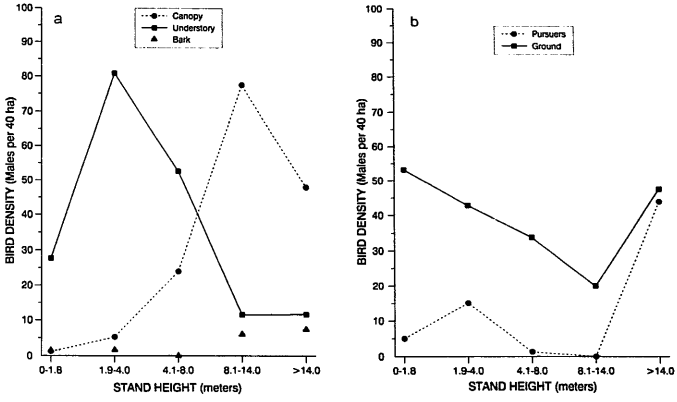

Fig. 2. Average populations of five avian foraging groups in each of five stand height categories.

category. The three mature stands with denser shrub understory (Table 1) supported more bird species than stands with less understory, but differences were not significant. The best predictor of total number of bird species ($R^2=0.60$, degrees of freedom (df) = 16) was understory cover for all classes, but the number of species was uniformly higher in the first three height classes.

Populations of the five avian foraging groups changed with forest maturation (Fig. 2). At least two of the groups (ground foragers, understory gleaners) were directly or indirectly dependent on shrubs and saplings for foraging, singing, and/or nest support. As stand regeneration progressed, some bird species appeared and others were absent. Bird species are listed in Table 3 in order of first occurrence during regeneration. Numerically dominant ground-foraging sparrows were gradually replaced by understory warblers as stand height increased (Fig. 2, Table 3). In mature stands, bark-foraging birds, tree canopy species, and aerial pursuers were more prominent, and ground-foraging species were again common. Seventeen bird species were found only in mature forests in this study, but four of them can be found (personal observation) in younger stands outside this study.

Density and biomass

Avian density and species richness patterns were essentially parallel (Fig. 1) but the mature plots had a greater number of birds per species than other

TABLE 3

Density (no. per 100 acres) for each bird species in five stand height categories

Species	Foraging group[1]	0–1.8 m ($N=5$)	1.9–4.0 m ($N=6$)	4.1–8.0 m ($N=3$)	8.1–14.0 m ($N=1$)	>14.0 m ($N=5$)
House wren	U	0.8	0	0	0	0
Common snipe	O	0.6	0	0	0	0
Spotted sandpiper	O	0.6	0	0	0	0
Common nighthawk	O	0.4	0	0	0	0
Olive-sided flycatcher	P	0.4	0	0	0	0
Eastern kingbird	P	1.8	0.3	0	0	0
Red-winged blackbird	G	1.8	0.3	0	0	0
Killdeer	O	2.2	0.5	0	0	0
Common flicker	G/B	3.0	1.2	0	0	0.5
Rufous-sided towhee	G	1.2	0.7	0	0	0
Indigo bunting	U	4.0	4.3	0	0	0
Cedar waxwing	P	0.6	0.8	0	0	0
Alder flycatcher	P	0.8	10.0	0	0	0
American goldfinch	U/G	2.2	3.7	0	0	0
Ruby-throated hummingbird	U	0.8	1.8	0	0	0
American woodcock	O	0.6	2.2	2.0	0	0
Song sparrow	G	26.8	13.3	2.5	0	0
White-throated sparrow	G	11.2	12.3	5.0	0	0
American robin	G	4.8	1.5	2.0	0	1.1
Brown-headed cowbird	G	4.8	1.3	0	0	2.4
Yellow-billed cuckoo	P/C	0	0.7	0	0	0
Brown thrasher	G	0	1.0	0	0	0
Mourning warbler	U	16.2	14.3	14.7	3.0	3.2
Least flycatcher	P	0.6	0.3	0	0	34.1
Tree swallow	O	0.6	0.7	0	0	0
Red-eyed vireo	C	0.6	0.8	9.7	37.0	35.1
Nashville warbler	U	0.4	4.0	4.3	0	0.5
Black-billed cuckoo	P	0.4	3.3	1.3	0	0.4
Common yellowthroat	U	1.8	3.3	0.7	0	0
Northern oriole	C	0.6	0	0	0	0.6
Purple finch	P	0.4	0	0	0	0.4
Chestnut-sided warbler	U	2.6	37.3	20.0	0	6.9
Gray catbird	U/G	0	5.8	2.0	0	0
Golden-winged warbler	U	0	8.2	2.0	0	0
Veery	G	0	7.0	14.3	6.0	11.4
Rose-breasted grosbeak	U/C	0	5.7	13.0	17.0	1.5
American redstart	C	0	1.2	7.7	26.0	1.1
Blue jay	O	0	1.0	1.3	0	0.6
Black and white warbler	B	0	1.0	0	6.0	0.2
Connecticut warbler	U	0	0	0.7	0	0
Ovenbird	G	0	0	8.3	14.0	31.4
Canada warbler	U	0	0	2.7	0	0.2
Ruffed grouse	G	0	0	0.7	0	0.2
Black-capped chickadee	C	0	0	0	6.0	3.3
Eastern wood pewee	P	0	0	0	0	4.2
Red-breasted nuthatch	B	0	0	0	0	2.1
Great-crested flycatcher	P	0	0	0	0	3.6

TABLE 3 (*continued*)

Species	Foraging group[1]	0–1.8 m (*N*=5)	1.9–4.0 m (*N*=6)	4.1–8.0 m (*N*=3)	8.1–14.0 m (*N*=1)	>14.0 m (*N*=5)
Broad-winged hawk	O	0	0	0	0	0.8
White-breasted nuthatch	B	0	0	0	0	1.0
Philadelphia vireo	C	0	0	0	0	0.6
Scarlet tanager	P/C	0	0	0	0	2.2
Hairy woodpecker	B	0	0	0	0	1.5
Blackburnian warbler	C	0	0	0	0	0.5
Chipping sparrow	G	0	0	0	0	0.2
Black-throated green warbler	C	0	0	0	0	4.0
Yellow-bellied sapsucker	B	0	0	0	0	2.2
Yellow-throated vireo	C	0	0	0	0	0.6
Hermit thrush	G	0	0	0	0	0.5
Northern goshawk	O	0	0	0	0	0.4
Northern parula warbler	C	0	0	0	0	0.2
Downy woodpecker	B	0	0	0	0	0.1

[1]Foraging groups: G, ground feeders; U, understory gleaners; C, canopy gleaners; P, pursuers; B, bark foragers; and O, other (aerial, shorebird, raptor, generalist).

stand categories (Table 2). We found three dominant species (red-eyed vireo, least flycatcher (*Empidonax minimus*), and ovenbird (*Seiurus aurocapillus*)) in the mature stands (Fig. 3). The 4.1–8.0 m category had a few dominant species. In the 0–1.8 m stands, sparrows and understory warblers were the most common bird species. Although total avian density was more difficult to model than species richness, two asymtotic models were developed using tree height (R^2=0.66, df=13) and total cover (R^2=0.51, df=14). Both models indicate a positive relationship between avian density and stand age.

Although avian density and diversity were highest in the 1.9–4.0 m regeneration category, the avian biomass was highest in the mature (>14.1 m) category (Table 2). Most birds in the 8.1–14.0 m category were relatively small understory and canopy gleaners, while the mature category had larger birds such as woodpeckers, raptors, and ground foragers. The 0–1.8 m category also had a sizable contingent of ground foragers, thus explaining its relatively high avian biomass to density ratio.

Avian species composition

Species composition changed markedly as stand age increased (Table 3). Ground foragers such as sparrows and the American robin (*Turdus migratorius*) reached higher densities at an earlier stand age than understory gleaners (warblers, rose-breasted grosbeak (*Pheucticus ludovicianus*)), and peaked again in mature stands with dense understory. Ground foragers (veery (*Catharus fuscescens*), ovenbird) were found at high densities in all

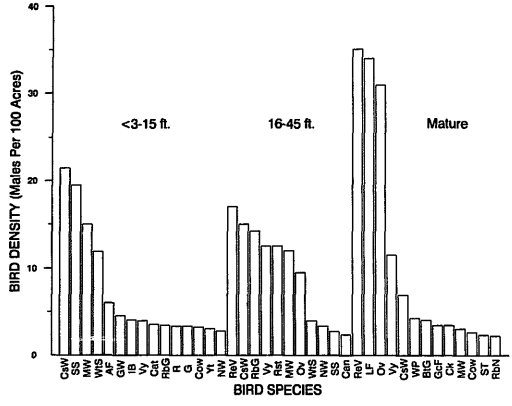

Fig. 3. Average density of the dominant species in three stand height categories. ALFL, alder flycatcher; AEWP, eastern wood peewee; AMGO, American goldfinch; AMRE, American redstart; AMRO, American robin; BCCH, black-capped chickadee; BHCO, brown-headed cowbird; BTNW, black-throated green warbler; CAWA, Canada warbler; COYE, common yellowthroat; CSWA, chestnut-sided warbler; GCFL, great-crested flycatcher; GRCA, gray catbird; GWWA, golden-winged warbler; INBU, indigo bunting; LEFL, least flycatcher; MOWA, mourning warbler; NAWA, Nashville warbler; OVEN, ovenbird; RBGR, rose-breasted grosbeak; RBNU, red-breasted nuthatch; REVI, red-eyed vireo; SCTA, scarlet tanager; SOSP, song sparrow; VEER, veery; WTSP, white-throated sparrow; YBSA, yellow-bellied sapsucker.

stand ages, ranging from 20 to 56 males per 40 ha. Ground-foraging species and aerial species were the only birds found in clearcuts less than 2 years old. No satisfactory model was found to explain relationships between ground-forager density and stand-age vegetation variables, in part because a different group of species was associated with each part of the bimodal bird density distribution with stand age. Populations of understory gleaners decreased in mature stands (relative to the 1.9–4.0 m category), and occurred rarely in mature stands with sparse understories. A quadratic model explains 71% of the variability (df=15) of understory bird populations in younger stands on the basis of dominant vegetation height (truncated at 9.4 m).

The abundance of canopy gleaners (vireos, warblers) and bark foragers (woodpeckers, nuthatches) increased in the older stands. Thus, an asymptotic model of tree height was used to predict log-transformed canopy gleaner populations ($R^2 = 0.76$, df=18). There were not enough older stands to model bark-forager densities, but research in oak forests in Pennsylvania suggests a strong relationship with average tree diameter (i.e. forest maturity) (Probst,

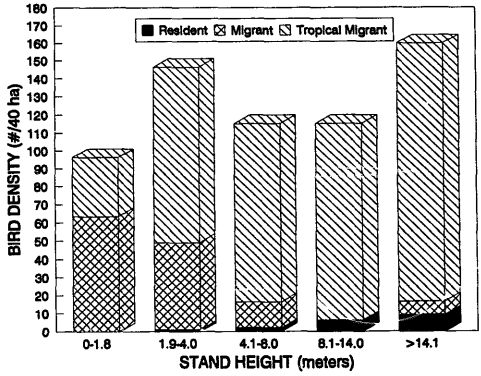

Fig. 4. Average proportionate density (No. males per 40 ha) of resident, migrant, and neotropical migrant birds in each of five stand height categories.

1976). Although all the bark foragers were recorded at low densities, their larger body size gave them a higher proportion of community biomass.

The pursuers (e.g. alder flycatcher (*Empidonax alnorum*)) as a group were present later in succession than the understory gleaners (Fig. 2), and were not present where dense sapling growth invaded regeneration stands. The least flycatcher and eastern wood pewee (*Contopus virens*) occurred in older stands with open tree canopies. Abundance of pursuers was predicted by tree height and shrub/sapling equitability ($R^2=0.86$, df=12). Tree height was positively related to the number of pursuers. At a given height, higher equitability results in a decreased number of pursuers based on height alone. In general, stands with both high shrub and sapling cover tend to have little open space for pursuers.

Four other foraging groups were not included in Figs. 2 or 3 due to their low frequencies and low population densities: shorebirds, aerial foragers, raptors, and a group of habitat generalists. A few species were placed in two groups in Table 3; for example the flicker (*Colaptes auratus*), was both a ground and bark forager in mature stands, but was principally a ground forager in regenerating stands.

Finally, we examined the proportion of resident vs. migrant birds in aspen stands (Fig. 4). Although resident species ($N=8$) are found in the northern Lake States throughout the year, individual birds may migrate. Summer resident species that migrate south of the Lake States were subdivided into species whose wintering range includes the southern USA (21 species) and those that winter in the neotropics almost exclusively (32 species). Resident spe-

cies were absent from the youngest aspen stand-age class, and were only a minor component in the older classes. Migrant species made up two-thirds of the birds in the youngest stand-age class (< 1.8 m) and one-third of the birds in the 1.9–4.0 m class. Tropical migrants represented two-thirds of the birds in the second age class and 86–95% of the individuals in stand-age categories greater than 4.1 m average tree height. Thus, tropical migrants are a significant or major component of avian communities in younger stands, and the predominant or nearly exclusive component of older stands.

Regular and common species

The initial avian composition of a clearcut area varies with the degree of tree canopy removal (Probst, 1979; Crawford et al., 1981). The overstory was completely removed in all of our clearcut plots, except the Ottawa No. 2 plot. The song sparrow (*Melospiza melodia*) was the most frequent (all plots) and abundant species overall in the first two stand-age classes (Table 3). Log-transformed song sparrow density had an asymptomatic relationship (Fig. 5) inversely related to dominant height ($R^2 = 0.80$, df = 18). The white-throated sparrow (*Zonotrichia albicollis*) was also a regular species in young regenerating stands. The mourning warbler, which was found in 14 of the 15 plots, was a numerically dominant species in the mid-aged and older regenerating stands. Thus, mourning warbler (log-scale) densities were best modeled by a positive response to cover and shrub/sapling equitability in the younger part of the gradient and a negative response to height toward the mature end

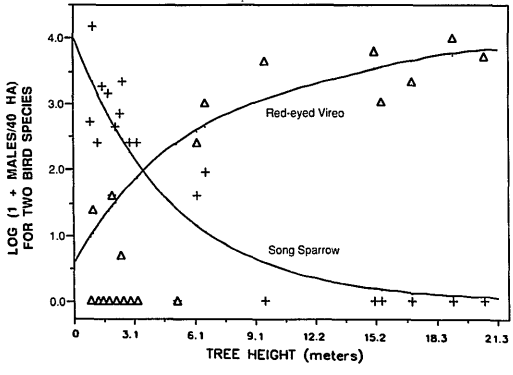

Fig. 5. Relationship of male song sparrow and red-eyed vireo populations to dominant tree height in Lake States aspen stands.

(R^2=0.75, df=14). In the older regenerating plots the chestnut-sided warbler (*Dendroica pensylvanica*) was the most abundant species.

The American robin was the only species recorded in all five stand-age classes, although it was not numerous in any of them. The brown-headed cowbird (*Molothrus ater*) was also widely distributed among stand ages. The 8.1–14.0 m class was composed of bird species that were more abundant in either the regenerating or mature classes, but the rose-breasted grosbeak and American redstart (*Setophaga ruticilla*) were exceptions to the pattern; we recorded their peak densities in 4.1–8.0 m aspen stands. The most successful model (Fig. 5) for rose-breasted grosbeak density integrates a positive response to cover and shrub/sapling equitability and a negative relationship to height (R^2=0.83, df=14). Common species such as the least flycatcher and red-eyed vireo occurred in some regenerating stands, but were most abundant in mature stands. Because of this, an asymptotic model utilizing dominant vegetation height (Fig. 5) provided a good explanation of red-eyed vireo populations (R^2=0.80, df=8), after excluding stands under 6.4 m.

Mourning and chestnut-sided warblers were regularly observed in mature stands with a dense shrub/sapling understory, but were absent in the other mature stands. A denser understory in the mature stands probably accounted for the greater number of least flycatchers. Mature stands with dense shrub and sapling layers supported considerably higher veery and ovenbird populations than those with sparse understories, but results were not significant. Ovenbirds were not present in stands of less than 4.6 m in height, and log densities of ovenbirds (in stands over 4.6 m) were predicted by a negative relationship (overall) to sapling cover (R^2=0.62, df=7). The veery was found at both extremes of stand maturity; its populations were best predicted by a parabolic model using shrub/sapling equitability and understory cover. Woodpeckers and nuthatches were regularly observed but not common in the mature plots. Canopy gleaners such as the black-throated green warbler (*Dendroica virens*) and northern parula (*Parula americana*) were found only in mature stands. Most of the year-round resident species were found in the mature stands (Fig. 4).

Less common species

Many species were restricted to a narrow range of habitats. Most canopy gleaners and bark feeders were restricted to the mature stands. Species such as the yellow-throated vireo (*Vireo flavifrons*) and olive-sided flycatcher (*Contopus borealis*) were limited by narrow habitat breadth. A specific vegetative component was required by some species; for example, the hermit thrush (*Catharus guttatus*), red-breasted nuthatch (*Sitta canadensis*) and blackburnian warbler (*Dendroica fusca*) required the presence of at least a few coniferous trees. The distribution of cavity-nesting species such as nu-

thatches, chickadees, and tree swallows (*Tachycineta bicolor*) depends on the occurrence of snags and/or primary cavity excavators. Other birds may have been rare in our censuses due to geographic range — for example, the Canada warbler (*Wilsonia canadensis*), Connecticut warbler (*Oporornis agilis*), and northern goshawk (*Accipiter gentilis*).

Other factors

Avian species composition can be influenced by plot size and edge effect. Small, isolated clearcut plots bordered on several sides by mature forest can be used by visitors from the mature forest. We did not observe this effect in our clearcut censuses, but least flycatchers and red-eyed vireos strayed into some of the older regenerating plots in one study plot and are not sampled reliably with our census techniques. Seventeen species were recorded only as visitors to our study plots, including regular species such as pileated woodpecker (*Dryocopus pileatus*) and yellow-rumped warbler (*Dendroica coronata*).

The presence of seasonally wet depressions accounted for the observations of most shorebirds in young stands. Common snipe, American woodcock (*Scolopax minor*), and killdeer bred in some clearcuts. Patches of residual mature trees accounted for the presence of some canopy gleaners (i.e. northern oriole (*Icterus galbula*)) in the clearcuts. The black and white warbler (*Mniotilta varia*) was also recorded in these residual trees.

DISCUSSION

The pattern of overlapping replacement of bird species with increasing aspen age is similar to that observed in other studies. New groups of species were added at three major periods during regeneration: (1) early aspen regeneration (1.9–4.0 m); (2) diverse mixture of herbs, shrubs, and saplings (4.1–8.0 m); and (3) development of open tree canopy and increased tree bark surface area (mature stands). The addition of species and foraging groups can be better understood by relating their presence to vegetation life forms such as herbs, shrubs, saplings, and trees (Karr and Roth, 1971; Probst, 1979) instead of foliage height intervals (MacArthur and MacArthur, 1961; and others).

Three of the numerically dominant bird species occurred in mature stands. The younger stands had a more equitable distribution of bird species average abundance. In the youngest stand-age classes, bird density and species richness may have been limited by amount of vegetation (see also Karr, 1968) and low structural complexity. However, maximum avian density and diversity were recorded in mature stands and those in the 1.9–4.0 m height range. More importantly, most species that are declining regionally or nationally occur in mature stands. As in almost all other studies, sapling-pole stands (8.1–

14.0 m) had lower densities and diversities relative to older or younger stands. Avian density and species richness patterns in mature stands and 1.9–4.0 m stands were similar, resembling those in oak forests and seres (Conner and Adkisson, 1975; Probst, 1979) where regenerating clearcuts often have more bird species and individuals than mature plots. Another study of aspen–northern hardwoods forests in Wisconsin showed little difference in avian density or species richness among stand ages (Steffen, 1984). Thus, it is incorrect to assume that bird populations always become progressively more diverse or numerous during succession. Oak forest censuses (Probst, 1979) suggest that peak bird density and species richness occur between 3 and 12 years in stand age. However, aspen stands usually reach the 1.9-4.0 m height range of peak populations at an earlier age (3–8 years), so average tree height is a better criterion than stand age for predicting avian development in eastern broadleaf forest types.

Habitat factors

In the younger regenerating plots the scarcity of both herbaceous and woody vegetation probably limited avian use. In later stages of regeneration, the number of bird species increased with the vertical complexity of the vegetation (MacArthur and MacArthur, 1961; Karr and Roth, 1971; Wilson, 1974; Probst, 1976, 1979) and the patchiness or horizontal heterogeneity (Roth, 1976). In contrast, there were few bird species in the 8.1–14.0 m (Fig. 1, Table 2) stands in this study, due to their simple vegetation structure. The structure of the stand is more important to avian species than foliage height intervals per se. Each layer or life form of the forest adds to avian diversity (Probst, 1979). Mature aspen stands with well-developed understories (Table 1) had more avian species than mature open stands, but samples were limited. We estimate that approximately half of the 61 species recorded in our censuses could have lower populations after natural or man-caused understory removal.

Avian species richness also was enhanced by more complex vegetation structure. For example, the number of species and individuals of bark foragers increased in more mature stands because of the larger tree trunks. Large, spreading tree canopies were beneficial to both gleaners and pursuers. If plant succession causes partial or total replacement of one vegetational layer by another, the changes in number of species may be compensatory; thus, species turnover may be more pronounced than species richness changes as forests mature.

Management implications

Studies that compare pre and postharvest bird communities are difficult to apply to a whole stand rotation, because they examine only the terminal points

of stand life. Bird censuses conducted over a range of stand ages show that regenerating stands quickly develop an avian density and species richness similar to mature habitats; but species composition is altered relative to mature forests. Furthermore, tree harvesting under balanced rotation insures a greater variety of species than could exist if only one age category were present. However, some silvicultural systems can decrease overall diversity of habitat types. For example, intensively managed, short-rotation systems forests eliminate mature stands in favor of pole stands – the poorest stand-age class for avian density or unique species in almost all studies.

Studies to date have shown varying effects of tree harvest on avian richness and diversity (Franzreb, 1977; Webb et al., 1977; DeByle, 1981; Crawford et al., 1981; Scott and Gottfried, 1983; Niemi and Hanowski, 1984; Steffen, 1984), perhaps due to differing degrees of canopy removal (Probst, 1979). Some harvesting systems have a greater short-term effect on species composition than others; shelterwood or patch-cut systems should have the least impact on bird species turnover.

Understory vegetation is critical to breeding birds in both regenerating and mature stands. At least one-fourth to one-half of the bird species and individuals present in complex forests are absent in stands without a well-developed understory. Almost all the birds in younger stands are dependent on shrubs and saplings for nesting or foraging. These species presumably will be eliminated or reduced in stands where such vegetation is removed by herbicides or other means.

Finally, local habitat factors such as are reported here are not the sole determinant of bird species abundance. Forest stands must be viewed within the context of larger scale population processes and landscape patterns. Landscapes that are altered by deforestation, road building, or land clearing may have different nest predation rates (Andren and Angelstam, 1988; Small and Hunter, 1988) than those in mostly forested areas. As a result, different landscapes may have different bird species compositions at local scales even when vegetation is quite similar (Ambuel and Temple, 1983). Bird populations at the local level may also reflect regional population increases or declines (Askins and Philbrick, 1987), so the results of local studies should be interpreted carefully.

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